

Evidence of blue marlin, *Makaira nigricans*, spawning in the vicinity of Exuma Sound, Bahamas

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Abstract. Exuma Sound is a semi-enclosed body of water bounded by islands of the Bahamas. During July 2000, sampling for larval billfish was carried out throughout the Sound's surface waters as well as in adjacent open waters of the Atlantic Ocean. A total of 99 larval billfish (Istiophoridae) was collected. Ninety of the larvae were identifiable as blue marlin (*Makaira nigricans*) and three as sailfish (*Istiophorus platypterus*). The remaining larvae were also istiophorids, unidentified to species owing to damage; no larval *Xiphias gladius* were collected. Larval blue marlin densities ranged from 0 to 3.4 larvae/1000 m²; their sizes ranged from 3.1 mm notochord length to 22.6 mm standard length. Densities tended to be highest north-east of the Sound's central axis, especially within the two regions where exchange with the Atlantic is greatest. Mean densities tended to decrease in the direction of mean flow; mean lengths increased from 8.08 mm at the Sound's mouth to 14.7 mm standard length at its upper reaches. Length-based estimates of larval age ranged from 2.2 to 17.2 days. Given these age estimates and assuming passive surface transport, the blue marlin larvae collected were likely the result of recent spawning in waters that include Exuma Sound and may extend some 200 km south-east of its mouth. This study suggests that Exuma Sound functions as a nursery area for blue marlin, and possibly other billfish species, at least during the summer. Limited sampling just outside Exuma Sound, in the Atlantic Ocean proper, also yielded blue marlin larvae.

Extra keywords: age and growth, Istiophoridae, larval billfish, nursery grounds.

Introduction

The term billfish refers to fishes of the family Istiophoridae, which includes the sailfish, spearfish and marlin species that inhabit the coastal and offshore waters of all tropical and subtropical seas (Collette *et al.* 1984). Four billfish species occur in the Western Atlantic Ocean and Caribbean Sea; sailfish (*Istiophorus platypterus*), longbill spearfish (*Tetrapturus pfluegeri*), white marlin (*Tetrapturus albidus*), and blue marlin (*Makaira nigricans*). The blue marlin is the largest of these fish, attaining up to 910 kg and 4.5 m (Robins and Ray 1986). Its size, beauty and spectacular fighting ability make the blue marlin one of the most sought after saltwater gamefish (de Sylva 1974). These apex pelagic predators support billion-dollar sportfishing industries throughout their range, especially along the US east coast, in the Gulf of Mexico and in the Caribbean Sea (IGFA 1996).

Fishing has led to significant declines in billfish stocks, particularly those of Atlantic blue and white marlin. In recent assessments by the International Commission for the Conservation of Atlantic Tunas and by the US National Marine Fisheries Service, both Atlantic marlins were characterized

as overfished (ICATT 2000; NMFS 2000). Longstanding concerns over billfish stock levels have led to restrictions on commercial and recreational fisheries and, in the case of the marlins and sailfish, the promotion of catch and release programmes among recreational anglers. Despite these measures, however, population indices for Atlantic marlins suggest their populations continue to decline (ICATT 2000). For example, the most recent Atlantic blue marlin stock assessment found that: (i) population biomass is currently at about 40% of the level needed to provide maximum sustainable yield; (ii) overfishing has been taking place for about three decades; and (iii) fishing mortality appears to be about 4 times the level that would support maximum sustainable yield (ICATT 2000). The assessment found that the situation is even worse for white marlin.

These findings stress the need for rapid and appropriate action. However, a major barrier to effective management is the dearth of fundamental biological knowledge on these highly evolved oceanic predators and the dynamics of their 'blue water' environment. Because adult billfish are large, pelagic and highly migratory, scientific observations and

data on them are especially difficult to obtain (Prince and Brown 1991). Indeed, the available quantitative scientific stock assessment information derives mainly from fisheries statistics, with the majority of data on billfish being recorded as bycatch and/or discards.

Data pertaining to larval billfish distribution, abundance and seasonality are uncommon (Leis *et al.* 1987). In all but a few cases (e.g. Ueyanagi 1962; Post *et al.* 1997), the studies that contain information on young billfish were neither designed or executed for the purpose of quantifying the larval and juvenile stages, or for estimating when and where they were spawned. Rather, data on the early stages of billfish appear in the literature as incidentally caught specimens collected in studies designed to obtain a suite of biotic and abiotic oceanographic data in a given region (e.g. Bartlett and Haedrich 1962) and/or to characterize larval fish communities associated with coral reefs (e.g. Leis *et al.* 1987; Limouzy-Paris *et al.* 1994). This, combined with the great difficulty in identifying young billfish to species (Richards 1974), has limited our understanding of their distribution and abundance as well as the timing and location of spawning activity. Without knowledge of the spatio-temporal extent of spawning and nursery grounds, fishery managers cannot consider the use of such measures as time-area fishing closures (e.g. Goodyear 1999) and protecting critical habitats (Govoni *et al.* 1999).

This study was conducted in and adjacent to Exuma Sound, a semi-enclosed body of water bounded by islands of the

Bahamas. Colin (1995) and Hickey *et al.* (2000) provide details of the Sound's physical oceanography. The Sound's basin is approximately 175 km long, 75 km wide and averages 2 km in depth. It has two major openings to the Atlantic; the larger opening is about 50 km wide and 2000 m deep, and the smaller opening is about 30 km wide and 25 m deep. Surface currents within Exuma Sound are dominated by both eddies and jets with a general north-westward movement along its south-east–north-west central axis. Because most reports on billfish larvae (e.g. Bartlett and Haedrich 1968; Masumoto and Kazman 1974; Post *et al.* 1997) have encountered them in the neuston (i.e. the air–sea interface), the objectives of the present study were: (i) to explore the Sound's surface waters for the early life stages of the Atlantic billfish; (ii) to examine patterns, if any, of larval billfish occurrence, density and size; and (iii) to project when and where spawning likely occurred. These objectives were pursued in July 2000 by sampling for larval billfish throughout the Sound's surface waters as well as by conducting a limited effort in adjacent open waters of the Atlantic Ocean.

Materials and methods

Sampling design and protocol

Larval billfish were sampled over a 6-day period (beginning 23 July 2000), between 0830 and 1700 h each day, along seven transects (Fig. 1). Similarly positioned to those of Hickey *et al.* (2000), six transects were located within the Sound, each in a line approximately normal to the south-east–north-west central axis. These were numbered consecutively

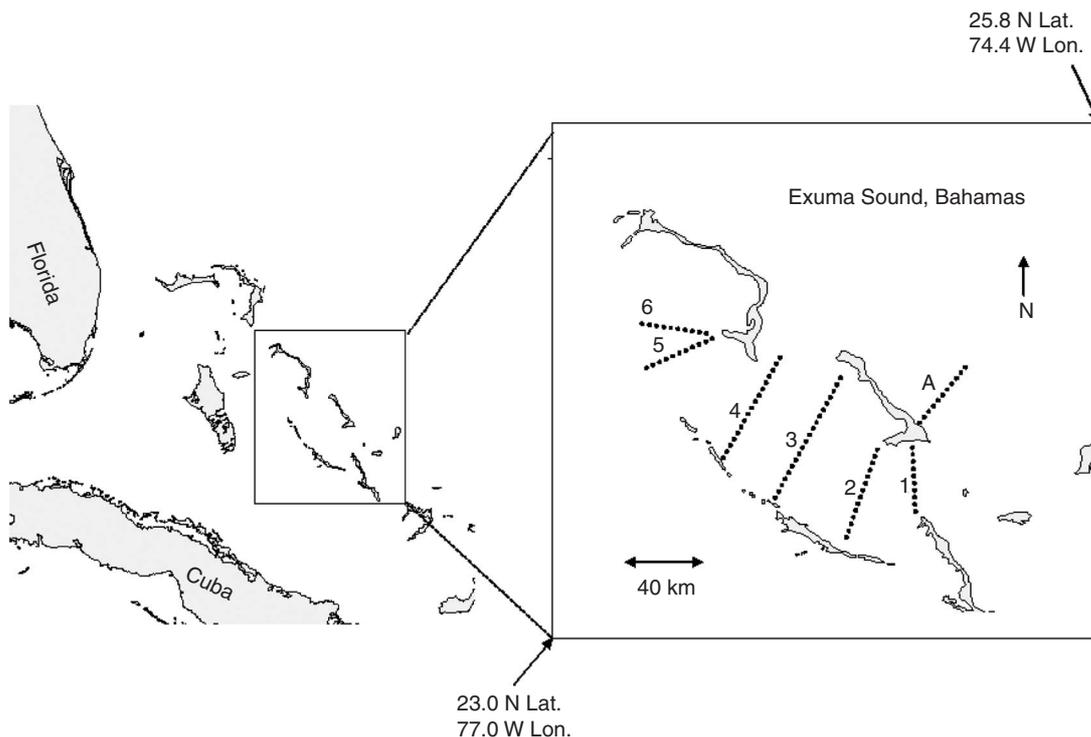


Fig. 1. Location of Exuma Sound, Bahamas, and position of the seven sampled transects.

in the direction of mean flow, with transect 6 being furthest downstream from the Sound's major opening. Our seventh transect (transect A) was located outside of the Sound, stretching north-east from the south-east coast of Cat Island and into the Atlantic Ocean proper. Between seven and 13 stations were sampled per transect for a total of 67 neuston collections.

The neuston net consisted of a 2×1 -m rectangular aluminium frame attached to 1 mm mesh netting with a cylindrical, polyvinyl chloride cod-end. A flow meter was suspended in the bottom corner of the net's frame to measure tow distance. To ensure that the relatively undisturbed neuston was filtered, the vessel's lifeboat davit was used to tow the gear off the port side of the boat. Heading and speed were adjusted accordingly such that the upper frame edge was above the water, with the lower edge below. Towing speed was approximately 3 knots. Nominal tow time, defined as the period from when the net was in proper fishing position until the start of net retrieval, was 10 min. At the beginning and end of each tow, location coordinates were obtained from an onboard global positioning system with a differential beacon. During each tow, surface water temperature ($^{\circ}\text{C}$) and salinity were measured using a multi-probed water quality instrument (Hydrolab, Austin, TX, USA). Nets were washed after each tow and each sample was fixed and stored in a 75% ethanol solution saturated with butylated hydroxytoluene, a compound that enhances the preservation of pigments.

Laboratory and data analyses

In the laboratory, billfish larvae were separated from other organisms and debris and examined under a dissecting microscope. Each larva was identified based on snout morphology and gular pigment patterns (Matsumoto and Kazama 1974; Richards 1974) and measured to the nearest 0.1 mm using an OPTIMAS image analysis system (Media Cybernetics, Carlsbad, CA, USA). In addition to providing precise lengths, this system allowed for measurement of curved specimens through automated tally of length segments. Notochord length (NL) or standard length (SL) was measured for preflexion- and postflexion-stage larvae respectively.

Larval age was estimated from length using a combination of age-length relationships and raw data described by Prince *et al.* (1991). They analysed the otolith microstructure of larval through adult blue marlin and found that an S-shaped, Gompertz equation best characterized growth for specimens from 10 to 110 days of age, with 10 days corresponding to a 6.22-mm larvae. For larvae ≥ 6.22 mm, therefore, we used the Prince *et al.* (1991) length-at-age equation to convert our measured lengths to estimate ages. However, because the Prince *et al.* (1991) growth curve yielded what seemed to be an unreasonable length at age zero (i.e. a hatch size of 0.51 mm), it was only used for age estimation of specimens ≥ 6.22 mm. For smaller larvae, we used a non-linear regression (SAS/STAT 1990) to fit an exponential growth model to the raw size and age data for the 18 larvae described by Prince *et al.* (1991):

$$L_t = L_0 \times e^{Gt}$$

where L_t is larval length at age t , L_0 is length-at-hatch and G is the instantaneous growth rate coefficient. The parameter L_0 was set at 2.5 mm NL; this length corresponding to the smallest blue marlin larvae reported (Ueyanagi and Yabe 1959; Leis *et al.* 1987). With an estimate of G , and solving for t , age estimates for larvae < 6.22 mm were computed. To make inferences about spawning time and location, overall and transect-specific age- and length-frequency distributions with 1-mm and 1-day age intervals were examined.

Larval densities were calculated as number of larvae per area towed (i.e. tow distance times net width) and mapped along with concurrently collected surface salinity and water temperature data, using ArcView geographical information system (GIS) software (ESRI, Redlands, CA, USA). Salinity and temperature fields were generated through cubic interpolation of data points using Matlab computer software (The MathWorks Inc., Natick, MA, USA). Scatter plots and Pearson correlation coefficients were also generated to examine relationships between blue marlin larvae and the characteristics of surface waters from which they were collected. Specifically, we examined as dependent variables: (i) the frequency of occurrence (proportion of positive tows) of larvae in each transect; (ii) mean larval density (number of blue marlin larvae/1000 m^2) in each transect; and (iii) the mean larval length in each transect. These transect-specific values were then plotted and regressed against average salinity and water temperature values for each transect. We also examined how the dependent variables varied in the direction of mean flow. For this we used the measuring tool in our GIS software to estimate linear distances from the centre of each transect to the centre of transect 1 (i.e. the transect located at the Sound's mouth), and then performed a simple linear regression, with distance the independent variable. Throughout, statistical significance was declared at $P < 0.05$.

Results

Surface water temperature and salinity ranged from 28.5 to 30.0 $^{\circ}\text{C}$ and 35.8 to 36.8 respectively (Table 1). Both water quality variables tended to increase in the direction of mean flow as indicated by highly significant, positive, linear correlations among mean transect surface water temperature, salinity and downstream distance (i.e. $r^2 > 0.80$ and $P < 0.016$). These patterns are consistent with the increasing influence of the shallow banks that encompass Exuma Sound and on the water masses that traverse over them (i.e. higher rates of heating and evaporation; Hickey *et al.* 2000).

A total of 99 larvae of the family Istiophoridae was collected. Ninety larvae were identifiable as blue marlin and three as sailfish. The remaining six billfish larvae were damaged and unidentifiable to species level. The blue marlin

Table 1. Number of samples per transect, mean distance of each transect from the mouth of Exuma Sound, and surface water quality data collected during July 2000

Transect	Date	Samples (<i>n</i>)	Mean distance (km)	Surface temperature ($^{\circ}\text{C}$)			Surface salinity		
				Min.	Mean	Max.	Min.	Mean	Max.
1	26 July 2002	11	0	28.7	28.86	29.0	36.1	36.15	36.2
2	25 July 2002	11	28.3	28.5	28.91	30.0	36.1	36.38	36.6
3	24 July 2002	13	68.2	28.8	29.08	29.4	36.1	36.31	36.5
4	23 July 2002	11	100.3	29.1	29.21	29.8	36.3	36.39	36.5
5	28 July 2002	7	160.2	29.5	29.72	29.9	36.5	36.69	36.8
6	28 July 2002	7	169.0	29.2	29.47	29.7	36.6	36.74	36.8
A	27 July 2002	7	-46.8	28.9	28.98	29.1	35.8	35.96	36.1

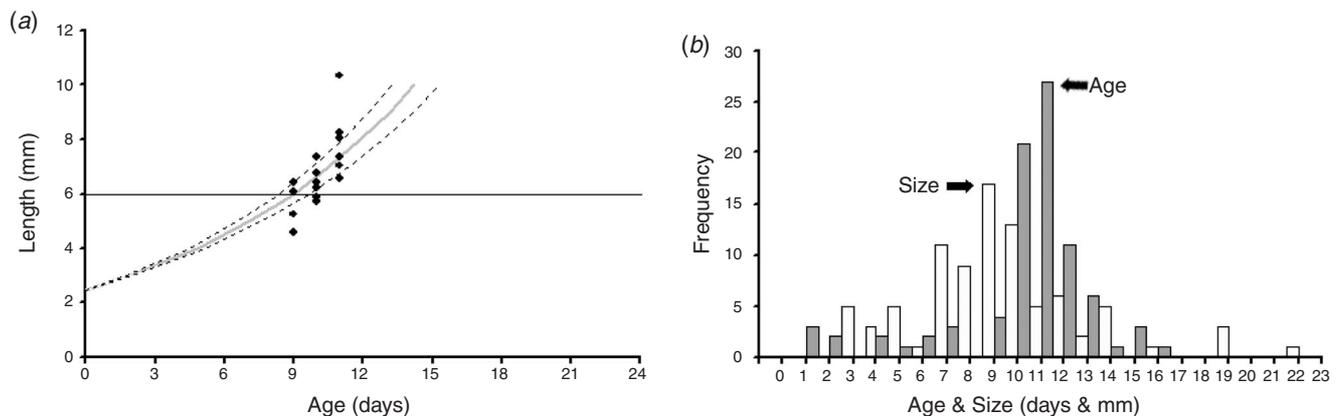


Fig. 2. Age and length of larval blue marlin. (a) Age-length relationship. Black dots indicate raw data described by Prince *et al.* (1991). Central grey line indicates exponential growth model (see text for details) and dotted lines indicate 95% confidence intervals. (b) Overall age/length-frequency distribution of collected larvae.

larvae ranged from 3.1 mm NL to 22.6 mm SL, with 85% measuring greater than 6.22 mm. For these, length-based age estimates were generated using the Gompertz growth model of Prince *et al.* (1991). For the 13 specimens measuring less than 6.22 mm, ages were estimated using the results of our exponential growth model that assumed length-at-hatch was 2.5 mm. The regression yielded an instantaneous growth rate of 0.0976, with lower and upper 95% confidence limits of 0.0904 and 0.1048 respectively (Fig. 2a). Using both the exponential and the Prince *et al.* (1991) models, our length-based estimates of the age of our blue marlin larvae ranged from 2.2 to 17.2 days.

Blue marlin larvae were collected in 58% of our 67 samples. Between 45% and 73% of tows within the Sound were positive, and 57% along the open ocean transect (i.e. transect A) were positive. The probability of catching one or more blue marlin larvae was not significantly correlated with mean transect salinity, temperature or distance from the Sound's mouth (Fig. 3a–c). In general, larval blue marlin densities were highest north-east of the Sound's central axis, especially within the two regions where exchange with the Atlantic is greatest and salinity tended to be relatively low (Fig. 4). Linear declines in mean larval density were evident with increasing salinity, temperature and distance downstream of transect 1 (Fig. 3d–f). At 1.1 larvae/1000 m², mean density of blue marlin collected at the Sound's mouth was about twice that observed at the Sound's upper reaches and also twice that observed along the open ocean transect. Whereas mean density of larvae declined, mean length increased linearly as salinity, temperature and distance increased (Fig. 3g–i). At 14.7 mm SL, larvae collected in the Sound's upper reaches (i.e. transect 6) averaged almost twice the size of those at the Sound's mouth (8.08 mm SL, transect 1); mean length of larvae collected along transect A was 10.25 mm.

Overall age- and length-frequency distribution plots indicated major modes at 12 days and 9 mm respectively (Fig. 2b).

Transect-specific age-frequency plots (Fig. 5) revealed that whereas fish >12 days were found along all transects, fish aged <7 days were restricted to the three southernmost transects within the Sound (i.e. transects 1–3). Given our larval age estimates (2.2 to 17.2 days) and assuming passive surface transport in a north-westerly direction at 15 cm s⁻¹ (Colin 1995), our larvae likely were the result of recent spawning at or the near the mouth of Exuma Sound, but this area may possibly extend south-east beyond the mouth some 200 km.

Discussion

Results of this study indicate that blue marlin spawned less than 18 days prior to sampling and in the vicinity of Exuma Sound. Clearly, this semi-enclosed water body can function as a nursery area for blue marlin, and possibly other billfish species, at least during the summer. However, before the Sound's importance as blue marlin nursery habitat can be ascertained, further sampling is required to assess the frequency and magnitude of larval entrainment into the Sound and growth and survivorship rates of those entrained.

The present collection of 90 blue marlin larvae in 67 10-min neuston collections, for an overall catch rate of 8.06 larvae h⁻¹, appears to be the highest reported for this species. For example, Jones and Kumaran (1962) reported on the capture of 36 larval blue marlin after 141 h of plankton sampling in the Indo-Pacific for an overall catch rate of 0.26 larvae h⁻¹. Similarly, Bartlett and Haedrich (1968) collected 85 blue marlin off the eastern coast South America between Brazil and Argentina. Total net tow duration in their study was 224 h, producing an overall catch rate of 0.38 larvae h⁻¹. Our catch rate greatly exceeds those reported in reviews by Masumoto and Kazama (1974) and Nishikawa *et al.* (1985). Masumoto and Kazama (1974) examined the results of over 20 years of plankton and neuston surveys made in the central Pacific Ocean: a total of 4279 net tows, most of 30-min duration,

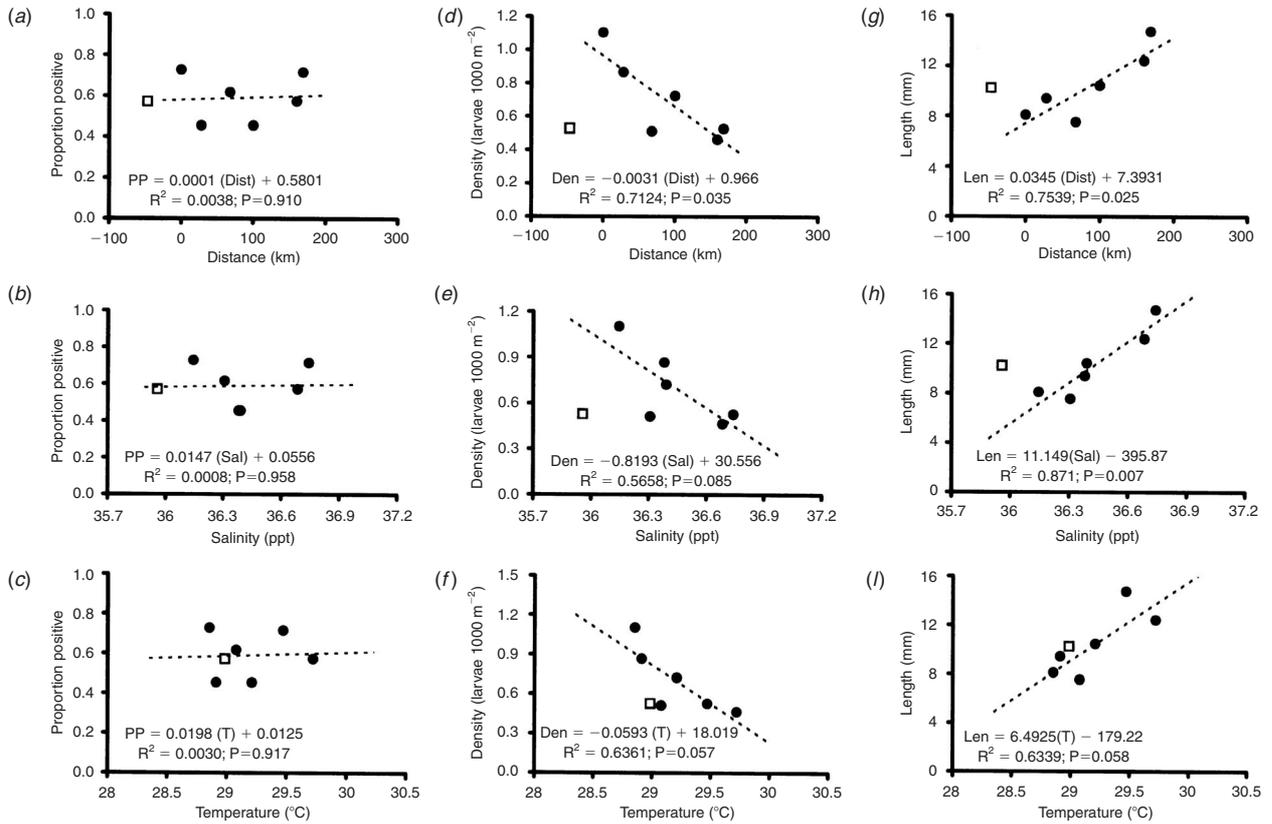


Fig. 3. Relationships among blue marlin frequency of occurrence, density and size versus mean transect distance (from the Sound’s mouth), mean surface water salinity and mean surface water temperature of each transect. Black dots refer to transects located within the Sound (transects 1–6), the open square refers to the transect located just outside in the open ocean waters (transect A).

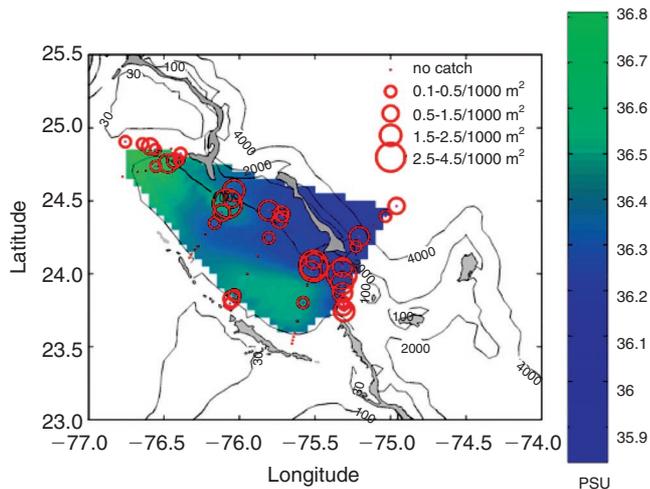


Fig. 4. Distribution of surface salinity and density of blue marlin larvae within Exuma Sound and in adjacent open Atlantic waters. Isobaths are in metres.

yielded 209 larval blue marlin for an approximate catch rate of 0.003 larvae h⁻¹. Nishikawa *et al.* (1985) reported on 21 years sampling for larval tuna and billfish larvae throughout the Atlantic, Pacific and Indian Oceans. By our calculations,

their overall larval blue marlin catch rates for the Atlantic, Pacific and Indian Oceans were 0.08, 0.45 and 0.58 larvae h⁻¹ respectively.

The larval blue marlin catch rate that we obtained is probably of the same order as that of Leis *et al.* (1987). They made plankton and neuston collections along transects that stretched from a lagoonal area inshore of the Great Barrier Reef to about 19 km offshore into the Coral Sea. Net tow duration, exact quantity of larvae captured and the total number samples collected are somewhat unclear in the Leis *et al.* (1987) paper. However, judging from their descriptions, an effort similar to ours (comprising about 100 samples) yielded about 40 blue marlin for estimated catch rates of 2.4 blue marlin larvae h⁻¹. Our blue marlin catch rate is less than that obtained for sailfish larvae by Post *et al.* (1996) in the Straits of Florida off Miami, Florida, USA. They collected 288 larval sailfish in 315 2-min tows for an overall catch rate of 27.4 sailfish larvae h⁻¹.

It is likely that our overall blue marlin catch rate would be lower had we not: (i) made all our collections during the putative peak of the blue marlin reproductive season in the North Atlantic (Erdman 1968; de Sylva and Breder 1997); (ii) specifically targeted larval billfish by making relatively high-speed neuston tows from the sampling vessel’s side with 1 mm

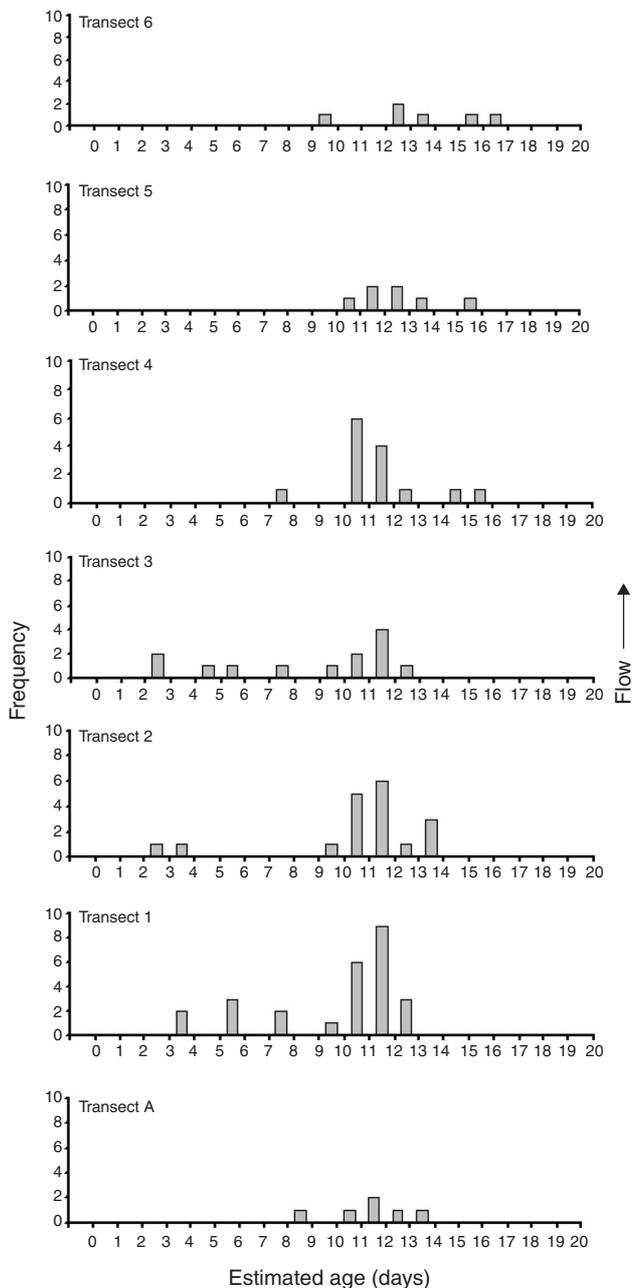


Fig. 5. Transect-specific age–frequency plots. Ages were estimated from length. Arrow indicates approximate direction of surface water flow.

mesh netting; and (iii) sampled within a relatively restricted area compared with most other studies. Conclusions from the above catch rate comparisons must be drawn with caution owing to the many differences between studies, especially in their respective objectives and methodologies. For example, the very low catch rates of Masumoto and Kazama (1974) and Nishikawa *et al.* (1985) were likely owing to poor fishing performance of the nets that they used (Davies *et al.* 1989). In addition to providing specifics on gear, future studies

should routinely report larval abundance in units of catch-per-volume and/or area filtered so that improved inter-study comparisons can be made.

Whereas our study yielded relatively high numbers of larval blue marlin, the length range that we captured (3.1 NL to 22.6 mm SL) was similar to those previously reported (e.g. Bartlett and Haedrich 1968; Masumoto and Kazama 1974; Fahay 1975; Leis *et al.* 1987; Prince *et al.* 1991). Presumably, this reflects similarities among studies in the size-selectivity of the various towed gears that were utilized as well as diurnal utilization of the neuston layer by larvae of this species.

Gorbunova and Lipskaya (1975) stated that blue marlin hatch at 4 mm in length (measurement type, e.g. TL or NL, unspecified). However, our collection of five specimens ranging from 3.1 to 3.6 mm NL as well as collections by others reporting larvae measuring <3 mm (Ueyanagi and Yabe 1959; Leis *et al.* 1987; W. J. Richards, National Marine Fisheries Service, unpublished data) indicates length-at-hatch is probably closer to 2 mm than 4 mm. This seems reasonable given the description by Erdman (1968) that blue marlin eggs ‘flowing out of the ovary’ measured 1 mm in diameter. Owing to the great difficulties identifying marine species at the egg stage, this issue (as well as duration of the egg stage) will probably only be resolved if ‘strip-spawning’ of mature adults yields fertilized eggs that subsequently hatch, as was done with swordfish (Sanzo 1922; Yasuda *et al.* 1978).

The range of estimated ages of larvae collected in this study suggest that spawning is occurring in Exuma Sound and probably in waters some distance south-east of its mouth. This appears to be the case because the youngest larvae (i.e. estimated to be <7 days) were only collected in the southern portion of the Sound. Furthermore, the oldest individuals (i.e. >14 days) were only collected in the northern half of the Sound. Given that the mean flow in the Sound is from the south-east to north-west at $11\text{--}19\text{ cm s}^{-1}$ (Colin 1995), with overall transit times of the surface waters of 10–20 days (Hickey *et al.* 2000), this age distribution is consistent with spawning occurring at or near the southern entrance of Exuma Sound and an alongaxis transport of larvae towards the north-west. Collection of older larvae near the mouth may be the result of some entrapment in the recurring mesoscale eddy reported by Hickey *et al.* (2000) (i.e. not all larvae are transported northwards) and/or from spawning further south-east of Sound’s mouth, possibly as far as 200 km away.

In addition to the alongaxis pattern in larval distribution, there was a clear acrossaxis pattern; very few larval blue marlin were collected in the western half of the Sound. A possible contributor to this pattern was that the winds prior to and during sampling were typical of tradewind conditions, that is consistently from the south-east. Under such wind conditions, surface waters would tend to be pushed some $15\text{--}45^\circ$ to the right of the wind, owing to Ekman drift. Given the near-surface distribution of the sampled larvae and the

orientation of the Sound, surface waters carrying the larval blue marlin would tend to move to the north-east, away from the western half of each transect. In addition, Hickey *et al.* (2000) reported that relatively salty water flows off the banks along the western edge of the Sound, resulting in higher salinities in the western half of the Sound. This high salinity water eventually sinks before reaching mid-axis, leaving less saline surface waters on the eastern half of the Sound. Thus, the possibility exists that the higher salinity surface water serves to restrict larval blue marlin to the eastern half of the Sound either physically or through active avoidance, or some combination of the two.

It is important to note that our limited sampling, just outside Exuma Sound in the Atlantic Ocean proper, also yielded blue marlin larvae. Therefore, insight into the nursery role of Exuma Sound and other semi-enclosed pelagic waters relative to open ocean environments may be gained through further sampling and comparison of larval condition, diet and growth rate. Also, sampling to examine the seasonality of larval blue marlin abundance in the vicinity of Exuma Sound as well as in other suspected spawning/nursery areas is warranted. Behavioural and physiological studies of larval billfish locomotion (i.e. vertical as well as horizontal swimming) are also needed. Results from these, when coupled to physical oceanographic models, may shed light on the relative importance of physical and biological factors in determining the spatio-temporal distribution of billfish larvae and, hence, their fate. Research of this type may represent a first step towards the ultimate protection of areas that appear important for blue marlin and possibly other highly migratory, pelagic fishes.

We intend to attempt to directly age the specimens collected in the present study through otolith microstructure analysis following Prince *et al.* (1991). If only half of our 90 blue marlin larvae can be aged, this would represent a 2.5 times increase in the knowledge of larval growth rate variation for this species. A further benefit of continuing with larval sampling in the vicinity of Exuma Sound is that our abundance values for blue marlin larvae may have utility as fishery-independent indices of spawning stock biomass (Scott *et al.* 1993), provided that the study area is expanded and a time-series is developed. These represent potentially important new lines of investigation on an exceedingly valuable, heavily exploited pelagic resource.

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