

Abstract—Ichthyoplankton surveys were conducted in shelf and slope waters of the northern Gulf of Mexico during the months of May–September in 2005 and 2006 to investigate the potential role of this region as spawning and nursery habitat of sailfish (*Istiophorus platypterus*). During the two-year study, 2426 sailfish larvae were collected, ranging in size from 2.0 to 24.3 mm standard length. Mean density for all neuston net collections ($n=288$) combined was 1.5 sailfish per 1000 m², and maximum density was observed within frontal features created by hydrodynamic convergence (2.3 sailfish per 1000 m²). Sagittal otoliths were extracted from 1330 larvae, and otolith microstructure analysis indicated that the sailfish ranged in age from 4 to 24 days after hatching (mean=10.5 d, standard deviation [SD]=3.2 d). Instantaneous growth coefficients (g) among survey periods ($n=5$) ranged from 0.113 to 0.127, and growth peaked during July 2005 collections when density within frontal features was highest. Daily instantaneous mortality rates (Z) ranged from 0.228 to 0.381, and Z was indexed to instantaneous weight-specific growth (G) to assess stage-specific production potential of larval cohorts. Ratios of G to Z were greater than 1.0 for all but one cohort examined, indicating that cohorts were gaining biomass during the majority of months investigated. Stage-specific production potential, in combination with catch rates and densities of larvae, indicates that the Gulf of Mexico likely represents important spawning and nursery habitat for sailfish.

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Distribution, growth, and mortality of sailfish (*Istiophorus platypterus*) larvae in the northern Gulf of Mexico

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Declining populations of Atlantic sailfish (*Istiophorus platypterus*) (ICCAT, 2001) emphasize the need for a better understanding of their biology, especially processes affecting growth and mortality during early life because these mechanisms often regulate recruitment (Fuiman, 2002). To date, studies on sailfish biology during the early life interval are limited; however, recent research conducted in the Straits of Florida indicates that sailfish grow rapidly and experience high mortality during early life (Luthy et al., 2005; Richardson et al., 2009a). Although our understanding of the early life ecology of sailfish has improved in recent years, work to date has been limited in geographic scope and basic life history data on sailfish are limited or not available for other regions of the Atlantic that may represent essential spawning and nursery habitat of sailfish. In particular, bycatch data from pelagic longline fisheries in the Gulf of Mexico indicate that catch rates for sailfish are twofold higher in the Gulf than in other areas of the North Atlantic during the presumed spawning season (May–September; de Sylva

and Breder, 1997; NMFS¹). Because spawning stock biomass appears high in this region, a better understanding of the role of the Gulf of Mexico as spawning and early life habitat of Atlantic sailfish is essential.

The Gulf of Mexico supports one of the most productive fisheries in the world (Chesney et al., 2000), and oceanographic features within the Gulf are influenced by inflow from the Mississippi River and large-scale oceanographic features, such as the Loop Current and associated warm and cold core eddies (Govoni and Grimes, 1992; Sturges and Leben, 2000). Physicochemical conditions and primary production vary markedly within and across these features (Grimes and Finucane, 1991; Biggs, 1992), and have been shown to affect the distribution and growth of pelagic larvae in the Gulf (Govoni et al., 1989; de Vries et al., 1990; Lang et al., 1994). Namely, higher densities

¹ NMFS (National Marine Fisheries Service). 2008. NMFS Pelagic Longline Logbook data, (<http://www.sefsc.noaa.gov/flslandingsdata.jsp>, accessed December 2008).

and increased growth have been observed for larvae within frontal features created by riverine discharge and hydrodynamic convergence (Lang et al., 1994; Hoffmeyer et al., 2007). It is likely that oceanographic features also influence the early life ecology and population dynamics of sailfish in this region, and therefore an improved understanding of the effects of these features on distribution, growth, and survival will aid in determining the value of the Gulf as spawning and nursery habitat for sailfish.

The objectives of this research were threefold: 1) to characterize spatial and temporal patterns of abundance of sailfish larvae in the northern Gulf of Mexico; 2) to relate spatial variation in distribution and growth to oceanographic features to determine the causal factors responsible for recruitment variability; and 3) to estimate demographic parameters within and across years to determine whether these traits varied temporally. Estimates of growth (G) and mortality (Z) were combined ($G:Z$) to determine indices of stage-specific production potential and to assess the functional role of the Gulf as spawning and nursery habitat of this species.

Materials and methods

Field collections

Five ichthyoplankton surveys were conducted in shelf and slope waters of the northern Gulf during spring and summer of 2005 (May, July, and September) and summer of 2006 (June and August). Surveys were conducted in an area bounded by 27° to 28°N latitude and 88 to 94°W longitude. This sampling area was selected because bycatch rates of adult sailfish by U.S. longliners were high in this region during the presumed spawning period of Atlantic sailfish (NMFS¹). Istiophorid larvae were collected with paired neuston nets (2-m width×1-m height frame) with two mesh sizes (500 µm and 1200 µm) to account for potential differences in capture success between mesh sizes. Nets were towed through the top meter of the water column at approximately 2.0 knots for 10 minutes. Paired tows were taken at 60 to 70 sampling stations spaced approximately 15 kilometers (km) apart during each survey. Sampling was conducted at 15-km intervals to allow coverage of a large area encompassing multiple oceanographic features. The September 2005 survey was shortened (39 stations sampled) because of inclement weather.

At each station, sea surface temperature (°C), salinity (ppt), and dissolved oxygen (mg/L) were recorded by using a Sonde 6920 Environmental Monitoring System (Yellow Springs Instruments Inc., Yellow Springs, OH). A probe malfunctioned during sampling in August 2006, preventing dissolved oxygen measurements. Sea surface height (cm) for each station was determined from archived satellite altimetry data provided by the Colorado Center for Astrodynamic Research (CCAR) Real-Time Altimetry Project (argo.colorado.edu; R. Leb-

en, personal commun.²). Flowmeters (General Oceanics, model 2030R, Miami, FL) placed within each net were used to determine the surface area sampled by each net. A formula provided by the manufacturer was used to determine distance towed during each collection which was multiplied by net width to determine surface area sampled during each collection (m²): $surface\ area\ sampled\ (m^2) = distance\ sampled\ (m) \times 2\ m\ (net\ width)$.

Fish larvae and associated biota were preserved on-board in 95% ethanol and istiophorids were sorted from each sample in the laboratory with the use of a Leica MZ stereomicroscope and stored in 70% ethanol. Istiophorid larvae were photographed and standard length (SL) was measured to the nearest 0.1 mm. Istiophorids do not have a full complement of fin rays until reaching 20 mm SL (Richards, 1974), and 99.8% of specimens collected in the Gulf were less than 20 mm. Even though a small number of our largest specimens were over 20 mm and may be considered early juveniles ($n=3$), for the purposes of this study, all sailfish collected are referred to as larvae.

Genetic identification

A percentage of istiophorid larvae (22.2%) were identified to the species level by following the protocol of Bangma (2006). The protocol was subsequently modified and the remaining istiophorid larvae (77.8%) were identified according to the protocol of J. Magnussen and M. Shivji (personal commun.³). Briefly, a single eyeball was removed from each larva and DNA was extracted by using a QIAGEN DNeasy blood and tissue kit (QIAGEN #69506, Valencia, CA). A multiplex polymerase chain reaction (PCR) was performed by using an Eppendorf mastercycler gradient, QIAGEN Hot Star Taq DNA Polymerase (QIAGEN #203203), and PCR grade dNTP mix (QIAGEN #201901). Four primer pairs were used in each PCR reaction: a universal billfish primer set, and species-specific primers for sailfish, white marlin, (*Kajikia albida*), and blue marlin (*Makaira nigricans*). PCR reactions were examined by means of gel electrophoresis with 1% agarose gels containing ethidium bromide and species identification was based on gel banding patterns. This multiplex assay was employed to identify sailfish larvae as follows. For samples consisting of less than 10 individuals, all specimens were assayed. For samples with 10–50 istiophorid larvae, 40–60% of larvae were processed. For samples with >50 istiophorid larvae, 25% of larvae were processed. If all larvae in a particular subsample were identified as conspecific, remaining larvae from the sample were assigned to that species. If more than one istiophorid species was detected in a subsample, all remaining larvae from the sample were identified genetically.

² Leben, Robert. 2008. Colorado Center for Astrodynamic Research, Univ. Colorado, Boulder, CO.

³ Shivji, Mahmood. 2007. Guy Harvey Research Institute, Nova Southeastern Univ., Ft. Lauderdale, FL.

Density and catch rate

The total number of sailfish caught at each sampling station was divided by the surface area sampled to determine the density of larvae in number of individuals per 1000 m². Mean density did not vary between the two mesh sizes (500 µm and 1200 µm) in any survey (paired *t*-test, all $P \geq 0.05$), indicating no difference in capture success between net sizes. However, mean standard length was smaller in the 500-µm net gear (5.2 mm vs. 5.6 mm; $F_{(1,3116)} = 21.3$, $P < 0.01$), indicating that a larger fraction of small larvae were retained by the finer mesh. Frequency of occurrence was calculated for each survey as the number of collection stations which produced at least one sailfish larva by using the equation

$$\text{Frequency of occurrence} = \frac{\text{number of stations with} \geq 1 \text{ larva}}{\text{total number of stations during survey}} \times 100. \quad (1)$$

In order to compare catch rates with those from other ichthyoplankton studies, catch per unit of effort (CPUE) of sailfish larvae was estimated with the equation

$$\text{CPUE (larvae per hour)} = \frac{\text{number of larvae collected}}{[\text{number of tows} \times \text{tow length (min)} \times 2 (\text{number of nets towed})] / 60}. \quad (2)$$

Oceanographic features

Remotely sensed sea surface height (SSH) data were used to delineate oceanographic features into one of four categories (Leben et al., 2002). Briefly, stations with a SSH greater than 17 cm were considered to be within the core of the Loop Current or an associated eddy system and classified as “anticyclones” (warm core eddies) (Leben et al., 2002). Further, the core of adjacent “cyclones” (cold core eddies) were identified by a SSH of less than -10 cm. Frontal features associated with the Loop Current and anticyclones have been reported to extend up to 60 km from the 17-cm contour. Therefore, stations between 17 cm and -10 cm SSH and within 60 km of the 17 cm SSH contour were classified as being in a “front” (Tidwell, 2008). Remaining stations were classified as “open ocean.”

Analysis of otolith microstructure

Sagittal otoliths were extracted, cleaned of tissue in immersion oil, and preserved in mounting media (Flo-texx, Fisher Scientific #14-390-4, Pittsburgh, PA) for a subset of sailfish larvae. Mounted otoliths were photographed under high magnification (400×) with an Olympus BX41 light microscope, and daily growth increments were enumerated with the use of Image-Pro Plus software (vers. 4.5, Media Cybernetics Inc., Bethesda, MD) by counting the first visible increment beyond the hatch check as day one (Luthy et al.

2005). Inner increments of large otoliths are occasionally difficult to enumerate; therefore a regression of growth increment radius on age was used to predict the number of increments at various distances from the core (Rooker et al., 1999). The number of increments within unclear regions was estimated with this regression and added to the increment count for the enumerated section to produce final age estimates. Less than 25% of age estimates were corrected with this method, and if the unclear region comprised more than 33% of the final age estimate, the otolith was not used for age and growth assessments. Two independent readings of daily increments were conducted by a single reader for each otolith. When two readings were within 10% variance of each other, one reading was randomly selected for analysis. If readings differed by >10%, a third reading was performed. If the third reading was within 10% variance of one of the former readings, one of the two similar readings was randomly selected for analysis. If each reading differed from the others by >10%, the otolith was not used for further analysis ($n=94$, 7.1%).

Growth, mortality and hatch dates

Growth rates were determined by using otolith-derived age estimates ($n=1236$) and standard length data. Because ages varied among surveys, growth rates were based on a limited age range (≤ 17 days or the oldest larva in May 2005 collections) to minimize any effect of variable age ranges on growth analyses (Rilling and Houde, 1999). Daily instantaneous growth coefficients (g) were calculated from an exponential model:

$$L_t = L_0 e^{gt}, \quad (3)$$

where L_t = length (mm SL) at time t ;
 L_0 = estimated length at hatching;
 g = instantaneous growth coefficient (d); and
 t = otolith-derived age (days after hatching).

Ages of sailfish without an otolith-derived age were predicted by using age-length relationships ($n=1118$). A small number of sailfish larvae were damaged ($n=72$), and therefore length and age estimates could not be determined for these larvae.

Daily mortality was estimated for each survey from regressions of the decline in $\log_e(\text{abundance}+1)$ on age. In order to minimize the influence of gear avoidance by larger larvae (Houde, 1987), mortality estimates were determined over a short time interval (10 days), and thus for a limited size range of larvae (<10 mm). Mortality was calculated for several time intervals ranging from 5 to 10 days and differences were negligible, indicating that the 10-day duration was appropriate for the target life stage. The age of peak abundance for each cohort was used as the initial point for catch-curve analysis and ranged from 9 to 11 days after hatching. Daily instantaneous mortality rates (Z) were calculated from the exponential model

Table 1

Mean environmental conditions (\pm standard deviation [SD]) by oceanographic feature for ichthyoplankton collections in the northern Gulf of Mexico in 2005 and 2006. Environmental parameters were recorded at the surface at each sampling station.

Feature	Temperature ($^{\circ}$ C)	Salinity (ppt)	Dissolved oxygen (mg/L)
Anticyclone	29.1 (1.6)	36.1 (0.4)	6.8 (0.8)
Front	28.9 (1.4)	36.1 (0.4)	6.6 (0.5)
Open ocean	29.3 (1.6)	35.5 (1.2)	6.7 (0.8)
Cyclone	28.2 (2.0)	35.6 (0.6)	7.2 (1.3)

$$N_t = N_0 e^{-Zt}, \tag{4}$$

where N_t = abundance at time t ;

N_0 = estimated abundance at hatching;

Z = instantaneous mortality coefficient (d); and

t = otolith-derived age.

Dry weight (mg) was calculated for all larvae with a measured length by using the length-weight relationship for sailfish larvae by Luthy et al. (2005): $weight$ (mg) = $0.002(SL[mm])^{3.012}$. Weight-at-age data were fitted with exponential growth models to determine instantaneous weight-specific growth coefficients (G) for each survey by using the equation

$$W_t = W_0 e^{Gt}, \tag{5}$$

where W_t = dry weight (mg) at time t ;

W_0 = estimated weight at hatching;

G = instantaneous weight-specific growth coefficient (d); and

t = otolith-derived age.

Indices of stage-specific production potential were assessed for each cohort by examining the ratio of instantaneous weight-specific growth to daily mortality ($G:Z$). This ratio incorporates growth and mortality and was used as an index of stage-specific production of larval cohorts (Rilling and Houde, 1999; Rooker et al., 1999; Wells et al., 2008). A cohort with a $G:Z > 1.0$ was considered to be gaining biomass, which indicates that individuals had increased survival and production potential (Houde and Zastrow, 1993; Wells et al., 2008).

Hatch dates for larvae were determined by subtracting age from date of collection. Otolith-derived ages were used when available, and remaining ages were predicted by applying cohort-specific age-length keys. Given that larger, older larvae in our collections hatched earlier and experienced greater cumulative mortality than larvae that hatched later, adjustments for mortality were made to more effectively represent the hatch dates of survivors in our collections by using the equation

$$N_0 = N_t / e^{-Zt}, \text{ (Powell et al., 2004),} \tag{6}$$

where N_0 = estimated number of larvae at hatching;

N_t = number of larvae at time t ($N_t=1$ because N_0 was calculated for each individual larva);

Z = cohort-specific daily instantaneous mortality rate; and

t = age of larva in days.

Data analysis

Spatial and temporal variation in environmental conditions and density of sailfish larvae was examined with a two-way analysis of variance (ANOVA) (factors: oceanographic feature and survey). Because of uneven replicates in 2005 and 2006, separate one-way ANOVAs were conducted to assess inter- and intra-annual variation in length and age of sailfish with year or survey as a fixed factor. In order to minimize heteroscedasticity, estimates of density were $\log_e + 1$ transformed, whereas standard length and age data were \log_e transformed. In cases where variances were unequal, nonparametric analyses (Brown-Forsythe F -Test; Brown and Forsythe, 1974) were performed; however, results were consistent with parametric tests (ANOVA) and thus only parametric analyses are presented. *Post-hoc* differences among levels of the main effect(s) were examined with Tukey's honestly significant difference (HSD) test when variances were equal and with a Dunnett's T3 test when variances were unequal (Zar, 1996). Analysis of covariance (ANCOVA) was used to test for spatial and temporal variations in growth and mortality (covariate: age) with models to determine if the slopes of the regression lines differed (slopes test). All data analyses were performed with SPSS, vers. 15.0 (SPSS Inc., Chicago, IL) with $\alpha=0.05$.

Results

Environmental conditions

Spatial and temporal variations in environmental conditions were observed during Gulf collections. Temperatures were not significantly different among oceanographic features (ANOVA, $F_{(3,270)}=2.2$, $P=0.09$), albeit temperature was lowest within cyclones (28.2° C) compared with other oceanographic features (28.9 – 29.3° C) (Table 1). Mean temperature was 28.8° C and 29.4° C in 2005 and 2006, respectively, and varied significantly among the five surveys (ANOVA, $F_{(4,270)}=354.0$,

Table 2

Mean environmental conditions (\pm standard deviation [SD]) for ichthyoplankton surveys in the northern Gulf of Mexico in 2005 and 2006. Environmental parameters were recorded at the surface for each sampling station. Dissolved oxygen is not reported for the August 2006 survey because of a probe malfunction (NA).

Year	Survey	Date	Temperature ($^{\circ}$ C)	Salinity (ppt)	Dissolved oxygen (mg/L)
2005	May	17–22	26.4 (0.9)	35.5 (0.7)	7.1 (0.7)
	July	23–28	30.4 (0.7)	35.2 (1.3)	6.8 (1.2)
	September	16–19	29.8 (0.6)	36.5 (0.6)	6.3 (0.4)
	All surveys		28.8 (2.0)	35.6 (1.1)	6.8 (1.0)
2006	June	15–20	28.7 (0.5)	35.8 (0.4)	6.6 (0.1)
	August	31 July–5 Aug	30.1 (0.3)	36.2 (0.4)	NA
	All surveys		29.4 (0.8)	36.0 (0.5)	NA

Table 3

Total catch, frequency of occurrence, and density (\pm standard deviation [SD]) of sailfish (*Istiophorus platypterus*) larvae collected from the northern Gulf of Mexico in 2005 and 2006 arranged by survey. Number of stations during each survey (n) shown. Percent frequency of occurrence was based on collection stations during each survey that yielded 1 or more larvae.

Survey	n	Sailfish catch	Frequency of occurrence	Density (\pm SD) (no./1000m ²)	Maximum density	Larvae/hour
May 2005	60	212	26.7	0.6 (1.8)	10.5	10.6
July 2005	62	755	56.5	2.1 (7.5)	51.4	36.5
Sept 2005	39	134	46.2	0.6 (1.3)	4.5	10.3
June 2006	62	691	48.4	2.0 (4.7)	22.1	33.4
Aug 2006	65	634	47.0	1.7 (3.0)	10.2	25.4
Total	288	2426	45.0	1.5 (4.5)		24.4

$P < 0.01$) (Table 2). Spatial variation in salinity was detected among oceanographic features (ANOVA, $F_{(3, 270)} = 16.8$, $P < 0.01$), and lowest salinity observed within open ocean and cyclonic features (35.5 ppt and 35.6 ppt, respectively) and higher salinity in anticyclonic and frontal features (36.1 ppt and 36.1 ppt, respectively) (Table 1). Mean salinity was 35.6 ppt and 36.0 ppt in 2005 and 2006, respectively, and significant variation was observed among the five surveys (ANOVA, $F_{(4, 270)} = 11.1$, $P < 0.01$) (Table 2). Dissolved oxygen (DO) varied significantly among oceanographic features (ANOVA, $F_{(3, 270)} = 2.7$, $P = 0.048$) and surveys (ANOVA, $F_{(4, 270)} = 38.9$, $P < 0.01$) (Table 2). Lower DO levels were observed within anticyclones, fronts, and the open ocean (6.8 mg/L, 6.6 mg/L, and 6.7 mg/L, respectively) compared to those within cyclonic features (7.2 mg/L) (Table 1).

Spatial and temporal patterns of abundance

A significant interaction effect between oceanographic feature and survey on the density of sailfish was detected (ANOVA, $F_{(10, 271)} = 2.1$, $P = 0.02$), and highest densities were observed within frontal features in three of five surveys and in the open ocean during the remaining surveys (Fig. 1). No individual effect of oceanographic

feature or survey on density was observed (feature $P = 0.06$, survey $P = 0.11$), although density was lowest within cyclones during all surveys. When data from all surveys were combined, significant spatial variation in the density of sailfish among oceanographic features was observed (ANOVA, $F_{(3, 285)} = 3.3$, $P = 0.02$); density within cyclones was lower than that within other features ($P < 0.05$).

Frequency of occurrence and relative abundances were highest in June (48.4%), July (56.5%), and August (47.0%) surveys and lowest during the May 2005 survey (26.7%) (Table 3). The overall density of sailfish was 1.5 larvae per 1000 m²; lowest densities were observed in May and September 2005 surveys (0.6 larvae per 1000 m² and 0.6 larvae per 1000 m², respectively) and higher densities during July 2005 (2.1 larvae per 1000 m²), June 2006 (2.0 larvae per 1000 m²), and August 2006 (1.7 larvae per 1000 m²) (Table 3). Catches peaked in July 2005 and June 2006 when maximum densities of 51.4 larvae per 1000 m² and 22.1 larvae per 1000 m² were observed, respectively (Table 3). The overall catch per unit of effort (CPUE) for sailfish in the northern Gulf was 24.4 larvae per hour, and highest CPUEs were reported for July 2005 (36.5), June 2006 (33.4), and August 2006 (25.4) (Table 3).

Table 4

Exponential growth models arranged by survey and oceanographic feature for sailfish (*Istiophorus platypterus*) larvae collected from the northern Gulf of Mexico in 2005 and 2006. Number of larvae collected within each feature is given (*n*). Cyclones excluded from analysis because of low sample sizes within this type of feature. * indicates significant growth difference among features.

Survey	Feature	<i>n</i>	Growth model
July 2005	Anticyclone	135	$1.289e^{0.128(age)}$
	Front	45	$1.458e^{0.122(age)}$
	Open ocean	108	$1.331e^{0.124(age)}$
June 2006	Anticyclone	21	$1.713e^{0.101(age)}$
	Front	108	$1.415e^{0.120(age)}$
	Open ocean	118	$1.526e^{0.112(age)}$
August 2006	Anticyclone	131	$1.682e^{0.105(age)*}$
	Front	166	$1.480e^{0.114(age)}$
	Open ocean	149	$1.442e^{0.117(age)*}$

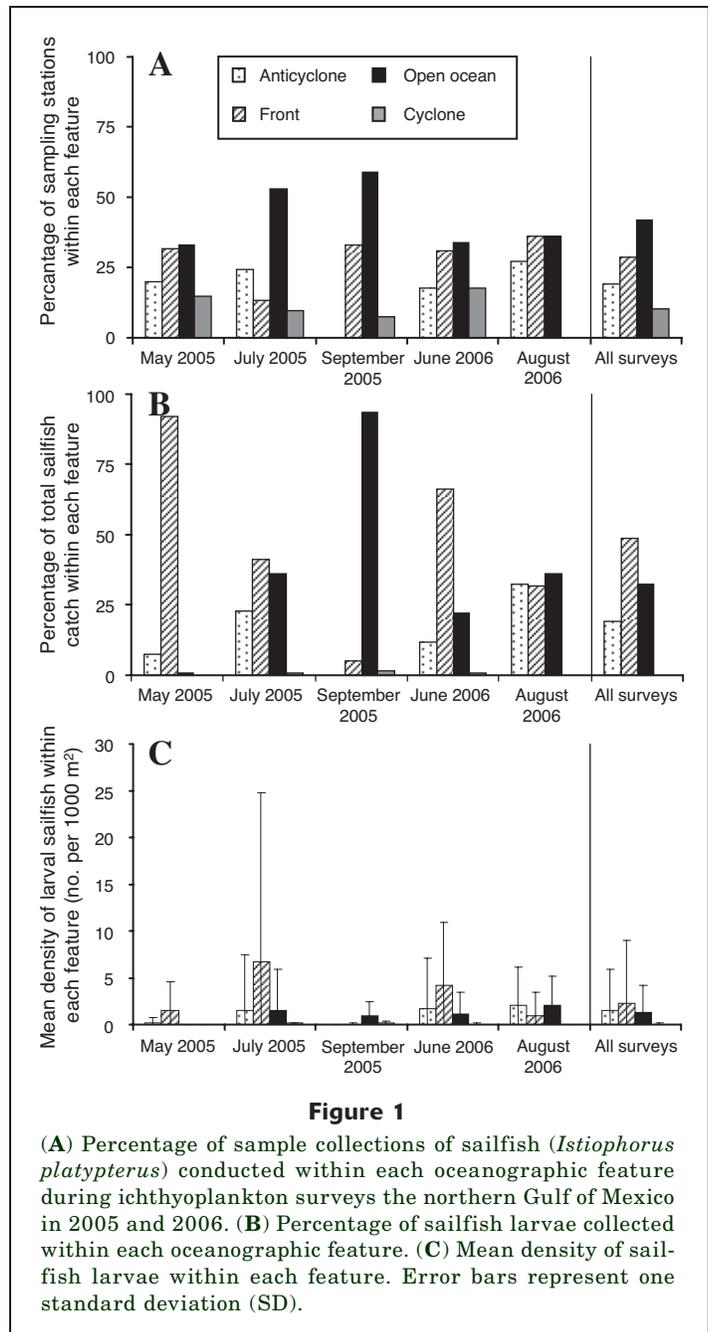
Sailfish length and age distributions

No significant difference in mean standard lengths of sailfish was observed between 2005 (5.1 mm, standard deviation [SD]=2.1) and 2006 (4.9 mm, SD=2.0) (ANOVA, $F_{(1, 2352)}=3.3, P=0.07$) (Fig. 2). Sailfish were most abundant in the 3–6 mm size range, with 70.4% and 65.9% of the catch in this size range in 2005 and 2006, respectively. Intra-annual differences in mean lengths of sailfish were observed in 2005 (ANOVA, $F_{(2, 1034)}=62.6, P<0.01$) and 2006 (ANOVA, $F_{(1, 1315)}=75.8, P<0.01$); smallest mean lengths were observed in May 2005 (4.1 mm, SD=1.6) and June 2006 (4.5 mm, SD=1.6), and larger larvae were collected in July 2005 (5.4 mm, SD=2.2) and August 2006 (5.4 mm, SD=2.3).

Mean ages were statistically similar between 2005 (10.1 days, SD=3.1 days) and 2006 (10.5 days, SD=3.2) (ANOVA, $F_{(1, 1234)}=2.7, P=0.10$) (Fig. 2). Sailfish larvae were most abundant in the 7–11 day range, with 60.7% and 53.9% of the catch in this age range in 2005 and 2006, respectively. Significant intra-annual variation in sailfish mean ages was observed in 2005 (ANOVA, $F_{(2, 521)}=51.6, P<0.01$) and 2006 (ANOVA, $F_{(1, 710)}=47.9, P<0.01$), when youngest mean age was observed in May 2005 (8.0 days, SD=2.3) and June 2006 (9.4 days, SD=3.1), and older larvae were observed in July 2005 (11.0 days, SD=3.3) and August 2006 (11.0 days, SD=3.1).

Spatial and temporal patterns of growth

Spatial variation in growth was analyzed across oceanographic features (anticyclone, front, and open ocean) for three of the five surveys, and significant differences in



growth were observed during August 2006 collections (Table 4). Cyclones were excluded from our analysis because of low sample sizes within this type of feature. During the August 2006 survey, daily instantaneous growth rates (*g*) of larvae collected within anticyclones ($g=0.105$) was significantly slower than growth of larvae collected in the open ocean ($g=0.117$) (ANCOVA, slopes, $F_{(2, 440)}=3.4, P=0.03$) (Table 4). In contrast, growth did not differ significantly among the three features in July 2005 (anticyclones $g=0.128$, fronts $g=0.122$, and open ocean $g=0.124$) and June 2006 (anticyclones $g=0.101$, fronts $g=0.120$, and open ocean $g=0.112$) (ANCOVA,

slopes, $F_{(2, 282)}=0.4$, $P=0.67$ and ANCOVA, slopes, $F_{(2, 241)}=2.5$, $P=0.09$, respectively).

Interannual differences in daily instantaneous growth rates of sailfish were detected between 2005 ($g=0.123$) and 2006 ($g=0.114$) (ANCOVA, slopes, $F_{(1, 1205)}=21.4$, $P<0.01$) (Fig. 3). Further, significant intra-annual variation in growth was observed in 2005 (ANCOVA, slopes, $F_{(2, 507)}=5.1$, $P=0.01$); larvae collected in September ($g=0.113$) displayed slower growth than larvae collected in July ($g=0.127$) (Fig. 4). In contrast, growth was statistically similar between surveys in 2006 (ANCOVA, slopes, $F_{(1, 692)}=0.7$, $P=0.39$).

Temporal variation in mortality

Estimates of daily instantaneous mortality (Z) did not differ significantly between 2005 ($Z=0.288$) and 2006

($Z=0.394$) (ANCOVA, slopes, $F_{(1, 46)}=1.0$, $P=0.33$) (Fig. 5, Table 5). Mortality rates ranged from 0.228 to 0.345 among survey periods in 2005, but rates were statistically similar (ANCOVA, slopes, $F_{(2, 24)}=2.1$, $P=0.15$) (Fig. 6). Further, mortality rates were not significantly different between survey periods in 2006, ranging from 0.344 in June to 0.381 in August (ANCOVA, slopes, $F_{(1, 16)}=0.5$, $P=0.48$).

Production potential ($G:Z$)

Instantaneous weight-specific growth coefficients (G) were 0.371 in 2005 and 0.347 in 2006, and G was indexed to daily instantaneous mortality (Z) to assess stage-specific production potential, $G:Z$ (Table 5). Annual estimates of $G:Z$ were 1.29 in 2005 and 0.88 in 2006. Production potential was highest in May 2005 (1.30) and July 2005 (1.66). In contrast, $G:Z$ ratios of the September 2005 (1.01), June 2006 (1.02), and August 2006 (0.91) surveys were lower.

Hatch-date distribution

Age-based estimates of hatch date indicated that sailfish in our collections were spawned from May to September (Fig. 7). Hatching of sailfish peaked in mid-July, and the majority of larvae hatched in July: 56.1% according to back-calculated estimates, 73.4% according to mortality adjusted estimates. The percentage of total catch from July for mortality-adjusted hatch dates was 52.1% in 2005, and 77.1% in 2006. Because the majority of sailfish were <20 days of age and sampling was conducted bimonthly, hatch-date distributions comprised multiple cohorts from separate spawning events throughout the spawning season.

Discussion

The relative abundance of sailfish larvae collected in the present study was comparable to or higher than values reported from other putative spawning grounds of sailfish. Llopiz and Cowen (2008), collected 7.3 sailfish larvae per hour in neuston tows over a two-year period in waters of the Straits of Florida; their catch rate was lower than the catch rate of 27.4 sailfish larvae per hour reported by Post et al. (1997) in the same region. Further, Richardson et al. (2009b), during a single week, reported a catch rate of 298 sailfish larvae per hour in the Straits of Florida; this catch rate indicates that very high, but ephemeral, abundances occur in this region. Catch rates of istiophorid billfishes (sailfish, white marlin, and blue marlin) reported in other areas,

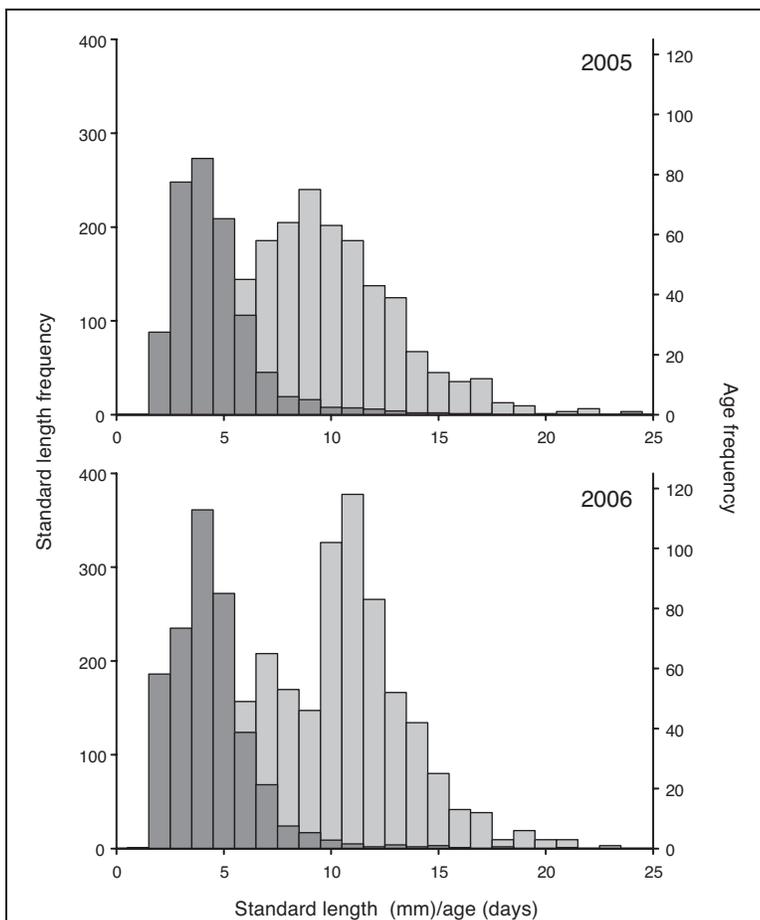


Figure 2

Standard length and age-frequency distributions of sailfish (*Istiophorus platypterus*) larvae collected from the northern Gulf of Mexico in 2005 and 2006. Standard length distributions are shown in dark bars ($n=1037$ and $n=1317$ in 2005 and 2006, respectively). Age distributions are shown in light bars ($n=524$ and $n=712$ in 2005 and 2006, respectively). Note: 72 larvae indicated in Table 2 were damaged and no length measurements were taken for these larvae.

including the Bahamas (Serafy et al., 2003) and the Dominican Republic (Prince et al., 2005), were less than 10 istiophorid larvae per hour, which is markedly lower than rates reported in our study for the Gulf of Mexico (24.4 sailfish larvae per hour). Sailfish frequency of occurrence from the Gulf (45.0%) also corresponds closely to the 41.1% occurrence reported in the Straits of Florida and Bahamas by Luthy (2004), which included all Atlantic billfishes. Although CPUE was standardized for tow length, sampling gear, and number of tows, variations in towing methods as well as in the timing of sampling may have affected differences in catch rates of larvae. However, the relatively high catch rate of sailfish larvae reported in our study supports the premise that this region is an important spawning and nursery ground of sailfish—a contention supported by high bycatch rates of adult sailfish during summer months (NMFS¹).

The highest density of larvae was reported within mesoscale frontal features and highest catch rates were observed from June through August. Lowest densities of sailfish larvae were observed in cold core features during all surveys; however, as with other pelagic species (Richards et al., 1993; Hoffmeyer et al., 2007), catches were higher within fronts and anticyclones associated with the western margin of the Loop Current. In fact, highest densities were observed within frontal features during three of five surveys and over the course of all surveys combined. Higher catches of marine fish larvae have been reported at frontal features created by riverine discharge or converging oceanic currents in both temperate and tropical oceans (Hoffmeyer et al., 2007; Richardson et al., 2009b). The accumulation of larvae near or within fronts may simply be due to hydrodynamic convergence which has been shown to aggregate marine larvae in the Gulf and other regions (Govoni and Grimes, 1992; Bakun, 2006). Alternatively, elevated primary and secondary production within frontal features often increases the availability of planktonic prey (Govoni et al., 1989; Grimes and Finucane, 1991) and therefore may effect higher survival for larvae within these oceanographic features (Grimes and Finucane, 1991; Biggs, 1992). In a recent study in the Straits of Florida, larval sailfish density was observed to peak at eddy frontal zones where there was a corresponding increase in density of common sailfish prey items (Llopiz and Cowen, 2008; Richardson et al., 2009b). This finding supports the premise that larvae are more abundant at fronts because of the increased availability of prey. As with spatial trends in sailfish density, temporal patterns in Gulf collections were comparable to those in the Straits of Florida; sailfish larvae were more abundant during spring and summer months (Post et al., 1997; Luthy, 2004). Elevated catches of sailfish in the summer correspond to peak spawning activity of

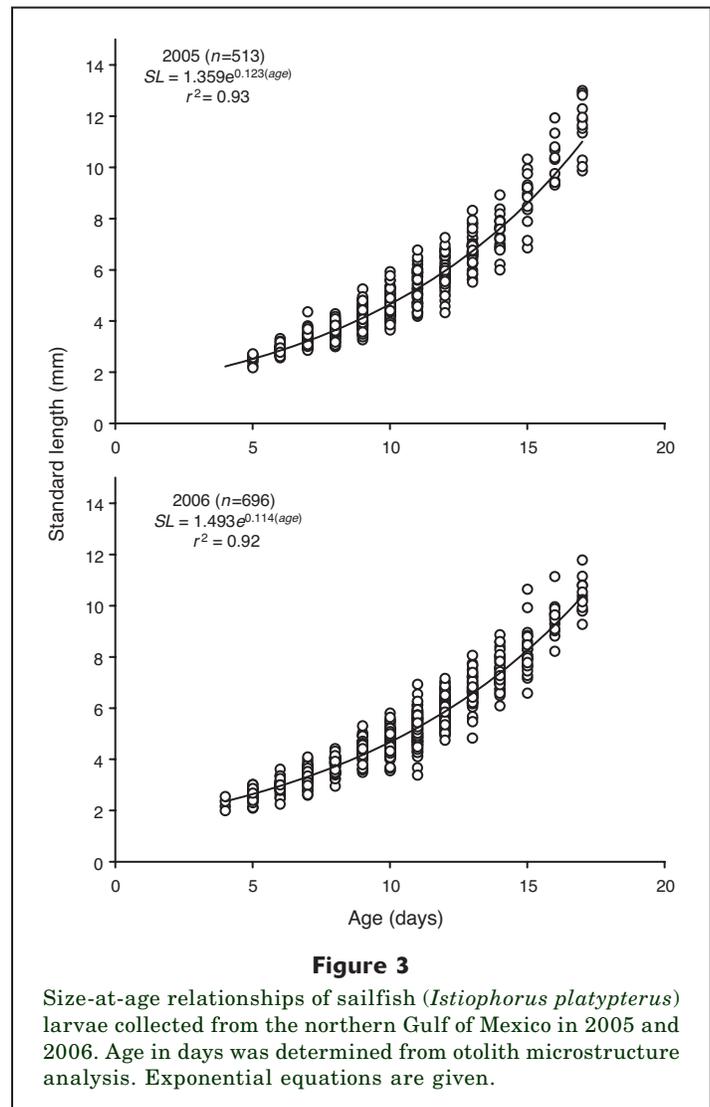


Figure 3

Size-at-age relationships of sailfish (*Istiophorus platypterus*) larvae collected from the northern Gulf of Mexico in 2005 and 2006. Age in days was determined from otolith microstructure analysis. Exponential equations are given.

sailfish in the North Atlantic (de Sylva and Breder, 1997; Richardson, 2007).

Spatial variation in growth of sailfish was limited despite elevated densities of sailfish larvae within fronts. The general lack of growth variation in sailfish among oceanographic features is somewhat unexpected given that cyclonic and frontal features often display increased primary productivity relative to anticyclones (Grimes and Finucane, 1991; Biggs, 1992) and that growth variation during early life is influenced by primary productivity and prey availability (de Vries et al., 1990; Wexler et al., 2007). The lack of variation in growth among oceanographic features may be attributed to the fact that larvae in the northern Gulf likely spend time in multiple oceanographic features during early life. Oceanographic currents in this region have been observed to have speeds up to 0.8 meters per second (69.1 kilometers per day) (Govoni and Grimes, 1992), and higher velocity currents have been recorded within the Loop Current (1.0 meters per sec-

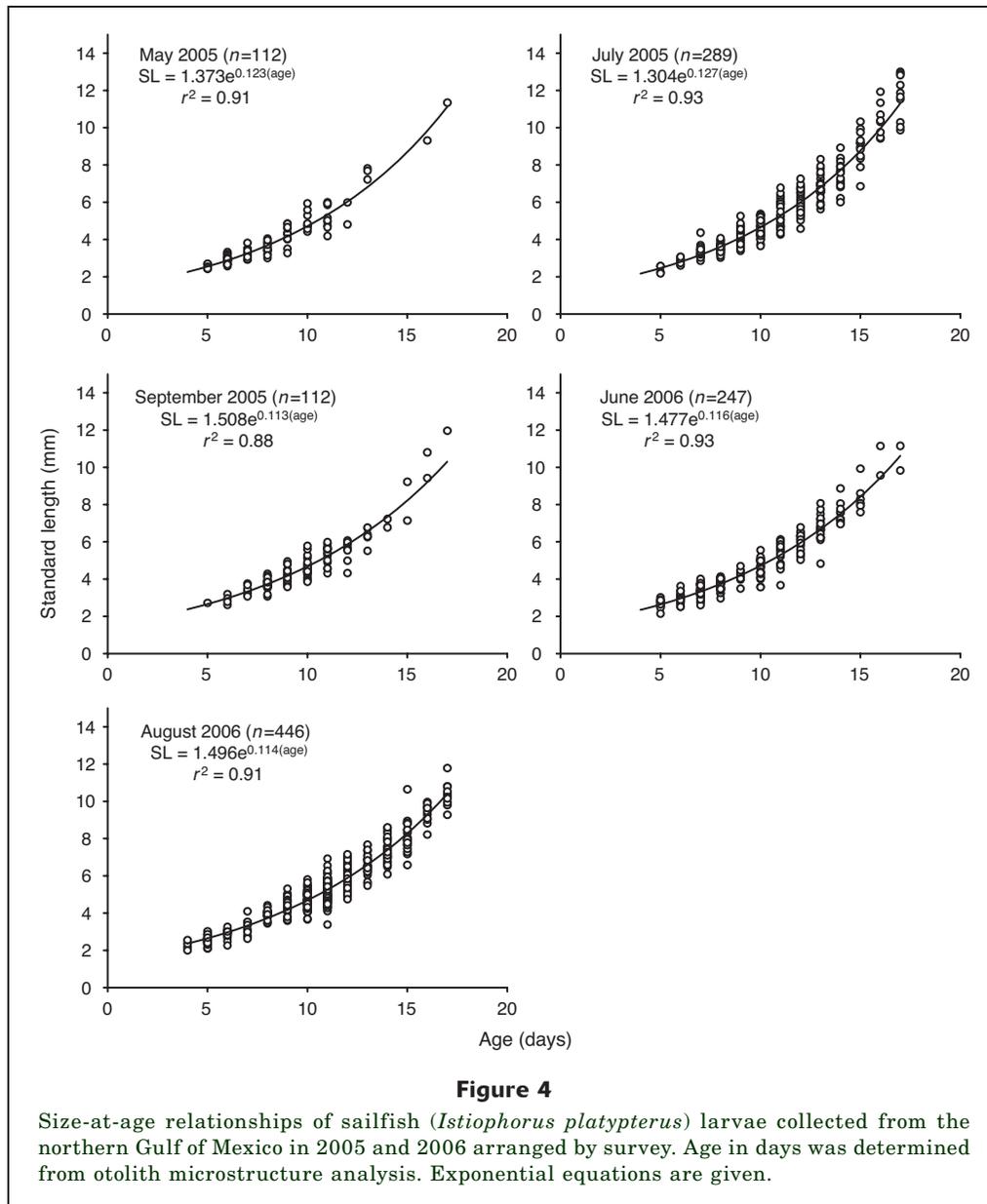


Figure 4

Size-at-age relationships of sailfish (*Istiophorus platypterus*) larvae collected from the northern Gulf of Mexico in 2005 and 2006 arranged by survey. Age in days was determined from otolith microstructure analysis. Exponential equations are given.

Table 5

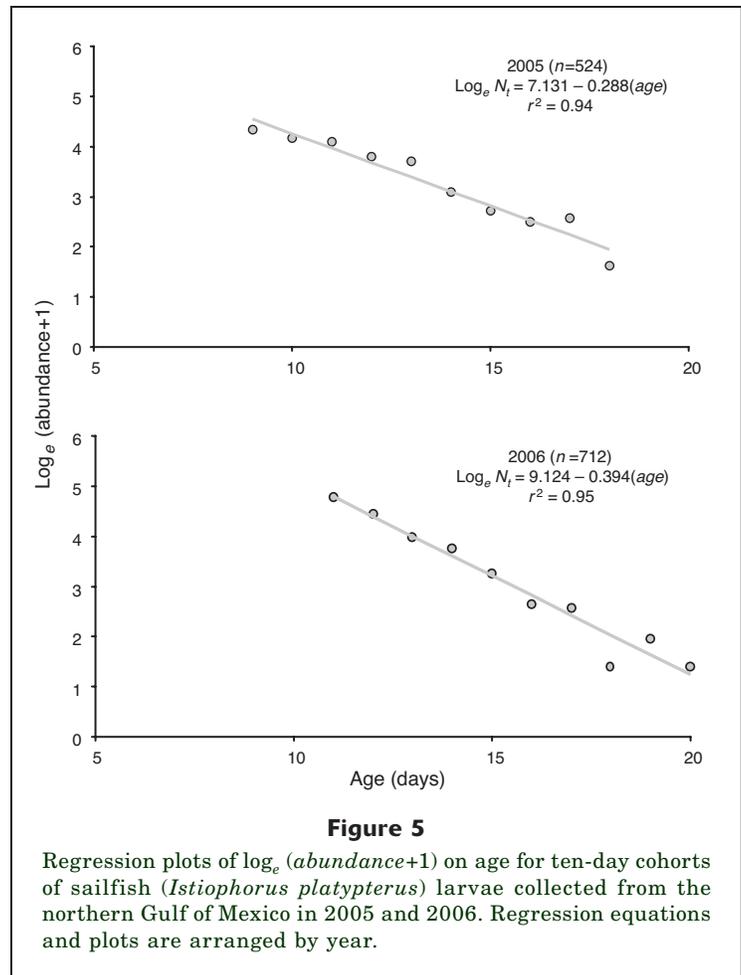
Instantaneous weight-specific growth (*G*) and mortality (*Z*) coefficients of sailfish (*Istiophorus platypterus*) larvae collected from the northern Gulf of Mexico in 2005 and 2006. Percentage per day was calculated from instantaneous growth and mortality coefficients. The *G*:*Z* index of stage-specific production potential is also shown.

Year	Survey	<i>G</i>	%/day	<i>Z</i>	%/day	<i>G</i> : <i>Z</i>
2005	May	0.371	44.9	0.285	24.8	1.30
	July	0.378	45.9	0.228	20.4	1.66
	September	0.347	41.5	0.345	29.2	1.01
	All surveys	0.371	44.9	0.288	25.0	1.29
2006	June	0.351	42.0	0.344	29.1	1.02
	August	0.347	41.5	0.381	31.7	0.91
	All surveys	0.347	41.5	0.394	32.6	0.88

ond; Vukovich and Maul, 1985), which indicate that planktonic larvae may encounter multiple oceanographic features during their planktonic larval duration. Further, pelagic larvae from broad oceanic areas have been reported to accumulate within frontal zones (Richards et al., 1993; Bakun, 2006), making it difficult to determine where individuals spend the majority of their lives and therefore, in which feature(s) most of their early growth occurs.

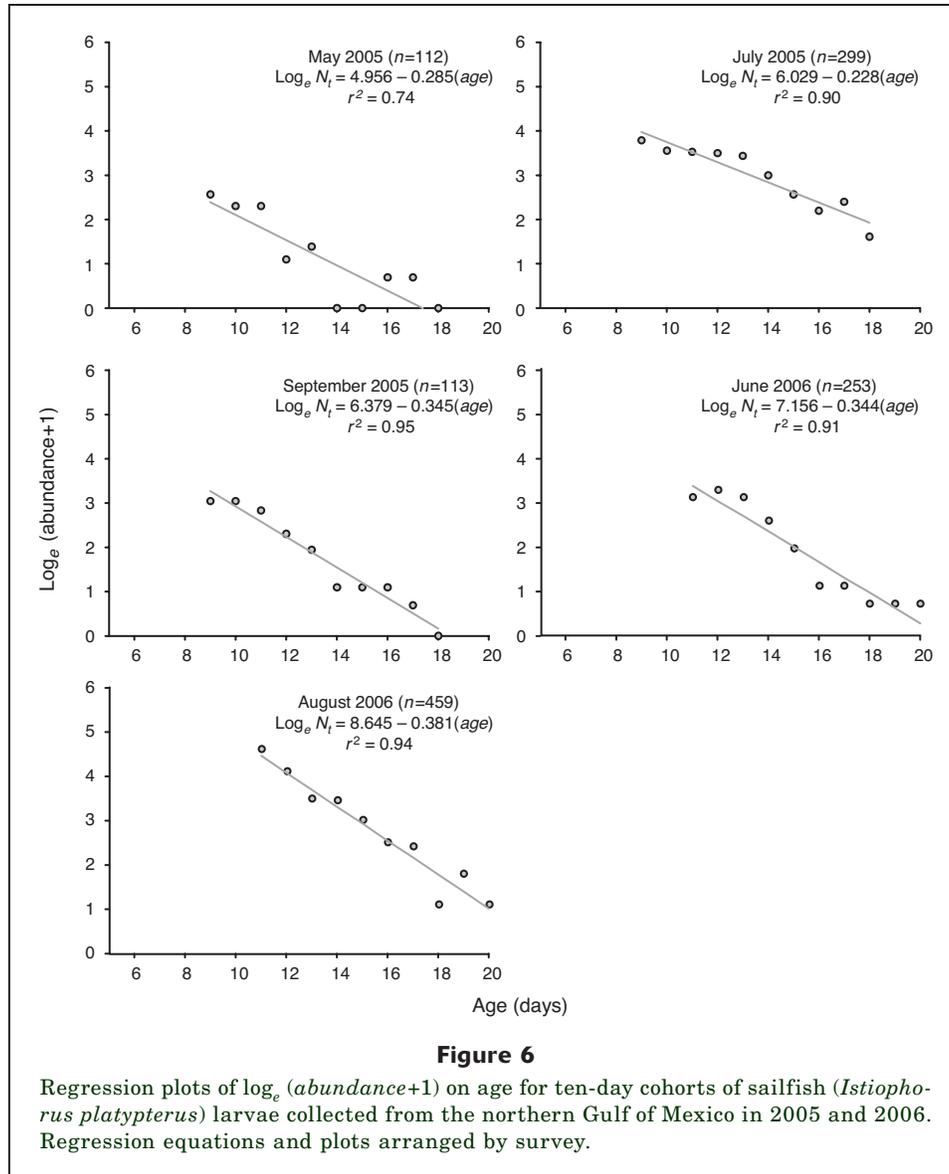
Estimated growth of sailfish in the Gulf ($g=0.113$ to 0.127) varied temporally and rates were comparable to or slightly slower than those reported for sailfish in the Straits of Florida ($g=0.130$ to 0.146 ; Luthy et al., 2005; Richardson, 2007; Richardson et al., 2009a) and blue marlin from the Bahamas ($g=0.098$ to 0.125 ; Serafy et al., 2003; Sponaugle et al., 2005) and the Straits of Florida ($g=0.089$ to 0.114 ; Sponaugle et al., 2005; Richardson, 2007). Observed differences in growth among studies are minor and similarities are not unexpected because the timing of collections and environmental conditions between the regions were comparable. Sampling in the Straits of Florida was conducted between April and September in waters ranging from 26.1°C to 30.6°C (Luthy et al., 2005; Richardson, 2007). This range of temperatures is similar to temperatures present in the Gulf during our May to September sampling period (26.4 – 30.4°C). Moreover, observed ranges in salinity were nearly the same between the Straits of Florida (34.0 – 36.7 ppt) and Gulf (35.2 – 36.5 ppt). Temporal variations in growth of marine larvae have been shown to be correlated with temperature (Rilling and Houde, 1999), and the most rapid growth of sailfish larvae was observed during July 2005 when the warmest mean temperature was reported. Nevertheless, the second fastest growth rate for sailfish was observed during May 2005 when the lowest mean temperature was reported. Thus, other factors known to affect growth, such as density of conspecifics or prey availability (Jenkins et al., 1991; Lang et al., 1994; Wexler et al., 2007), may be responsible for observed variations in growth of sailfish larvae.

Although intra-annual differences in mortality were limited, losses were substantial throughout the early life interval examined ($Z=0.23$ to 0.38). Daily instantaneous mortality rates reported in our study are 10 – 45% lower than mortality rates for sailfish and blue marlin larvae from the Straits of Florida and Exuma Sound, Bahamas (Richardson et al., 2009a). However, the losses reported in our study are comparable to those of other pelagic larvae, such as bluefin tuna (*Thunnus thynnus*) ($Z=0.20$; Rooker et al., 2007), yellowfin tuna (*Thunnus albacares*) ($Z=0.33$; Lang et al., 1994), and members of the suborder Scombroidei, which includes tunas, billfishes, and the barracuda *Sphyrna barracuda* ($Z=0.34$; Houde and Zastrow,



1993). Predation has been observed to be a major cause of mortality during the early life interval of pelagic species (Leggett and Deblois, 1994; Houde, 2002) and it may be responsible for high losses of sailfish larvae. Recent studies indicate that istiophorids are preyed upon by conspecifics and congeners (Llopiz and Cowen, 2008; Tidwell, 2008) and, if so, cannibalism or predation pressure by other istiophorids may represent an important source of mortality for sailfish during early life.

Observed $G:Z$ ratios were greater than 1.0 during all but the August 2006 survey, indicating conditions were likely favorable for production during the life stage examined. Houde and Zastrow (1993) reported a mean $G:Z$ ratio of 0.89 for marine fish larvae (pooled across several taxa), which is lower than the range reported in our study for sailfish (0.91 – 1.66). However, indices reported for individual species or taxonomic groups ranged from 0.26 to 2.42 for larvae abundant in upwelling and shelf zones, indicating wide-ranging stage-specific production potential for pelagic fishes. Collection of larvae peaked in July and it is possible that increased $G:Z$ coincided with increased temperature or prey availability, both of which have been

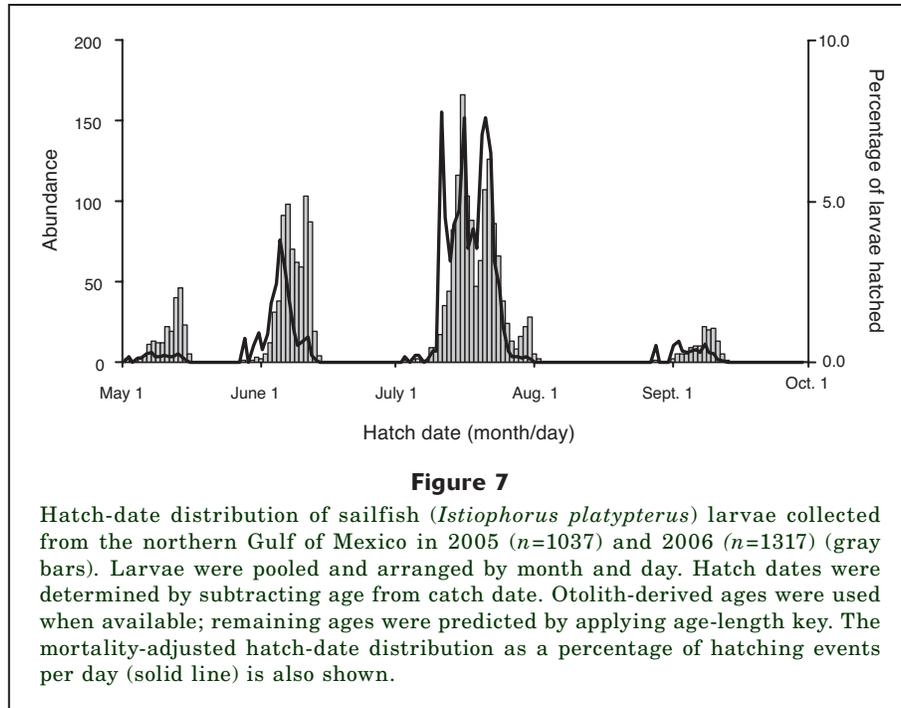


shown to increase stage-specific production potential (Rilling and Houde, 1999).

Hatch dates of sailfish larvae collected in this study indicate that spawning is protracted in the northern Gulf and peak activity occurs during July. To date, sailfish spawning has not been documented in the northern Gulf, but sailfish are known to have protracted spawning in other regions of the Atlantic and Pacific oceans (de Sylva and Breder, 1997; Chiang et al., 2006; Richardson, 2007). Although the timing of sampling likely influences hatch-date distributions of sailfish in the Gulf, resulting in a multimodal distribution, spawning has been shown to occur from May to September in the western North Atlantic Ocean (de Sylva and Breder, 1997) and from April to September in the eastern Pacific (Chiang et al., 2006), corresponding to the spawning range observed in this

study. Additionally, data from studies indicate that peak spawning occurs in mid to late summer because increased frequencies of mature ovaries have been observed in sailfish landed in July and August (de Sylva and Breder, 1997; Chiang et al., 2006; Richardson et al., 2009a).

Questions remain regarding the specific factors regulating observed variations in distribution, growth, and mortality of sailfish, as well as the extent of spawning in the northern Gulf. Regardless, high densities and broad distributions of larvae combined with rapid growth and high production potential indicate that sailfish larvae spawned or hatched in the northern Gulf potentially contribute to Atlantic sailfish populations. This study provides strong evidence that the northern Gulf serves as an important spawning and nursery habitat for Atlantic sailfish.



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