Growth variation in larval *Makaira nigricans*

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The Atlantic blue marlin *Makaira nigricans* larvae were collected from Exuma Sound, Bahamas and the Straits of Florida over three summers (2000–2002). Sagittal otoliths were extracted and read under light microscopy to determine relationships between standard length (*L*₂) and age for larvae from each year and location. Otolith growth trajectories were significantly different between locations: after the first 5–6 days of life, larvae from Exuma Sound grew significantly faster than larvae from the Straits of Florida. Exponential regression coefficients were similar among years for Exuma Sound larvae (mean instantaneous growth rate, \( G_L = 0.125 \)), but differed between years for larvae from the Straits of Florida (\( G_L = 0.086–0.089 \)). Differences in larval growth rates between locations resulted in a 4–6 mm difference in *L*₂ by day 15 of larval life. These differences in growth appeared to be unrelated to mean ambient water temperatures, and may have been caused by location-specific differences in prey composition or availability. Alternatively, population-specific differences in maternal condition may have contributed to these differences in early larval growth.

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Key words: age and growth; billfish larvae; Exuma Sound; Istiophoridae; otoliths; Straits of Florida.

INTRODUCTION

The Atlantic blue marlin *Makaira nigricans* Lacepède is the largest of the istiophorid billfishes in the Atlantic Ocean and adjacent seas. Despite its great popularity and economic value to recreational fisheries, relatively little is known about the early life history of this ‘apex’ predator. Until recently, the collection and identification of billfish larvae has been a challenge. To date the only published data on ageing is a study based on 18 larval blue marlin collected off Florida over a 2 day period (Prince *et al*., 1991). Later efforts re-examined these age-length data to estimate the ages of additional larvae collected from Exuma Sound, Bahamas (Serafy *et al*., 2003). Because so little empirical data on the

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age and growth of billfish larvae are available, the scope of variation, and possible factors contributing to it, have not been examined.

Over the last decade there has been increasing interest in defining, and ultimately protecting, those habitats that are essential to the sustainability of exploited fish populations. This concept was incorporated into U.S. legislation and has become a major avenue of fisheries research. Consequently, much effort has focused on nearshore, coastal habitats within the management jurisdiction of the U.S. Much less work, however, has addressed the importance of offshore habitats to fisheries resources, particularly to pelagic fish populations. Different offshore habitats probably exhibit variability in physical, chemical and biological conditions that render them more or less favourable to the growth and survivorship of the pelagic fishes that occupy them. Coupled with distribution studies to identify larval abundances and survivorship in different water masses, the examination of growth variability should offer insight into the relative value of particular habitats.

This study was undertaken to examine the early growth of blue marlin in two geographically and oceanographically distinct areas over 3 years. Exuma Sound is a semi-enclosed body of water in the central Bahamas (Fig. 1). Surface currents move through the 175 km long, 75 km wide, 2 km deep basin in a

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**Fig. 1.** Map of locations where blue marlin larvae were collected in the vicinity of Exuma Sound, Bahamas (●) from 2000 to 2002, and in the Straits of Florida during 2000 and 2002 (○). Larvae collected from the Straits of Florida during 2001 (□) could not be aged.
roughly north-westward direction at speeds averaging 10–20 cm s\(^{-1}\) (Colin, 1995; Hickey et al., 2000). In contrast, the Straits of Florida is a relatively steep-sided, narrow passage through which a strong western boundary current, the Florida Current, passes. Moving eastward from the Loop Current in the Gulf of Mexico, the Florida Current ‘bends’ northward as it is ‘pinched’ between Florida and the Bahamas (Fig. 1), moving at average speeds of 160 cm s\(^{-1}\) through the study area (Richardson et al., 1969; Niiler & Richardson, 1973). The present study tested the null hypothesis that early growth of blue marlin larvae is similar in both habitats and among years.

**MATERIALS AND METHODS**

**FIELD SAMPLING**

Blue marlin larvae were collected from the vicinity of Exuma Sound, during three 1 week cruises each during the month of July (2000–2002). Transects were distributed both within and adjacent to the Sound (Fig. 1). By day, billfish larvae are typically concentrated within surface waters (Bartlett & Haedrich, 1968; Matsumoto & Kazama, 1974; Post et al., 1997), thus sampling exclusively concentrated on the neuston layer. Stations were sampled with a 2 \(\times\) 1 m neuston net with 1 mm mesh towed at ca. 5-6 km h\(^{-1}\) (3 knots) for 10 min off the port side of a sport fishing vessel. An onboard global positioning system was used to determine the starting and ending points of each tow and water temperature and salinity were measured during each tow with a multi-probe water quality instrument (Hydrolab, Austin, TX, U.S.A.). After each tow, the net was washed down and the sample retrieved from the codend. The sample was fixed in 95% ethanol and stored in 70% ethanol. Blue marlin larvae were collected in the Straits of Florida using identical gear and methods, employing either a 30 m research vessel or a 16 m sport fishing vessel; five cruises were conducted in 2000, three cruises in 2001 and one cruise in 2002. Unidentified problems with the preservative in 2001 resulted in the loss of all otoliths from the larvae collected during this year.

**DAILY AGE AND GROWTH ESTIMATION**

All of the collected blue marlin larvae were dissected for otolith age estimation. Larvae were sorted from the samples and identified as blue marlin based on snout morphology and gular pigment patterns (Matsumoto & Kazama, 1974; Richards, 1974; Luthy, 2004). Identification was confirmed for some specimens with genetic analysis (Luthy, 2004). Prior to dissection, standard \((L_S;\) of larvae \(\geq\) post-flexion stage) or notochord length \((L_N;\) of preflexion larvae) was measured to the nearest 0.1 mm with the aid of a Leica MZ12 dissecting microscope equipped with a CoolSNAP-Pro\(^\text{\texttrademark}\) monochrome camera (Media Cybernetics, Carlsbad, CA, U.S.A.). Camera output fed into a computer with frame grabber and Image-Pro\(^\text{\texttrademark}\) Plus (version 4.5) image analysis software (Media Cybernetics). Prior to length measurement, each larva was soaked briefly in tap water to re-hydrate and improve its flexibility; no corrections were made for shrinkage. The entire larva was then placed in medium viscosity immersion oil for at least 24 h and examined under polarized light. Locating the lapillar and sagittal otoliths prior to removal was important given their very small size (e.g. radius of a sagitta from a 5 mm was larva \(c.\) 30–40 \(\mu\)m). Dissection involved placing each oil-soaked specimen on a microscope slide, with the ventral side up and the anterior tip of the jaw facing away. With the head stabilized with one set of forceps on the anterior junction of the lower jaw, another set of forceps was used to grasp the isthmus at the junction of the gill arches, and pull it back, thereby separating the head from the body. Focusing on the head, the gular membrane was teased apart to expose the ventral side of the skull and surrounding tissue, and thus reveal the otoliths (Fig. 2). The lapilli are located just posterior to the eye and medial to the

pterotic spine; anterior and slightly dorsal of the sagittae. The sagittae are located in the skull cavity, just under the surface at the widest point before the skull tapers to meet the first cervical vertebra (Fig. 2). The otoliths were removed using very fine dissecting needles and placed in a drop of immersion oil on a microscope slide where they were left for several days prior to reading.

Whole otoliths were examined under a Leica DMLB transmitted light compound microscope at ×1000; images were captured using the same camera, computer and image analysis software system as above. From each image, increments were enumerated along the longest growth axis of the otolith from the core to the outer edge. Daily increment deposition in blue marlin has not been directly validated, however, Prince et al. (1991) found that back-calculated spawning dates of blue marlin larvae generally matched known adult spawning patterns. Daily deposition has been validated for many other pelagic fish species (Radtke, 1983; Jenkins & Davis, 1990; Jones, 2002; Tanabe et al., 2003). Therefore, each increment was assumed to reflect 1 day of growth. Strong daily increments can be distinguished from less clear, subdaily marks [Prince et al. (1991)]. Otolith length (radius)-at-age was recorded for every day in the larval period.

A standard protocol was followed for reading and interpreting the otoliths. First, all unclear, abnormally shaped (non-linear growth axis) otoliths were discarded. A sagitta and lapillus from each specimen was read twice independently. Comparisons between the total number of increments on sagittae and lapilli revealed no substantial differences. Thus, due to overall higher clarity of the sagittae, these were used for age analysis. Two independent readings were made of each sagitta; where increment counts between two
readings were within 10% of each other, one measurement was randomly selected for analysis (Meekan & Fortier, 1996). Where increment counts differed by >10%, the otolith was re-read. If the increment counts from the third reading differed from the other readings by >10%, the otolith was discarded. If the difference on the third count was <10% of one of the former readings, then one of these two measurements was randomly selected for analysis.

Relative otolith growth was examined by comparing mean increment widths for larvae collected from the two geographical locations each year. To avoid issues with lack of independence of points along increment width trajectories (i.e. a series of daily measurements from each fish; Searcy & Sponaugle, 2000), mean otolith increment widths were compared at separate points (days 1, 5 and 10) during early life using separate ANOVA techniques (SYSTAT version 8.0; Wilkinson, 1992). Few large larvae from the Straits of Florida were collected during 2002, which precluded the inclusion of these fish in the ANOVA analysis of older (day 10) fish.

Somatic instantaneous growth rates ($G_L$) for larvae from each location and year were estimated by regressing $L_S$ on age (otolith increment counts). No additional ‘incubation’ days were added to the estimates of age in this study as was done by Govoni et al. (2003) who aged larval swordfish *Xiphias gladius* L. based on otolith increments. Linear and exponential relationships were fitted to the data and they had generally similar $r^2$ values. Because the exponential regressions provided the most realistic estimates of size-at-hatch (i.e. intercepts), they were deemed the most suitable and further testing was performed on these estimates. Regressions for each location and year were compared using standard ANCOVA techniques (Sokal & Rohlf, 1981). Because the smaller size range of the larvae from the Straits of Florida could lead to differences in the shape of the growth curves, ANCOVA was also used to compare the length-to-age relationships only for fish ≤14 days old (the oldest larvae collected from the Straits of Florida). Finally, mean $G_L$ for each location and year were compared to mean water temperatures during each month of collection. To validate the temperatures measured *in situ*, additional data on sea surface temperatures (SST) from satellite data were obtained for each study period. The SST images were obtained from the MODIS high-resolution sensor (http://modis.marine.usf.edu/index.html).

**RESULTS**

Larval blue marlin ranged in size from 2 to 19 mm, with two individuals of 23-3 and 26-0 mm collected from Exuma Sound. The full complement of fin rays is not present in fish ≤20 mm $L_S$ (Richards, 1974), thus all but these two larger specimens were clearly larvae. Although these two specimens may be considered pre-juveniles, for simplicity, this terminology distinction is not made. Ninety-five per cent of all collected larvae were estimated to be between 5 and 15 days old (Fig. 3). Larvae from the Straits of Florida were generally smaller and encompassed a smaller size (and age) range than those collected from Exuma Sound (Fig. 3). Note that the length frequency distribution for the 2001 blue marlin collected in the Straits of Florida is included, but these fish could not be aged due to preservation problems.

Mean otolith increment widths of larvae from Exuma Sound were generally similar. Otolith growth was more rapid for Exuma Sound 2000 larvae early in larval life (days 1 and 5) than for larvae collected during 2002, but by day 10, growth was similar for all Exuma Sound larvae (Fig. 4). Increment widths were not significantly different for Straits of Florida larvae between the two collection years. Larvae from the Straits of Florida tended to have consistently smaller otolith increment widths than larvae from Exuma Sound. This
The difference was significant at days 1 and 5 between both Straits of Florida years and Exuma Sound 2000. By day 10, all 3 years of Exuma Sound larvae had significantly larger mean increment widths than larvae from the Straits of Florida (Fig. 4).

ANCOVA revealed growth differences among geographical locations and sampling years (Fig. 5). The age-length exponential regressions of Exuma Sound blue marlin were similar among years (ANCOVA: $F$, d.f. = 2, $P = 0.525$), thus the data were pooled to yield a single relationship for Exuma Sound larvae. Growth of larvae from the Straits of Florida differed between years (ANCOVA: $F$, d.f. = 2, $P = 0.003$), and was significantly lower than growth of larvae from Exuma Sound (ANCOVA: $F$, d.f. = 2, $P = 0.003$; Tukey: Straits of Florida 2000, $P = 0.001$; Straits of Florida 2002, $P = 0.003$). The fit of the exponential regressions generated ‘reasonable’ $r^2$ values, although the small size range of larvae from the Straits of Florida in 2002 resulted in a somewhat lower $r^2$ (Table I). The calculated $G_\text{L}$ for Exuma Sound larvae (0.125) was c. 40% higher than that for Straits of Florida larvae (2000: 0.089; 2002: 0.086; Fig. 5 and Table I).

Fig. 3. (a) Standard length and (b) age frequency distributions of blue marlin larvae collected from Exuma Sound, Bahamas (EX), and the Straits of Florida (SF) over 3 years (2000–2002). Note that larvae from the Straits of Florida 2001 could not be aged, so no age data are available.
Differences in the length-to-age regressions were not a result of the smaller size range of Straits of Florida larvae. When the data were re-analysed by comparing only larvae 14 days old, instantaneous growth rates of Exuma Sound larvae were in fact slightly higher ($G_L=0.128-0.131$) and $r^2$ values were similar (0.70–0.92). Because no larvae were eliminated from the Straits of Florida data, these regressions were unchanged. Thus, eliminating larger larvae did not substantially influence the results (differences between sites became slightly more pronounced).

No relationship between growth rate and ambient water temperature was apparent. Sea surface temperatures were consistently warm, ranging from 28.7 to 29.1°C in Exuma Sound over the three collection years, and 28.2–29.7°C in the Straits of Florida (Table II). In fact, water temperatures tended to be slightly higher in the Straits of Florida where blue marlin larval growth rates were lower.

**DISCUSSION**

This study is the most extensive ageing effort for young blue marlin conducted to date. The otoliths of 193 blue marlin larvae (Exuma = 148; Straits of Florida = 45) were aged to examine the relationship between length and age and
to measure the scope of variability in growth of larvae inhabiting two oceanographically distinct locations over multiple years. The growth rates estimated here are comparable to other pelagic species such as the Atlantic sailfish \textit{Istiophorus platypterus} (Shaw) \((G_L = 0.137; \text{Luthy, 2004})\), and dolphinfish \textit{Coryphaena hippurus} L. \((G_L = 0.087; \text{Benetti, 1992})\), and faster than that of several species of mackerel and tuna \([\text{e.g. Spanish mackerel} \textit{Scomberomorus maculatus} \text{(Mitchill)}, \text{king mackerel} \textit{Scomberomorus cavalla} \text{(Cuvier)}, \text{yellowfin tuna} \textit{Thunnus albacares} \text{(Bonnaterre)} \text{and southern bluefin tuna} \textit{Thunnus T}\)].

![Graph showing standard length and age relationships for blue marlin larvae collected from Exuma Sound, Bahamas (EX) and the Straits of Florida (SF) over 3 years (2000-2002). Lines represent exponential curves fitted to the raw data (see Table I for regression equations).](image)

**Table I.** Exponential regression of standard length \((L_S)\) or notochord length \((L_N)\) on age for Atlantic blue marlin from the vicinity of Exuma Sound, Bahamas (EX), and the Straits of Florida (SF). The equation fitted to the data was \(L_i = L_0 e^{G_L t}\), where \(L_i\) is length at time \(t\), \(L_0\) is mean ± s.e. length-at-hatch and \(G_L\) is the mean ± s.e. instantaneous growth rate.

<table>
<thead>
<tr>
<th>Site</th>
<th>Year</th>
<th>(n)</th>
<th>Size range ((L_N \text{ or } L_S)) (mm)</th>
<th>(L_0) (mm)</th>
<th>(G_L)</th>
<th>(r^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>EX</td>
<td>2000</td>
<td>76</td>
<td>3.5–23.3</td>
<td>2.18 ± 0.20</td>
<td>0.128 ± 0.007</td>
<td>0.80</td>
</tr>
<tr>
<td>EX</td>
<td>2001</td>
<td>22</td>
<td>3.6–16.0</td>
<td>2.00 ± 0.36</td>
<td>0.126 ± 0.016</td>
<td>0.75</td>
</tr>
<tr>
<td>EX</td>
<td>2002</td>
<td>45</td>
<td>3.9–26.9</td>
<td>2.28 ± 0.15</td>
<td>0.116 ± 0.005</td>
<td>0.91</td>
</tr>
<tr>
<td>EX</td>
<td>ALL</td>
<td>148</td>
<td>3.5–26.9</td>
<td>2.16 ± 0.12</td>
<td>0.125 ± 0.004</td>
<td>0.83</td>
</tr>
<tr>
<td>SF</td>
<td>2000</td>
<td>34</td>
<td>3.3–9.8</td>
<td>2.65 ± 0.20</td>
<td>0.089 ± 0.007</td>
<td>0.81</td>
</tr>
<tr>
<td>SF</td>
<td>2002</td>
<td>11</td>
<td>2.9–6.0</td>
<td>2.29 ± 0.44</td>
<td>0.086 ± 0.021</td>
<td>0.64</td>
</tr>
</tbody>
</table>

maccovii (Castelnau): 0.32–1.6 mm day\(^{-1}\); Brothers et al., 1983; DeVries et al., 1990; Jenkins & Davis, 1990; Lang et al., 1994]. Swordfish larvae significantly exceed these values (larvae >11 mm can grow at 5.6 mm day\(^{-1}\); Govoni et al., 2003).

The present results suggest that blue marlin larvae from two geographical locations differ in their early growth rates, with those collected from the Straits of Florida growing at significantly reduced rates. Although there was some interannual variability in mean otolith increment widths among Exuma Sound larvae very early in their lives, by day 10, increment width differences were minor, as were differences among years in their length and age regressions. The length and age regressions for larvae from the Straits of Florida differed between the 2 years examined. Sample sizes, however, were consistently lower in the Straits of Florida; this probably contributed to the somewhat lower regression \(r^2\) values and possibly produced a false indication of higher growth variability. It is unlikely that the truncated size range of the larvae contributed to the apparent differences in growth curves because analyses based on only fish \(\leq 14\) days old produced the same results. If larvae are subjected to increased size-selective mortality over time, survivors (i.e. older fishes) may have relatively higher growth rates (Ricker, 1969; Anderson, 1988; Sogard, 1997). Inclusion of larger larvae from the Straits of Florida would help resolve the issue but unfortunately these were not collected during the present study. On the other hand, conditions in the Straits of Florida may be inherently more variable and thus drive variation in larval growth rates.

The different growth curves of blue marlin larvae collected from the two geographical locations resulted in substantial differences in length for fish of a given age. For example, 10 day old larvae were 5–6 mm \(L_S\) in the Straits of Florida and c. 7 mm \(L_S\) in Exuma Sound. The difference was exacerbated at older ages, e.g. by 15 days, Exuma Sound larvae were 4–6 mm larger than larvae.
from the Straits of Florida. Likewise, when back-calculating age from length, a 15 mm larva from Exuma Sound could be up to 6.5 days younger than one from the Straits of Florida; a 20 mm fish up to 7.5 days younger.

The value of $G_L$ calculated for Exuma Sound blue marlin larvae in this study was higher than that estimated for larvae <6.22 mm by Serafy *et al.* (2003). Presumably, this was because they used an age and length relationship that was based on specimens collected from the Straits of Florida. For larvae ≥6.22 mm, Serafy *et al.* (2003) adopted the Gompertz relationship of Prince *et al.* (1991); this led to estimates that generally followed the Exuma Sound larval growth trajectory until c. 14 days, after which length-at-age was increasingly overestimated (Fig. 6). Whether overestimation was due to the inclusion of juveniles in the Prince *et al.* (1991) study or the use of larger sample sizes in the present study is unknown. Clearly, it is preferable to either directly age larvae or, at a

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**Fig. 6.** Exponential regressions of length to age for blue marlin larvae collected from Exuma Sound, Bahamas (EX) and the Straits of Florida (SF) (—, SF 2000; --, SF 2002) over 3 years (2000–2002). Because there were no significant interannual differences in the growth of larvae from Exuma Sound, for simplicity, the data were pooled and a mean relationship obtained for all larvae from Exuma Sound (—) (see Table I). For comparison, the curve used in Serafy *et al.* (2003) is plotted. For larvae ≤6.22 mm $L_0$ (○), $L_0=2.5$, $G_L=0.098$; for larvae >6.22 mm (♦), the Gompertz equation fit to the data by Prince *et al.* (1991) was used (—), where 

$$L = 115.506e^{(-7.731e^{-0.039t})}.$$
minimum, use location-specific growth curves, especially when inferences about the timing and location of spawning are being made.

Growth variability is frequently related to water temperature differences (Houde, 1989; Pepin, 1991), but this was not the case in the present study. Differences in growth between larvae from Exuma Sound and the Straits of Florida could not be attributed to water temperature because temperatures were <1°C warmer in the Straits of Florida than in Exuma Sound. No data are available on the relative prey field between the two locations, but increased food availability, or access to a different prey composition may underlie the substantial differences in growth exhibited by young larvae. Otolith increment widths began to diverge in fish from the two locations between days 5 and 10. While otolith increment widths of larvae from the Straits of Florida continued to increase with age, increment widths of larvae from Exuma Sound increased more rapidly. It is possible that this divergence reflects a shift in prey for Exuma Sound larvae without a corresponding shift, or a shift to a different prey type, by larvae in the Straits of Florida. Govoni et al. (2003) found that a growth check occurred in the otoliths of larval swordfish between days 8 and 13, corresponding to a switch in diet from copepods to larval fishes. With consumption of prey of greater nutritional value, growth dramatically increased (Govoni et al., 2003). Blue marlin from the Pacific and Indian Oceans are also known to switch prey from a diet of copepods to increasing proportions of fish larvae >6 mm Ls (Gorbunova & Lipskaya, 1975). The timing of the onset of piscivory, coupled with differentiation of the digestive system, can significantly influence larval growth rates in different scombroid species (Tanaka et al., 1996). How such ontogenetic switches differ between oceans and geographic locations is unknown.

Access to prey may differ between locations due to the different hydrographic regimes. Exuma Sound experiences low flow (10–20 cm s⁻¹; Colin, 1995; Hickey et al., 2000) relative to the Straits of Florida (160 cm s⁻¹; Richardson et al., 1969; Niiler & Richardson, 1973), which should directly influence turbulence and indirectly, larval feeding success. Although turbulence has been recognized as an important component of larval feeding success (Rothschild & Osborn, 1988; MacKenzie & Kiorboe, 2000; Werner et al., 2001), field studies of turbulence and related feeding success of larvae are limited (Reiss et al., 2002). Data on the vertical position and gut contents of blue marlin larvae, their prey composition, availability and distribution, together with detailed measurements of physical variables would enable the testing of these hypotheses.

Other possibilities include genetic differences between adult spawning populations, or simply larger sizes of spawning females near Exuma Sound. In their review of genetic differences within and among Atlantic and Indo-Pacific istiophorid billfish species, Graves & McDowell (2003) found no evidence for within-ocean stock structuring for blue marlin. Recent work on the Pacific black rockfish Sebastes melanops Girard has demonstrated that the oldest and largest females in a population produce larvae that grow three times faster than those produced by younger females (Berkeley et al., 2004). Differences in the spatial distribution of small v. large females could result in spatially-explicit growth rates of young. Similarly, differential fishing-related truncation of adult ages and sizes between locations could potentially contribute to the observed differences in larval growth, but data with which to explore this possibility are not available.
Regardless of the underlying causes, results of this study provide some of the first evidence of habitat-specific differences in the growth of pelagic fish larvae. Oceanic habitat variability is difficult to study, yet it probably plays an important role in growth and survival of young pelagic fishes.

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