Importance of the Straits of Florida spawning ground to Atlantic sailfish (*Istiophorus platypterus*) and blue marlin (*Makaira nigricans*)

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ABSTRACT

Much of the uncertainty in managing highly migratory pelagic species results from the scarcity of fisheries-independent data relevant to determining long-term trends in abundance, migratory movements, and the relative importance of different spawning grounds. To address these issues, we used an ichthyoplankton-based method to quantify the overall level of spawning of sailfish (*Istiophorus platypterus*) and blue marlin (*Makaira nigricans*) in the Straits of Florida (SF). We estimated that during the 2 years (2003–2004) of the study, 4.60×10^{11} sailfish eggs and 4.49×10^{11} blue marlin eggs were produced on an annual basis in this region. These egg production values, when combined with estimates of annual fecundity for each species and the most recent stock assessment estimate of total biomass, indicate that about 2.1% of Western Atlantic sailfish spawning and 1.6% of Atlantic-wide blue marlin spawning occurs in the SF. Additionally, pop-up satellite tags deployed on sailfish at the start of the spawning season revealed their short residency times in the SF, suggesting that a large (≈13%) transient portion of the sailfish population is responsible for the SF egg production. Overall, this study provides a critically needed fisheries-independent method of

quantifying spatial and temporal trends in the abundance of highly migratory species. The application of this methodology in the SF indicated that above-average levels of sailfish and blue marlin spawning occur in this area and, possibly more importantly, that the SF is a migratory bottleneck for these species.

INTRODUCTION

Two of the fundamental goals of fisheries science are to delineate stock structure and to assess the abundance of individuals within different stocks (Begg *et al.*, 1999). Highly migratory large pelagic species present a unique challenge to accomplishing these two goals. For these species, the isolation of stocks may occur during just one portion of their annual movement, most commonly during spawning activity (Block *et al.*, 2001, 2005). Understanding the degree to which spawning grounds are isolated in space and/or time and, conversely, the degree to which individuals from the same spawning area overlap in different feeding areas, is thus critical for the management of these species (Lutcavage *et al.*, 1999; Magnuson *et al.*, 2001). However, for nearly all large pelagic species, spawning grounds are poorly delineated and individual-level migratory movements are unknown. Additionally, the stock assessments for these species rely almost exclusively on fisheries-dependent data. This runs counter to the well recognized need to incorporate fisheries-independent data, collected through a coordinated sampling effort, into stock assessments (National Research Council, 1998). The result is that there are high levels of uncertainty and limited consensus about the status of most highly migratory stocks (e.g., Myers and Worm, 2003; Hampton *et al.*, 2005), and a limited ability to devise spatially structured management approaches.

Ichthyoplankton surveys have long been used in the identification and assessment of fish stocks

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(Saville, 1964; Ahlstrom and Moser, 1976; Lasker, 1985; Hunter and Lo, 1993; Hare, 2005). The use of these surveys as part of the stock identification process has focused primarily on the determination of spatially and temporally isolated spawning grounds and their relation to adult movement patterns (Hare, 2005). Ichthyoplankton studies have been used to calibrate stock assessments by providing either an index of population trends (e.g., Scott *et al.*, 1993) or, when combined with an adult reproductive study, an estimate of the absolute abundance of spawning fish (Saville, 1964; Lasker, 1985; Pepin, 2002; Ralston *et al.*, 2003). The latter approach has proven particularly successful for small pelagic species, but has not been implemented on an operational basis with large pelagic species (reviewed in Stratoudakis *et al.*, 2006). Notably, the stock assessments for both groups share many of the same challenges, including the often poor relationship between catch per unit effort data and population trends, and the difficulty in developing fisheries-independent indices based on adult sampling (Pitcher, 1995; Freon *et al.*, 2005).

Blue marlin and sailfish are two large pelagic species that are critically important in a number of tropical and subtropical fisheries (Brinson *et al.*, 2006). Currently, blue marlin are managed as a single Atlantic stock, whereas sailfish are managed as separate western and eastern Atlantic stocks. Though uncertain, the stock assessments indicate that blue marlin are over-exploited and sailfish are at least fully exploited or possibly overexploited (ICCAT, 2002, 2007, Restrepo *et al.*, 2003; Die, 2006). Both species spawn in a number of locations throughout the western North Atlantic (e.g., Serafy *et al.*, 2003; Luthy, 2004; Prince *et al.*, 2005), although the relative importance of different spawning grounds and the full spatial extent of spawning are unknown. Tagging studies have revealed both long distance movements and a certain level of site fidelity (Ortiz *et al.*, 2003; Prince *et al.*, 2005; Orbesen *et al.*, 2008) but, with a few exceptions (e.g., Prince *et al.*, 2005), most of this work does not link these movement patterns to spawning.

Previous work has determined that the Straits of Florida (SF) is a spawning ground for sailfish and blue marlin (Luthy, 2004; Richardson *et al.*, in press-a). This relatively narrow (70–150 km) passage links the Gulf of Mexico and Caribbean Sea to the broader North Atlantic Ocean. Current patterns within this area are dominated by the Florida Current, with current speeds in excess of 2 m s^{-1}. The objective of this study was to quantify the importance of the SF spawning ground for sailfish and blue marlin. This work encompassed three specific tasks: (i) using larval surveys to estimate the annual egg production for both species in the SF, (ii) using published adult fecundity estimates and stock assessment data to evaluate the number of individuals spawning in the SF and the relative importance of SF spawning ground, and (iii) for sailfish only, using a pop-up satellite tagging study to determine residency times of adults on the spawning grounds and their interregional movement patterns.

MATERIALS AND METHODS

Assessment approach

A modification of the larval production method (Hunter and Lo, 1993; Ralston *et al.*, 2003) was applied to sailfish and blue marlin (Fig. 1). Traditionally, this method, and similar ichthyoplankton-based approaches, have two components to the field work and data analysis (Saville, 1964; Ahlstrom and Moser, 1976; Lasker, 1985; Stratoudakis *et al.*, 2006). The first component, fully implemented in this application of the methodology, is a comprehensive ichthyoplankton study used to estimate annual egg production (P_a) for a spawning stock. The second component, for which we relied upon published values, is an adult reproductive study used to determine egg production per female or per unit of biomass. Within this second component, we also incorporated an estimate of the total stock size to calculate the total stock egg production, and ultimately, the percentage of total stock spawning that occurs in the SF. Because of the highly migratory nature of these species, a third adult tagging component was used to quantify the turnover of individuals on the spawning ground, and ultimately, the percentage of the stock that likely migrates through the SF during the spawning season. Logistical constraints restricted this third component to sailfish. A comprehensive evaluation of the precision of the estimate of SF P_a (component 1) was performed; however, the nature of the available data prevented an assessment of the error of values estimated from the other two components.

Ichthyoplankton sampling and processing

Ichthyoplankton was sampled over a 2–3-day period along a 17-station transect crossing the SF at 25°30′N (Fig. 2a) on a monthly basis from January 2003 to December 2004 (Richardson *et al.*, in press-a). Two net systems were used to sample ichthyoplankton. The first, a combined neuston net, consisted of a 1 × 2 m 1000-μm mesh net attached to a 0.5 × 1 m 150-μm mesh net. This system was deployed with half of the frame out of the water and the volume of water filtered

Figure 1. Outline of the three main components of the larval production methodology. Parameters are enclosed in circles and equations are enclosed in brackets, with details of both listed in Table 1. For the ichthyoplankton component of the study, the final product is the SF annual egg production. The confidence intervals of this value are determined using Monte-Carlo simulations that take into account the error from the parameters in black circles. Variables in gray for the adult reproductive component of the study were taken from the published literature.
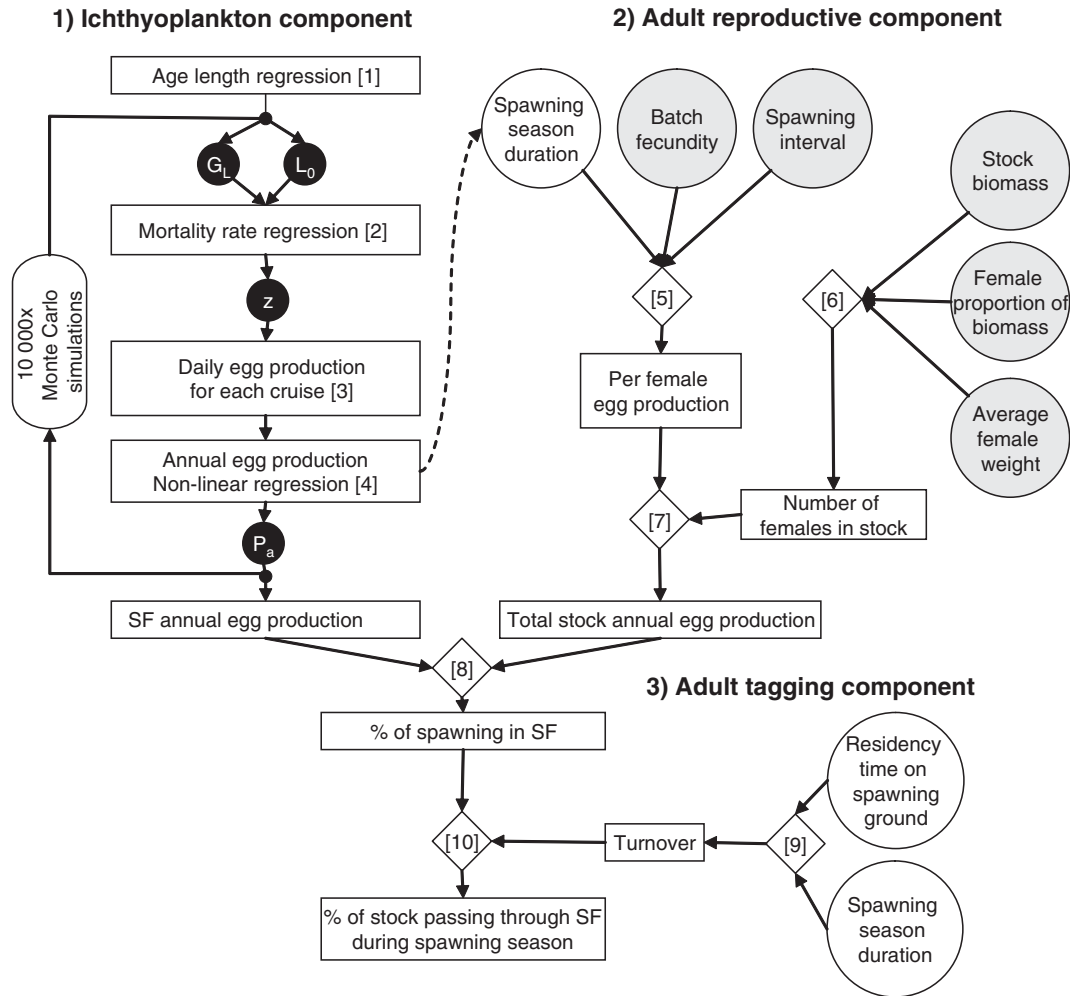

was measured with a General Oceanics flowmeter. The second, a combined MOCNESS (multiple opening and closing net and environmental sensing system) contained a 4 m^2 1000-μm mesh net and a 1 m^2 150-μm mesh net (Guigand *et al.*, 2005). This system allows for the precise opening and closing of individual nets at discrete depths with continuous measurements of the volume of water filtered. The MOCNESS was sampled from 100 m to the surface with nets triggered in 25-m intervals.

Billfish were removed from the plankton samples and were identified either morphologically following Luthy *et al.* (2005a) or molecularly following Richardson *et al.* (2007). Standard length measurements

were made using a dissecting microscope equipped with a digital camera and the IMAGE PRO PLUS image analysis software (Media Cybernetics, Bethesda, MD). For the samples collected in 2003, all of the nets were processed. Within these samples ≈0.5% of billfish larvae occurred in samples collected deeper than 25 m. Due to time constraints, the 2004 fine-mesh samples collected deeper that 25 m were not processed for billfish larvae. To account for the effects of net extrusion, all analyses were run using only data and individuals from the fine-mesh nets for the <4-mm length classes.

A total of 121 sailfish and 187 blue marlin larvae were aged using the protocol outlined in Sponaugle *et al.* (2005) and Luthy *et al.* (2005b). Measured and
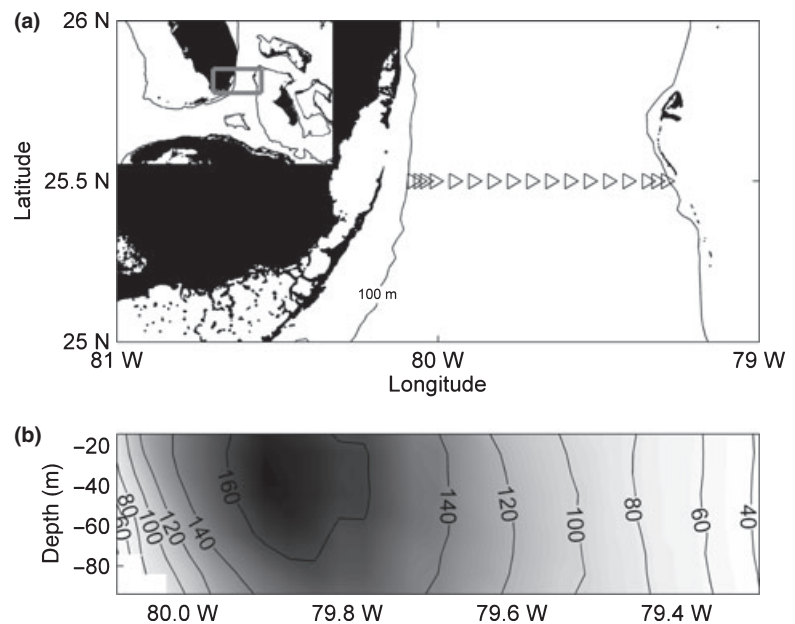
Figure 2. Location of sampling transect and current structure across the transect (a). Sampling stations (Δ) along the transect are indicated, (b) average north component of the current (cm s^{-1}) across the SF sampling transect.

aged otoliths from genetically identified yolk-sac billfish and published information on egg-stage durations (≈1 day) of scombroid larvae at >26°C (Margulies *et al.*, 2007) verified that the otolith-based ages accurately estimated time since spawning and did not require a correction factor.

Current measurements

The calculations of annual egg production required a measurement, concurrent to the collection of larvae, of the north component of the current. These measurements were obtained using an RD Instruments 150 kHz Acoustic Doppler Current Profiler (ADCP; RD Instruments, Poway, CA). Four steps were involved in the processing of these data. First, 1-min average files were created using the WINADCP software (RD Instruments, Poway, CA). Second, measurements with Percent Good-4 (percentage of measurements with four beam solutions) values below 80% were discarded. Third, measurements collected when the ship speed was <1.5 m s^{-1} were discarded, due to their reduced reliability on this sampling platform. Finally, measurements of the north component of the current were averaged across 0.01° longitude bins for both the outbound and return sampling of the transect. At the latitude of sampling the northward component of the surface current across the transect ranges between 220 and −10 cm s^{-1}, and averages 120 cm s^{-1} (Fig. 2b). The standard error for the north component of the average current was generally <5 cm s^{-1}, or about 4% of the average northward current speed across the sample transect.

Regional egg production

To use the larval production method, sampling should generally occur across the entire spatial extent occupied by the larvae of the assessed species or population, and sampling must occur sufficiently frequently to model the seasonal cycle of egg production (Pepin, 2002; Ralston *et al.*, 2003). For wide-ranging species such as blue marlin and sailfish that spawn in fast currents, the requirement of sampling the entire spatial extent occupied by their larvae is not achievable. As an alternative, we considered the flux of larvae across the sampling transect, eliminating the need to sample a large horizontal grid of stations. This in turn allowed sampling to occur more frequently in time, and along a more closely spaced set of stations.

The use of daily flux across a transect requires that an alternate means be used to estimate the area over which P_a is calculated. Both the regional current patterns and the age range of larvae used in the flux calculations determine the size and shape of this area. Additionally, the area of egg production does not contain hard boundaries, but rather there are locations upstream of the transect where only a portion of the egg production crosses the transect in the defined period of time. These issues were addressed using a larval transport model (Cowen *et al.*, 2006). The specific implementation of the model used the 1/12° (≈9 km) resolution HYbrid Coordinate Ocean Model (HYCOM) with a particle tracking code to simulate larval dispersal. Particles (*n* = 100) were released from a grid of 319 locations upstream of the SF on a

bi-weekly basis from 15 May to 9 October for the 2003 and 2004 model year runs. Particles remained in the upper layer of the model (5 m) and were passive. The vertical distribution of particles in the model is consistent with results from vertically stratified sampling of billfish larvae, which found a daytime concentration in the upper half meter of the water column, a nighttime subsurface concentration of larvae, and the near absence of larvae deeper than 25 m during all time periods (Llopiz and Cowen, 2008). Additionally, minimal shear occurs in the upper 25 m of the water column in this location. From each release location the percentage of particles crossing the transect in a 3–11-day period was quantified.

The implementation of the larval production method was a four-step procedure: (i) the age of each larva was estimated using a regression of age on length, (ii) an apparent mortality rate (z) (incorporates mortality and increasing net avoidance with age; Houde et al., 1979) was calculated using a regression of abundance-at-age on age, (iii) for each cruise daily egg production was calculated based on the age-specific

flux of larvae across the transect and the apparent mortality rate, and (iv) a non-linear regression of daily egg production versus ordinal day of year was used to calculate P_a (Fig. 1, Table 1). As with previous work with billfish larvae (Luthy et al., 2005b; Sponaugle et al., 2005), an exponential growth model was used. In contrast to those studies, length was treated as the dependent variable (equation 1, Table 1), though for consistency, and to aid interpretation, the instantaneous daily growth rate (G_L) and length at hatch (L_0) values are reported here, rather than the regression coefficients [i.e., $1/G_L$ and $1/G_L * \ln(L_0)$]. An exponential model (equation 2, Table 1) with age 3–11 days larvae, was used to calculate the mortality rates (Houde, 2002). Additionally, a Gaussian curve (equation 4, Table 1) was fit to the seasonal cycle of egg production (Saville, 1964; Ralston et al., 2003). This non-linear least-squares regression was performed using the *nlinfit* function in the MATLAB statistics toolbox (Mathworks, Natick, MA).

The one novel step in this four-step process was the methodology used to calculate the daily egg production

Table 1. Equation, parameter and derived variable list. The equation numbers are provided and referred to in the text and the broad outline of the methodology in Fig. 1.

# Equation	Parameters and derived variables	Description
[1] $age = \frac{1}{G_L}\ln(L_{age}) - \frac{1}{G_L}\ln(L_0)$	L_{age}	Length at age (days)
	L_0	Length at hatch (mm)
	G_L	Instantaneous growth rate (mm day^{-1})
[2] $N_{age} = N_0 e^{(-z \times age)}$	N_{age}	Abundance of larvae at age
	N_0	Abundance of spawned eggs
	z	Apparent mortality rate
[3] $P_d = C \sum\limits_{age=3}^{11} Flux_{age} \times e^{(z \times age)}$	P_d	Daily egg production
	C	Seconds per day constant = 86 400
	$Flux_{age}$	Age-specific flux of larvae across transect
[4] $P_d(t) = \frac{P_{a,SF}}{\sigma\sqrt{2\pi}} e^{\frac{(t-\mu)^2}{2\sigma^2}}$	$P_d(t)$	Daily egg production at time t
	$P_{a,SF}$	Annual egg production, Straits of Florida
	μ	Peak day of egg production
	σ	Standard deviation in days
[5] $F_a = \left(\frac{BF}{I}\right)S$	F_a	Annual fecundity
	BF	Batch fecundity
	I	Spawning interval
	S	Spawning season duration
[6] $N_F = \frac{B_{stock} \times PB_F}{W_F}$	N_F	Number of females in stock
	B_{stock}	Total biomass
	PB_F	Female proportion of biomass
	w_F	Average female weight
[7] $P_{a,stock} = N_F \times F_a$	$P_{a,stock}$	Total stock annual egg production
[8] $\%P_{a,SF} = \frac{P_{a,SF}}{P_{a,stock}}$	$\%P_{a,SF}$	% of stock egg production that occurs in the SF
[9] $T = \frac{S}{R_{SF}}$	T	Turnover on spawning ground during spawning season
	R_{SF}	Residency time in SF (days)
[10] $\%Transit_{SF} = \%P_{a,SF} \times T$	$\%Transit_{SF}$	% of stock transiting through the SF during the spawning season

value (equation 3, Table 1). To calculate daily egg production it was first necessary to determine the age-specific larval flux at each station, a product of the density of larvae in each sampling depth bin (ind m^{-3}) and the concurrent transport across that depth bin (m^3 s^{-1}) (Pepin *et al.*, 1995; Grothues *et al.*, 2002). Transport rates were determined from the ADCP measurements. A transect-wide age-specific larval flux rate was then calculated for each cruise using a linear interpolation between stations. This transect-wide age-specific flux of larvae was converted to the corresponding equivalent level of eggs using the apparent larval mortality rate (z). These values were summed across all age classes. A 3-day minimum age was used in this calculation based on the minimum age of larvae considered to be accurately quantified. The 11-day maximum age was set to ensure that each age class had an adequate sample size. Finally, a constant (86 400 = 60*60*24) was used to convert the flux rate for the transect as a whole from the units of egg s^{-1} to eggs day^{-1}.

The development of confidence intervals for the estimate of P$_a$ relied on a Monte-Carlo simulation approach (Fig. 1) that accounts for the error propagation inherent in the multiple step calculation of P$_a$. For each species, 10 000 Monte-Carlo simulations were performed. First, parameters of the growth equation were sampled from the multivariate t-distribution derived from the covariance matrix of the regression coefficients. These parameters were used to calculate the age of each larva based on its length. Subsequently, the abundance-at-age regression was performed and a mortality rate (z) and corresponding error were calculated. From the mortality rate distribution (*t*-dist; df: 7), a value was randomly selected. Using this set of parameters, a daily egg production value for each of the cruises was calculated, and the non-linear regression was performed. The MATLAB statistics toolbox *nlinparci* function was then used to obtain the confidence intervals of each of the non-linear regression parameters. A final P$_a$ value for that simulation run was randomly selected from its distribution. Values of μ and σ were also selected, though these values were not necessary to calculate P$_a$. For each simulation, a measure of year-to-year variability in the index was obtained by running the final daily egg production versus day of year regression using only data from a single year. Additionally, to evaluate the contributions of each individual regression model to the final error in estimating P$_a$, a new set (*n* = 2000) of simulations was run with errors from only a single regression incorporated into the simulations.

Unique to the calculation of confidence intervals for this study is the consideration of a single transect as

a unit of sampling. The extensive spatial autocorrelation of larval flux within transects does not allow for the use of standard techniques to estimate variance based on a station as a unit of sampling (Legendre and Legendre, 1998), while at the same time, the number of stations per cruise (17) and the non-stationarity of the data are not conducive to the use of standard geostatistical techniques, especially within a simulation framework. The occurrence of temporal autocorrelation in the flux estimates was not expected considering the ≈30-day period separating cruises.

Reproductive and stock assessment parameters

An assessment of relative importance of the SF as a spawning area was made by comparing the estimates of P$_a$ in the SF versus an estimate of total egg production for the entire Western Atlantic sailfish stock and Atlantic-wide blue marlin stock (Fig. 1). To estimate total stock P$_a$ it was necessary to consider the average annual female fecundity and the number of females in the stock (equation 7, Table 1).

Three parameters were required to estimate annual female fecundity: batch fecundity, interval between spawning, and the length of the spawning season (equation 5, Table 1). The spawning season duration was defined as the time period during which 95% of spawning occurs and was calculated based on the median σ value from the regression of daily egg production on day-of-year (equation 4, Table 1). The only comprehensive reproductive study of sailfish (Chiang *et al.*, 2006) and blue marlin (Tseng, 2002) is based on sampling from the waters offshore of Taiwan. The latitude (22–24°N), habitat (western boundary current), and spawning season length (≈5 months) around Taiwan are similar to the SF. For blue marlin, the exact values of the parameters obtained in the Pacific study were used. On the other hand, Pacific sailfish tend to be larger than Western Atlantic sailfish (Prince and Goodyear, 2006). Because of this, the average batch fecundity data for Western Atlantic sailfish was estimated using an approximated scaling factor of 70% of the average Pacific sailfish batch fecundity. This scaling factor is based on difference (19 versus 28 kg) in average size between Atlantic (Jolley, 1974) and Pacific females (Chiang *et al.*, 2006). The use of average fecundity values, versus a more comprehensive size structure-based analysis (e.g., Ralston *et al.*, 2003), was dictated by the available data. Specifically, fishing operations provide the only current size structure data on blue marlin and sailfish, though relative catch at length in these data is highly dependent on the gear being used. Moreover, sex-specific size information would be necessary for a size-

structured approach, but is not available in the catch records.

A calculation of the number of females in the stock (equation 6, Table 1) depended upon estimates of three parameters: stock biomass, female proportion of stock biomass, and average female weight. The stock biomass values used in the analysis were the median of the model runs presented in the stock assessments for blue marlin and sailfish (ICCAT, 2001, 2002). For each species, the model runs differed in the assumed model parameters and the relative weighting of each catch per unit effort index. The best available sailfish biomass estimates are based on model runs that were considered unsatisfactory by the assessment working group, and thus must be viewed with caution (ICCAT 2002). No estimates of female proportion of the biomass exist and thus this value was set at 0.5. In general, studies have found a higher proportion of males in spawning areas (Erdman, 1968), though this is likely offset by the higher weight of females. Average female weight was obtained from Tseng (2002) for blue marlin and Jolley (1974) for sailfish.

Adult tagging and analysis

The adult tagging component of the study was designed to address the residency time of individual adult sailfish in the SF, and the interregional movement patterns of adult sailfish during the spawning season. Twenty Wildlife Computers PAT-4 pop-up satellite tags were deployed on adult sailfish in the Straits of Florida between 25 April and 11 May 2005 (Table 2). These tags were programmed to record temperature, depth and light levels at 30-s intervals for a deployment duration of 120 days that coincided with the majority of the spawning season. The location (lower Florida Keys) at which most of the tags were deployed approximated the center of the spawning area that was assessed with the ichthyoplankton work. One additional tag used in this study was deployed offshore of Miami (25.70°N 80.17°W) on 30 April 2003 for 60 days.

Sailfish were caught using standard recreational fishing techniques. Those fish that were in poor condition after capture or were considered unlikely to be reproductively mature based on their size (<15 kg) were released without a tag. Fish handling, tag rigging and tag attachment followed an established protocol (Prince *et al.*, 2005). The function of pop-up satellite archival tags (PSAT) is described in detail elsewhere (Block *et al.*, 1998). Briefly, after their programmed deployment duration the tags are designed to release from the fish, float to the surface, and transmit data summaries via the ARGOS satellite system. Position

Table 2. Tagging data from adult sailfish.

Fish #	Track color	Estimated size (kg)	Deployment			Pop-off			Estimated residency time	Other regions visited
			Date	Lat	Lon	Date	Lat	Lon		
40606	Pink	18	30/4/2003	25.70	−80.17	1/7/2003	26.6	−73.67	10*	SS; NB
57176	Purple	18	25/4/2005	24.43	−81.92	23/8/2005	33.44	−78.55	6	SS;NB;SAS
57177	Brown	27	11/5/2005	24.50	−81.55	N/A			7	NB; SAS
57178	Yellow	20	28/4/2005	24.43	−81.89	26/8/2005	27.00	−79.97	43	SS; NB; SAS
57179	Blue	25	11/5/2005	24.49	−81.54	9/9/2005	27.44	−78.60	40	NB
57180	Red	18	3/5/2005	24.46	−81.69	31/8/2005	27.69	−95.26	13	EGOM; WGOM
57181	Green	20	8/5/2005	24.45	−81.76	5/9/2005	25.70	−79.97	34 + 5	EGOM
57182	Blue-green	18	8/5/2005	24.44	−81.80	5/9/2005	36.33	−72.21	5	SAS
57184	Cyan	18	10/5/2005	24.00	−81.00	7/9/2005	24.79	−84.55	25 + 14	EGOM
									Average = 24 days	

Track color corresponds to Figs 6 and 7. Residency times are best estimates based on the fish tracks. The residency time of fish 4060 was excluded from the average due to the short tag duration.
SS, Sargasso Sea; SAS, South Atlantic States; NB, Northern Bahamas; EGOM, Eastern Gulf of Mexico; WGOM, Western Gulf of Mexico.

estimates are made using light-based geolocation, a methodology that inherently has large latitudinal and smaller longitudinal errors (Sibert *et al.*, 2003). To partially account for this, the position data were processed using the manufacturer-provided software, a sea-surface temperature-corrected Kalman filter (Nielsen *et al.*, 2006), and a bathymetry filter (Hoolihan and Luo, 2007). Sailfish residency times in the Straits of Florida were estimated primarily based on the longitudinal portions of the tracks, which have smaller estimation errors. The longitudinal range associated with the Straits of Florida was present in deep (>25 m) waters only in the SF and south of Cuba, increasing the reliability of residency time estimates. The turnover of individuals on the spawning ground was based on the ratio of the spawning season duration to the residency times of adult sailfish (equation 9, Table 1).

Composite analysis

The final stage of the analysis involved uniting the results from the ichthyoplankton, adult reproductive and tagging components of the study (Fig. 1). The percentage of spawning estimated to occur in the SF (equation 8, Table 1) was determined from the estimate of SF total egg production (ichthyoplankton component) and total stock egg production (adult reproductive component). This, in turn, was combined with the estimates of turnover of adults in the SF (adult tagging component) to calculate the percentage of the stock that likely passes through the SF during the spawning season (Equation 10, Table 1)

RESULTS

Egg production estimates

In total, 648 blue marlin larvae (2.3–23.0 mm SL) and 684 sailfish larvae (2.3–22.8 mm SL) were collected. For both sailfish and blue marlin the correlation coefficients of the age-length regressions were high ($r^2 = 0.883$ and $r^2 = 0.943$, respectively; Fig. 3a,d). Relative to blue marlin, the sailfish L_0 was lower, G_L was higher, and the confidence intervals for both parameters were wider (Table 3). Using the median values of L_0 and G_L, the correlation coefficients of the mortality regressions (sailfish $r^2 = 0.982$; blue marlin $r^2 = 0.970$) were also high (Fig. 3b,e). Taking into

Figure 3. Regressions of (a,d) age on length (b,e) abundance-at-age on age, and (c,f) daily egg production on day of year for both sailfish and blue marlin in the Straits of Florida. The latter two regressions assume median parameters from the previous regressions.
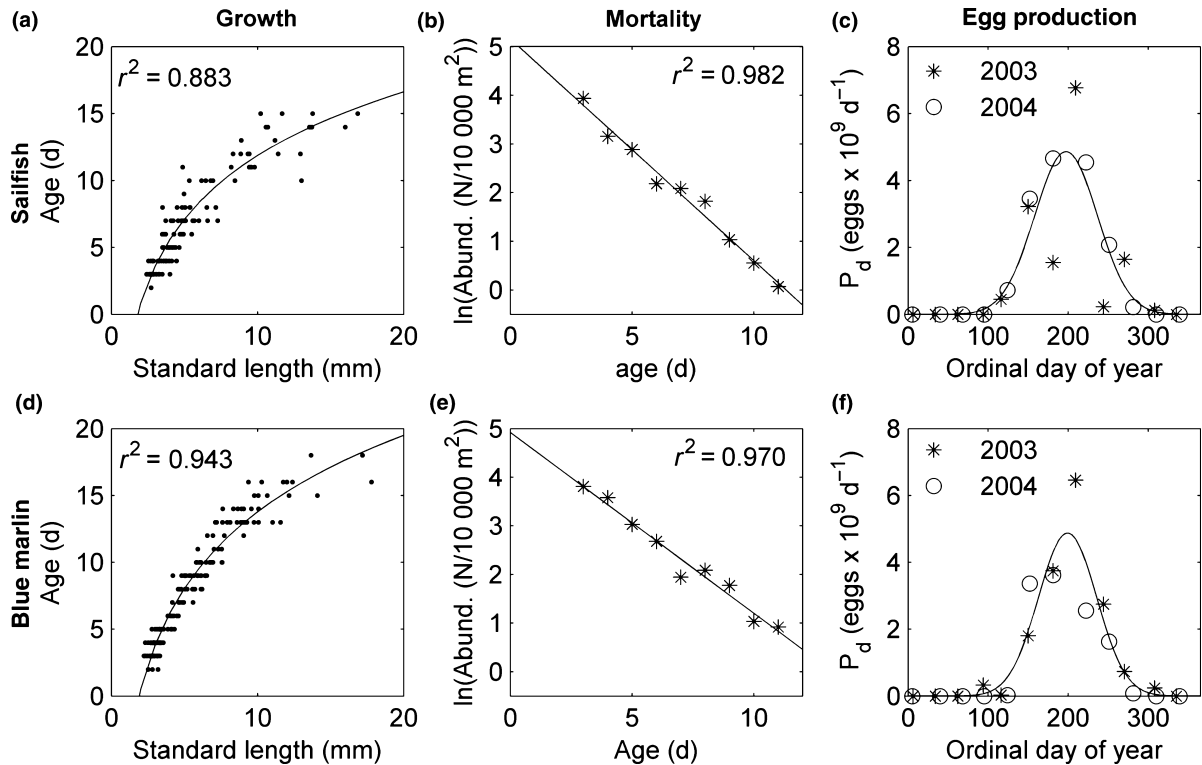
Table 3. Estimated parameters from egg production analysis. 95% confidence interval (CI) corresponds to the complete set (n = 10,000) of simulations with all parameters allowed to vary. Effect of error on P_a corresponds to the final egg production estimate when only the specified parameter is allowed to vary. The 95% CIs are in parentheses, and the magnitude of this error relative to the total model error is given.

| Parameter	Parameter name	Sailfish			Blue Marlin		
		Median	95% CI	Effect of error on P_a	Median	95% CI	Effect of error on P_a
G_L	Growth rate	0.146	0.137–0.156	15.2% (4.10–4.99 × 10^{11})	0.121	0.117–0.126	15.5% (4.06–4.96 × 10^{11})
L_0	Length at hatch	1.77	1.64–1.89		1.89	1.81–1.96	
z	Apparent larval mortality rate	0.45	0.36–0.53	64.6% (3.25–7.01 × 10^{11})	0.37	0.29–0.45	67.3% (2.93–6.84 × 10^{11})
$P_{a,all}$	Annual egg production	4.60 × 10^{11}	2.47–8.29 × 10^{11}	39.8% (3.60–5.92 × 10^{11})	4.49 × 10^{11}	2.46–8.27 × 10^{11}	24.6% (3.72–5.15 × 10^{11})
$P_{a,2003}$	Annual egg production in 2003	3.51 × 10^{11}	1.21–7.03 × 10^{11}		4.76 × 10^{11}	2.84–8.21 × 10^{11}	
$P_{a,2004}$	Annual egg production in 2004	5.16 × 10^{11}	2.84–9.44 × 10^{11}		3.92 × 10^{11}	1.91–8.17 × 10^{11}	
μ	Mid point of spawning season	195 (13-July)	184–207		200 (18-July)	193–207	
σ	Stdev of seasonal egg production	38.2	26.7–49.6		36.7	29.3–43.9	

account the variability in L_0 and G_L, the median estimate of z for sailfish was higher than the estimate for blue marlin (Table 3). The regression of daily egg production versus day of year indicated that the peak egg production day occurred on 13 July for sailfish and on 18 July for blue marlin (Fig. 3c,f, Table 3). The σ value quantifies the length of the SF spawning season. The median estimate indicated that 95% of spawning occurs between 29 April 29 and 25 September for sailfish and between 6 May and 28 September for blue marlin.

The median and confidence intervals of the P_a estimate were very similar for blue marlin and sailfish (Table 3). The Monte-Carlo simulations indicated a strong skew in the P_a distribution towards higher values. When the simulations were re-run using only data from a single year in the seasonality of spawning regression, the estimate of P_a for sailfish was higher for 2004 (5.16 × 10^{11}) than for 2003 (3.51 × 10^{11}). However, the confidence intervals substantially overlapped for the 2 yr and the difference was not significant. For blue marlin the 2003 estimate (4.76 × 10^{11}) was higher than the 2004 estimate (3.92 × 10^{11}), but again the differences were not significant (Table 3).

Between-simulation variability in the P_a values resulted from an interaction of the errors associated with estimating L_0, G_L, z and P_a. As such it is important to consider the relationship between each of these parameters, and how each of them contributes to the error in the calculation of P_a. A negative correlation was evident between L_0 and G_L (Fig. 4a). This correlation was derived directly from the covariance structure of the regression of age on length. The simulations revealed no relationship between the estimate of G_L and the estimate of either z or P_a (Fig. 4b,c). A strong exponential relationship was evident between the estimate of z and P_a (Fig. 4d).

Simulations, run while allowing the parameters derived from one regression to vary and keeping the others constant, revealed that the uncertainty in the z estimate was the dominant source of error in the P_a estimates (Table 3). With only the variability of z taken into account, the confidence interval of P_a for sailfish and blue marlin was 64.6% and 67.3%, respectively, of the width of the confidence interval when all the sources of error were taken into account. For both species, the error in the P_a estimate that was associated with the regression of daily egg production on day of year was of intermediate importance, and the error associated with the growth regression was of relatively minor importance.

Figure 4. Relationship between parameters derived from the 10,000 Monte Carlo simulations foe sailfish from the Straits of Florida. Each point represents values from a single simulation for the following parameter pairs: (a) growth rate and length at hatch, (b) growth rate and mortality rate, (c) growth rate and annual egg production, and (d) mortality rate and annual egg production.
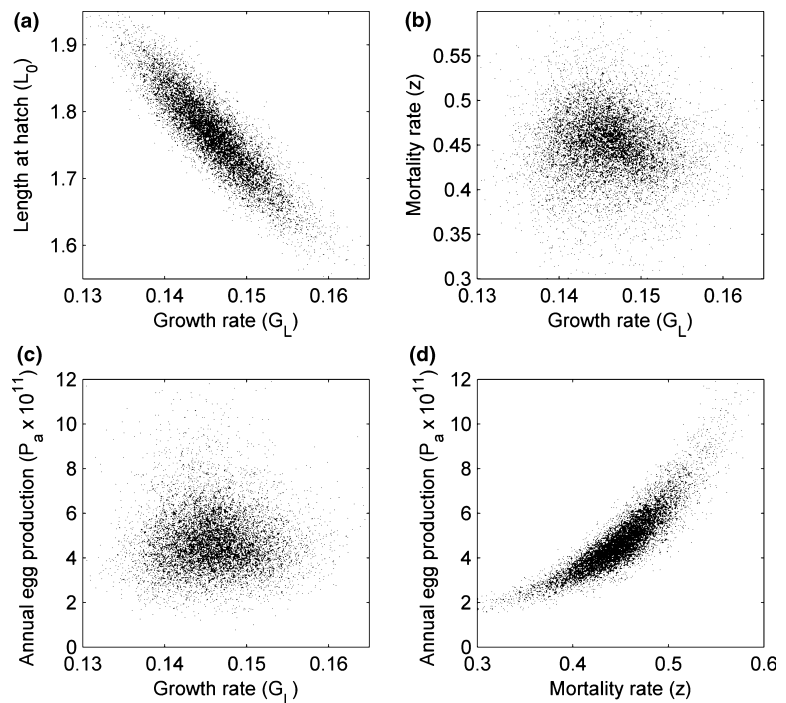
Area of egg production

The area of egg production estimated from the model encompassed most of the southern Straits of Florida, and to a lesser extent, portions of the Santaren Channel (Fig. 5). The distances upstream that contributed notable levels to the calculated egg production were shorter along the edges of the SF than in the center. Only a limited amount of spawning in the Gulf of Mexico was expected to result in larvae that cross the sampled transect in the designated 3–11-day period.

Adult movements

Data for the entire 120-day deployment duration were obtained from eight of the 20 tags deployed in 2005, and for a single 60-day deployment in 2003. One of the 120-day deployment tags was recovered 7 months after deployment still attached to the fish, having not successfully released at the programmed time. Of the remaining 12 tags, three released prematurely (<10 days) and reported by satellite, one was recovered shortly after deployment, damaged and without data, and eight remain unaccounted for.

Over the tagging period all of the fish moved away from the SF, including transits to the west into the Gulf of Mexico, to the north into the waters offshore of the South Atlantic States, and to the east into the Sargasso Sea (Fig. 6). The maximum distance a fish

Figure 5. Area over which egg production of sailfish and blue marlin was calculated. The use of larval flux rates, versus the sampling of a two-dimensional horizontal grid results in a lack of hard boundaries to the area being assessed. The color scale indicates the percentage of spawning at that location that would be expected to contribute to the calculated annual egg production in this study; that is, these values represent the percentage of virtual larvae in the transport model that cross the transect in a 3–11-day period of time, corresponding to the age range of larvae used in this assessment. The 319 particle release locations (x) are indicated.
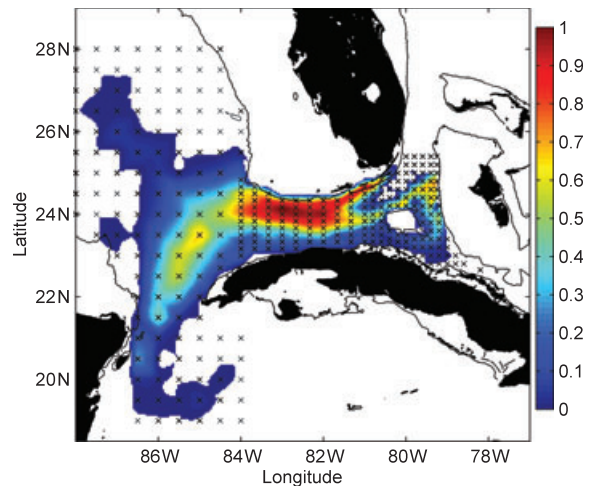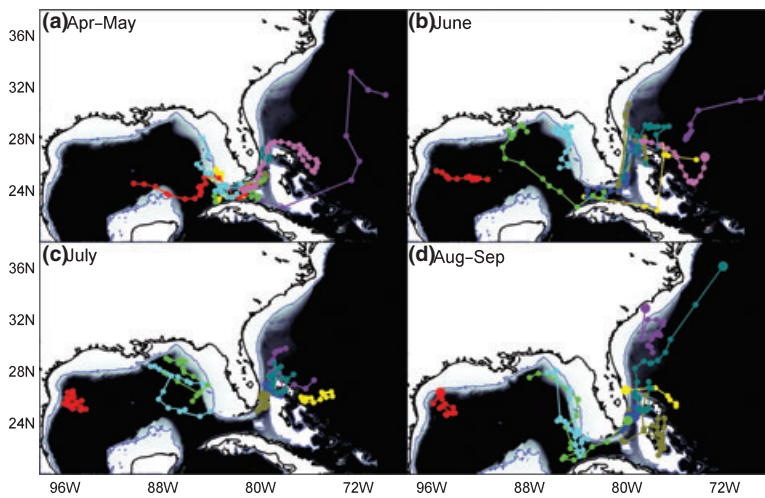
Figure 6. Tracks of the nine PSAT tagged sailfish for (a) April–May, (b) June, (c) July, and (d) August–September. Tag pop-off locations are indicated with a large circle. Position estimates were processed with a Kalman filter and a bathymetry filter.

moved away from the SF was ≈1500 km. Estimates of residency time ranged from 5 to 43 days and averaged 24 days, exclusive of the 60-day duration tag. Residency occurred only at the start of the tagging period for all other individuals, with two exceptions (Fig. 7). One fish made a rapid 5-day transit between the Gulf of Mexico and the east coast of Florida at the end of the tagging period. For a second fish, the track produced using the Kalman filter suggests a 2-week residency in the southwestern portion of the SF during August. This fish occupied the eastern Gulf of Mexico for the period preceding and following this SF residency.

Composite analysis

Annual fecundity was estimated at 72×10^6 eggs and 318×10^6 eggs for sailfish and blue marlin, respectively (Table 4). The total stock biomass value used in the analysis was the median of three model runs for sailfish (7348, 11390, 12590 mt) and blue marlin (15425, 17664, 20908 mt) from their most recent stock assessments (ICCAT, 2001, 2002). These values were used to estimate a western Atlantic stock of 299 700 female sailfish producing 21.6×10^{12} eggs and an Atlantic-wide stock of 88 320 female blue marlin producing 28.1×10^{12} eggs (Table 4). Based on the calculated egg production value for the SF, 2.13%

Table 4. Estimated reproductive and stock parameters used to calculate the measures of the relative importance of the SF spawning ground.

	Sailfish	Blue Marlin
Reproductive Characteristics		
Batch fecundity	0.91×10^6	5.4×10^6
Spawning interval	1.89	2.44
Spawning season duration	150	144
Annual female fecundity	72×10^6	318×10^6
Stock Assessment Values		
Total biomass	11,390 mt	17,664 mt
Female proportion of biomass	0.5	0.5
Average female weight	19 kg	100 kg
Total females	299,700	88,320
Composite Values		
Annual egg production, Stock	21.6×10^{12}	28.1×10^{12}
Annual egg production, SF	0.460×10^{12}	0.449×10^{12}
% of stock egg production that occurs in the SF	2.13%	1.60%
Residency time in SF (d)	24	–
Turnover on spawning ground during spawning season	6.1	–
% of stock transiting through the SF during the spawning season	13.0%	–
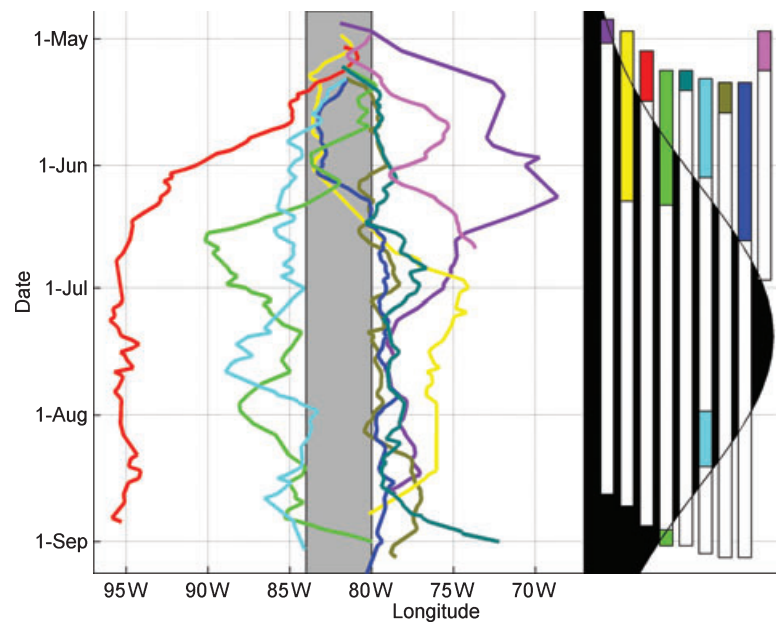
Figure 7. Longitude estimates of each tagged sailfish versus time. The Straits of Florida band of longitude is shaded. Estimated residency times for each fish are indicated in color on the right side of the figure. The shaded normal curve corresponds to the spawning season as indicated by the ichthyoplankton sampling.

(95% CI: 1.1–3.8%) and 1.60% (95% CI: 0.9–2.9%) of the total stock egg production for sailfish and blue marlin, respectively, occurs in the SF (Table 4). Given an estimated turnover of sailfish on the spawning ground of 6.1 times per season, the resulting percentage of the sailfish stock that moves through the SF is estimated at 13.0% (Table 4).

DISCUSSION

Fisheries-independent index

In evaluations of the billfish stock assessment process, Restrepo *et al.* (2003) and Die (2006) both noted the low reliability of the fisheries-dependent abundance indices currently in use, and the resulting uncertainty in estimates of population trends. This uncertainty highlights the appeal of developing a fisheries-independent index of abundance for blue marlin and sailfish. Annual egg production, which is estimated with relatively limited calculations and sampling requirements, is the variable best suited for indexing population trends. Although the 2 years of data presented here are not extensive enough for incorporation into the stock assessment process, they are sufficient to evaluate the benefits and drawbacks of the index development methodology.

Among the appeals of using ichthyoplankton-based methods to index stock abundance are the simple calculations based on readily measured variables (Hunter and Lo, 1993). For this methodology, three models – an exponential growth, an exponential mortality, and a Gaussian seasonality of spawning –

were used to estimate annual egg production. For both sailfish and blue marlin, the selected models appeared appropriate, with both the growth and mortality model yielding high correlation coefficients. However, despite the suitability of the models, the confidence intervals for annual egg production were relatively wide. The sensitivity analysis revealed that the mortality component contributed the most to this error. Given the already high precision of the mortality rate regression, appreciable gains in the precision of the egg production estimate seem unlikely. While increased precision is always desirable, such low precision in ichthyoplankton-based indices is not uncommon (Stratoudakis *et al.*, 2006). The critical question is whether this index, with its low precision but minimal bias, would improve the billfish stock assessment if extended over a longer time period. Two factors suggest it would. The first is the comparable, if not lower, precision of the available fisheries-dependent indices and the concerns about substantial bias in all of these indices (Restrepo *et al.*, 2003; Die, 2006). The second is the existence of methods to reduce noise in longer time series of fisheries-independent data (Stockhausen and Fogarty, 2007).

This study took advantage of two techniques, larval flux measurements and larval transport modeling, which have been frequently used in ichthyoplankton studies but have not previously been combined for use in larval index development. Previous calculations of flux rates have been instrumental in calculating levels of transport between regions or into estuaries (Rowe and Epifanio, 1994; Grothues *et al.*, 2002), and in

partitioning the decline in larval abundance with age between biological mortality and emigration (Taggart and Leggett, 1987; Pepin *et al.*, 1995). Larval transport models have been used to estimate connectivity (Cowen *et al.*, 2006), understand recruitment (Miller, 2007), and back-calculate spawning locations (Christensen *et al.*, 2007). In this study, the logistical aspects of sampling motivated the use of larval flux measurements and a transport model. Specifically, use of these two techniques enabled the assessment of a large area based on the sampling of a narrow transect. The unavoidable downside of this approach is the loss of hard boundaries to the area over which egg production was calculated. Moreover, at their current level of development, larval transport models may overestimate transport in the more complex nearshore currents (Paris *et al.*, 2007). This may be particularly problematic for sailfish that spawn in the Florida Keys frontal zone (Richardson *et al.*, in press-b), an area with a complex current structure that is poorly resolved by the models. If actual larval transport rates are reduced relative to the model, then the actual geographic boundaries of spawning in nearshore areas would be reduced relative to the model depiction. This would in turn indicate that the actual levels of spawning by sailfish within the geographic boundaries of the SF may be higher than this analysis indicates.

A more general downside of the approach used in this study, which limits its exportability to other regions, is that the use of a single sampling transect to assess spawning output over a large area of the SF is dependent on the fast current speeds in the area. In regions with low transport rates, a horizontal grid of stations, rather than a single transect of sampling, will be necessary to assess spawning output. However, with a horizontal grid of stations, larval flux measurements and transport models could still play an important role in quantifying egg production. Specifically, if it is possible to directly quantify age-specific larval emigration and immigration rates within the sampled area, the traditional requirement of sampling the entire spatial extent occupied by the larvae of the assessed spawning population becomes unnecessary. A number of studies have taken this approach of measuring both the standing stock of larvae in an area, and immigration and emigration rates (Taggart and Leggett, 1987; Pepin *et al.*, 1995; Helbig and Pepin, 1998). Although these studies focused on partitioning the loss of larvae from the system between emigration and biological mortality, the sampling and analysis could have been used for egg production calculations.

Importance of the Straits of Florida spawning area

One of the consistent challenges in studying migratory pelagic species has been to assess the relative importance of spawning areas. Billfish provide an excellent example of these issues. Serafy *et al.* (2003) reviewed the larval catch rates of blue marlin and other billfish in published studies, and noted the difficulty in making between-area comparisons due to differences in how data have been collected and reported. The incorporation of adult fecundity, movement, and stock assessment data into this ichthyoplankton study provided a means of evaluating the importance of the SF spawning area that was not dependent on the existence of comparable ichthyoplankton datasets.

This was done by addressing two questions: 1) what percentage of spawning in the stock occurs in the SF, and 2) for sailfish, what percentage of the stock transits through the SF during the spawning season? The answers to both these questions should be viewed only as rough estimates due to the use of uncertain stock assessment estimates of biomass, assumptions about the female proportion of the stock biomass, the use and modification of fecundity data from studies of Pacific billfish, and the small sample size of tagged adult sailfish used to determine residency time.

The estimated percentage of spawning that occurs in the SF for both sailfish (2.13%) and blue marlin (1.60%) reveals two aspects of the broader spawning patterns of the species. The first is that spawning levels for both species within the SF are higher than would be expected if the distribution of spawning was even across the area of the Atlantic occupied by both species. More specifically, the area over which this egg production was calculated is only about 0.3% of the area occupied by the Western Atlantic sailfish stock and 0.15% percent of the total area occupied by the Atlantic-wide blue marlin stock. The second is that the SF is likely one portion of a larger spawning area complex. The larvae of both species have been collected in numerous locations (e.g., blue marlin: Outer Bahamas, Mona Passage, Gulf of Mexico, South Atlantic offshore of Brazil; sailfish: Barbados, Gulf of Mexico, Outer Bahamas) throughout the Atlantic (Bartlett and Haedrich, 1968; Houde *et al.*, 1979; Serafy *et al.*, 2003; Prince *et al.*, 2005). Adult reproductive studies also indicate that many more spawning grounds likely exist (e.g., Luckhurst *et al.*, 2006). Pelagic species are generally considered to range in patterns of spawning, from the high spatially and temporally restricted spawning areas of bluefin tuna, to the much more broadly distributed spawning of skipjack tuna (Schaefer, 2001). While insufficient data

exist to fully characterize the spawning distribution of sailfish and blue marlin, this and other studies suggest that they exhibit a somewhat intermediate, if not more broadly distributed, regional spawning pattern.

Unlike the percentage of spawning that occurs in the SF, the percentage of the stock that transits through the SF during the spawning season suggests that this area is critical in the life history of sailfish, though this conclusion should be viewed with some caution given the low number of tagged fish. The short residency times of sailfish in the SF relative to their 4–5-month spawning season, indicates that a larger number of transient individuals, rather than a smaller number of resident individuals, must have accounted for the total egg production in the area. Assuming an average 24 days of residence, or about 16% of the spawning season, the percentage of the sailfish stock that transits through the SF during the spawning season would be ≈13%. Higher values would be obtained from shorter residency times and *vice versa*. Addressing this issue in more detail would require a larger dataset of tagged fish, including fish tagged elsewhere for which their entire movement through the SF is recorded in the tag data.

Implications for stock identification and management

For most highly migratory species, the development of spatial management options is hampered by the lack of understanding of the following areas: migratory movements, the relative importance of different spawning grounds, and the degree to which isolated stocks are present. This study revealed that individual adult sailfish tagged at the start of the spawning season in the SF, a restricted area known to support spawning, moved extensively over a much wider area (≈2500 × 1200 km) over the course of the season. This occurred to such an extent that all tagged individuals were absent from the SF during the peak of the spawning season. While based on a small sample size, these tagging data suggest that the SF is one portion of a much wider spawning area extending from the Gulf of Mexico to the Sargasso Sea.

To date, most of the debate with respect to spatial management options for migratory species has focused on whether closed areas provide substantial management benefits (Hyrenbach *et al.*, 2000; Walters *et al.*, 2007). Supporters for this approach have used fisheries-dependent data (Goodyear, 1998; Worm *et al.*, 2003) and, more recently, archival tag data (Block *et al.*, 2005) to determine hotspots of abundance of species of concern or diversity as a whole. The quantitative ichthyoplankton approach described here can

contribute to this goal of determining hotspots for migratory pelagic species. Additionally, this approach can be useful in delineating migratory bottlenecks which are commonly referred to in studies of migratory birds, but less commonly used in the marine literature. Migratory bottlenecks are restricted areas through which a notable portion (often set at >5%) of a population or species passes in a designated period of time, regardless of the abundance of individuals in that area at any one time (Bennun *et al.*, 2004). Our data strongly suggest that the SF is a migratory bottleneck for sailfish. This designation is not surprising given the narrowness of the SF and its position between the much larger expanses of the Gulf of Mexico, Caribbean, and North Atlantic Ocean.

One question raised by this study is: what management strategies are best suited for migratory bottlenecks that do not support a high abundance of individuals at any one time, but over time do contain a notable portion of the population? One of the primary motivations for time-area closures, particularly for bycatch species, is to reduce effort in areas with high catch per unit effort (Goodyear, 1998; Worm *et al.*, 2003). Bottleneck sites may not fall into this category, and thus would not be included in most of the current designations of critical habitat. On the other hand, in migratory birds, migratory bottlenecks and stopover sites are recognized to be critically important in assuring the success of the migration and the arrival of individuals in good condition at the end of migration (Moore *et al.*, 2005). Preserving the integrity of the ecosystem processes and the presence of a suitable forage base at these sites is critical in the management of the species that pass through them (Moore *et al.*, 1995; Newton, 2006), possibly more so than eliminating directed take of individuals. The importance of migratory bottlenecks in the broader lifecycle of any highly migratory pelagic fish species has not been demonstrated. However, in concept, it is evident that the abundance-based designation of conservation hotspots should be broadened to include categorizations for high turnover areas.

CONCLUSIONS

The absence of high-quality data, rather than the inadequacies of analytical procedures, is considered the primary underlying factor constraining marine fish stock assessments (National Research Council, 1998). For highly migratory species, the uncertainties in single species stock assessments and management are particularly severe, while at the same time there is an

increasing push to develop multi-species spatially informed management procedures that incorporate environmental variability (Pauly *et al.*, 2002). For such management approaches to be successful there is an overwhelming need for the development of high-quality fisheries-independent datasets. Our study demonstrates that an ichthyoplankton methodology can be used to quantify the interannual and spatial trends in the distribution of highly migratory species. Its application over 2 yr in the SF provided a measure of the relevance of this spawning ground to sailfish and blue marlin. The expansion of this approach over multiple years and in other areas would undoubtedly provide new insights into the population trends and spatial dynamics of these species. Such information is critical to the development of the more comprehensive management strategies currently being advocated.

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