

# Variation in pelagic larval growth of Atlantic billfishes: the role of prey composition and selective mortality

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**Abstract** Atlantic blue marlin (*Makaira nigricans*) and sailfish (*Istiophorus platypterus*) larvae were collected from 10 monthly cruises (June–October 2003 and 2004) across the Straits of Florida to test (1) whether growth differed between the more productive western region near the Florida shelf, and the less productive eastern region toward the Bahamas, and (2) whether growth was related to prey consumption. Examination of larval sagittal otoliths revealed that instantaneous growth and daily growth during the first 2–3 weeks of life did not vary significantly between the two regions for either species. However, recent growth during the last two full days prior to collection was greater in the west for blue marlin larvae. Recent growth of blue marlin larvae <9 mm SL (primarily zooplanktivorous) was significantly related to prey composition (faster growth when higher proportions of *Farranula* copepods were consumed). Western larvae grew faster and had higher proportions of *Farranula* in their guts. Trends for sailfish larvae were not significant. In both species, comparison of early growth between <9 and  $\geq 9$  mm SL size groups indicated that growth trajectories diverged around 5–8 mm SL, the time when billfish

larvae become capable of piscivory. Significantly faster growth of larger (older) larvae suggests that mortality was selective for fast growers and that the transition to piscivory may be a critical point in the early life of billfish.

## Introduction

The early life history of billfishes is characterized by exponential larval growth, a highly selective diet, and an early transition from invertebrate to fish prey (Govoni et al. 2003; Luthy et al. 2005b; Sponaugle et al. 2005; Llopiz and Cowen 2008). These characteristics reflect a strong adaptation to a pelagic existence, particularly in the relatively oligotrophic, warm waters of the tropics and subtropics where larvae must find and capture prey at a high rate to sustain fast growth. There is some indication that growth rates of Atlantic blue marlin larvae are higher in some semi-enclosed basins such as Exuma Sound (Bahamas), relative to more oceanic environments such as the Straits of Florida (SOF), but it is not known whether prey abundance, composition, or other oceanographic conditions underlie this differential growth (Sponaugle et al. 2005).

The SOF is a major spawning ground for stocks of Atlantic blue marlin (*Makaira nigricans*) and sailfish (*Istiophorus platypterus*; Richardson et al. 2009a). Larvae are spawned from late spring through early fall by transient adults moving through the SOF (Richardson et al. 2009b). Larvae of multiple ages occur in relatively high abundance, with blue marlin larvae occurring more frequently toward the central and eastern side of the SOF and sailfish larvae occurring in greatest abundance along the western portion of the SOF, closer to the Florida shelf (Richardson 2007; Llopiz and Cowen 2008; Richardson et al. 2009b). These distributions may reflect differential spatial occurrence of

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spawning adults coupled with local oceanography, or species-specific differences in larval growth and survivorship.

The SOF region is an oceanographically dynamic area dominated by the nearshore presence of a major western boundary current, the Florida Current (FC; Fig. 1). The FC flows at speeds of up to  $2 \text{ m s}^{-1}$  through the bathymetrically constrained SOF between the Florida shelf and the Bahamas Bank. The proximity of the FC to the Florida shelf causes predictable upwelling of deep nutrient-rich waters onto the Florida reef tract, which are further enriched by the frequent passage of mesoscale eddies along the western front of the FC. These oceanographic features create a gradient of relatively higher nutrient concentrations nearshore and more oligotrophic oceanic waters offshore, which supports similar onshore–offshore patterns in primary and secondary productivity (Lee et al. 1991; Hitchcock et al. 2005, P. Lane and S. Smith, RSMAS, unpublished data). Results of studies conducted simultaneously with the present effort have demonstrated that multiple zooplankton prey of larval fishes are distributed in a similar cross-SOF pattern, with generally higher abundances toward the west (Llopiz 2008; Sponaugle et al. 2009; Llopiz et al. 2009).

During the first few weeks of life, larvae of both blue marlin and sailfish have largely overlapping diets dominated by crustaceans until they eventually transition into exclusive piscivory (Llopiz and Cowen 2008). Feeding is highly selective relative to available prey types, with crustacean prey largely consisting of either a single genus of copepod (*Farranula*) or cladoceran (*Evadne*), and the

relative proportions of these consumed prey varying in both time and space. Although billfish larvae have high daytime feeding incidence, they also exhibit some variability in gut fullness, but it is unknown whether growth is food-limited during this early period. The goal of this study was to investigate the possibility for spatial and diet-related variation in larval growth of billfishes in these tropical/subtropical oligotrophic waters. Evidence for food limitation of billfish larvae in the SOF may exist if faster growth occurs in nearshore western portions of the SOF where prey availability is greater. Alternatively, growth may be related more to diet composition, potentially complicating any spatial patterns of growth. Because observed patterns of larval growth may also be due to differential survival, we also examined the possibility for selective mortality of larval billfishes.

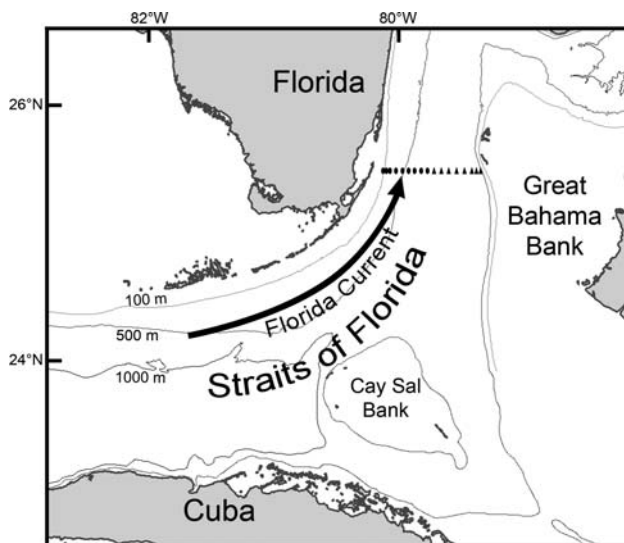
## Materials and methods

### Field sampling

For 2 days at the beginning of each of 24 months (2003–2004), ichthyoplankton samples were collected along a transect across the SOF between Miami, Florida, and the Bahamas at  $25.5^\circ\text{N}$  (Fig. 1). Samples were collected from 17 stations (numbered 1–17, W–E; spaced  $\sim 2 \text{ km}$  apart on both ends of the transect and  $\sim 5.5 \text{ km}$  apart in the center) during daylight hours. A Multiple Opening and Closing Net and Environmental Sampling System (MOCNESS) was modified to simultaneously sample ichthyoplankton and their prey ( $4\text{-m}^2$  mouth opening with 1-mm mesh nets, and  $1\text{-m}^2$  opening with  $150\text{-}\mu\text{m}$  mesh nets; Guigand et al. 2005) from discrete depth bins (0–25, 25–50, 50–75, and 75–100 m). A similarly designed double neuston net ( $2 \times 1 \text{ m}$  mouth opening with 1-mm mesh, and  $0.5 \times 1 \text{ m}$  opening with  $150\text{-}\mu\text{m}$  mesh; see Llopiz and Cowen 2008) was used to sample the surface layer to  $\sim 0.5 \text{ m}$ . Both net systems were outfitted with flow meters, and the MOCNESS also collected water temperature data during sampling. Samples (fixed in 95% ethanol and stored in 70% ethanol) were sorted in the laboratory to remove billfish larvae, and these were identified either morphologically (following Luthy et al. 2005a) or, when not possible, with high throughput DNA techniques (Richardson et al. 2007). Approximately 15% of sailfish and 76% of blue marlin larvae used in this study were identified molecularly.

### Otolith analysis

For 5 months (June–October) each year, when billfish larvae occurred along the entire transect, sailfish and blue marlin larvae were selected from two regions of the



**Fig. 1** Straits of Florida in the western Atlantic where billfish larvae were collected monthly at 17 stations distributed from the Florida shelf break to the Great Bahama Bank. Stations were numbered west–east and divided into western (stations 1–9; ovals) and eastern (stations 10–17; triangles) for analyses. Arrow indicates approximate position of the core of the Florida Current

transect (western vs. eastern stations) for otolith examination. Larvae were selected randomly from each 1 mm standard length (SL) size bin to ensure that all sizes were represented. Otoliths were used to obtain estimates of age and larval growth, since increments are thought to be deposited daily (Prince et al. 1991; Luthy et al. 2005b), enabling an accurate estimate of age and the instantaneous growth parameter (see below). Further, otolith increment widths can be used to compare the daily growth. These techniques have been used previously to estimate larval growth for both blue marlin and sailfish from the Bahamas (Sponaugle et al. 2005) and the SOF (Luthy et al. 2005b).

Prior to dissection, the SL of individual larvae was measured to the nearest 0.1 mm using a Leica MZ12 stereomicroscope with a Dage MTI video camera and frame grabber, and Image Pro Plus 4.5 image analysis software (Media Cybernetics). Heads of larvae were soaked overnight in immersion oil to render the tissue transparent and facilitate locating the otoliths. The flesh was then teased apart using insect pins, and sagittal otoliths were removed and placed in a clean drop of medium viscosity immersion oil. Otoliths were read at 1,000 $\times$  magnification (oil immersion) using a Leica DMLB microscope equipped with a polarized filter between the first stage and light source. As with the SL measurements, the image was captured with a video camera and frame grabber and analyzed using Image Pro image analysis software. Individual increments were enumerated along the longest axis, from the core (primordium) of the otolith to the outer edge, to determine larval age. The distance between each pair of increments provided a measure of daily growth. Each otolith was read blind (i.e., with no size or collection location information available) by a single reader, and when the analysis of all otoliths from each year was complete, the process was repeated using the otolith or the captured otolith image (without any previous age information). If the difference in age between the two reads was <5%, one of the two reads was chosen randomly as the final read. If there was a discrepancy in age of  $\geq 5\%$  difference between the two readings, the otolith was read a third time. If after a third read a high discrepancy in the readings remained, the otolith was discarded. In total, otoliths of 18 billfish larvae were rejected due to high variance in interpretation after the third read.

#### Gut contents analysis

We inspected the gut contents of larvae to examine whether larval growth was related to prey consumption or composition. Although cause and effect cannot be inferred due to the temporal lag between prey consumption and subsequent larval and otolith growth (e.g., Pepin et al. 2001), our simultaneous comparison of otolith growth and gut

contents is a valid and conservative means of examining the associations. An assumption is that larvae with particular gut contents were consuming the same prey in the days immediately preceding collection. Using a large number of larvae reduces some error; however, lack of an association could also be due to the inherent temporal mismatch of the approach. Sailfish and blue marlin larvae were analyzed for gut contents as part of a separate study (Llopiz and Cowen 2008). The entire alimentary canal was excised from each larva using a microscalpel and minuten pins and transferred to a drop of immersion oil. Prey were identified to the lowest taxonomic level possible and counted. The prosome of copepods and the longest dimension of other prey were measured. Length:dry weight relationships were established for dominant prey types, as were length:gut-free dry weight relationships for billfish larvae. These data were used to calculate a relative gut content biomass (i.e., prey dry weight as a percentage of predator gut-free dry weight) for each larva. A percent fullness value was calculated by assuming that the largest length:gut-free dry weight value represented a full gut, then dividing all other values by the largest value to produce a percent fullness. Larvae collected during the first 10% of daylight were excluded since larvae are just beginning to feed during this time.

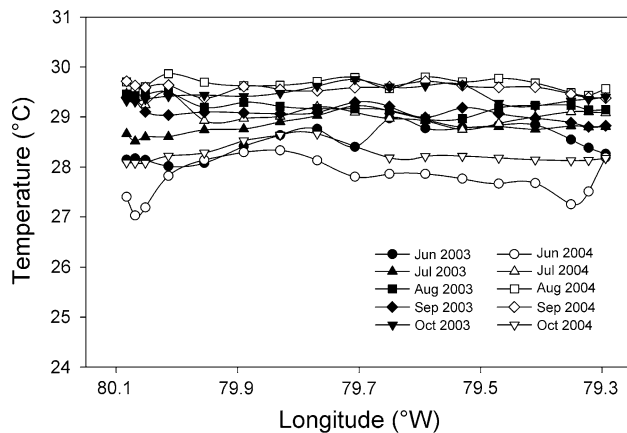
#### Data analysis

##### *Spatial differences in growth*

We used three separate analyses to examine the variation in larval growth of each species collected from western (stations 1–9) vs. eastern (stations 10–17; Fig. 1) regions: (a) Overall larval growth (instantaneous growth parameter,  $k$ ) from exponential regressions of SL-at-age, (b) daily otolith growth (individual increment widths) as a proxy for growth at specific ages during larval life, and (c) recent daily growth (as a detrended growth index computed from the last two complete otolith increment widths). For overall larval growth, the equation fit to the SL-at-age data was

$$L_t = L_0 e^{kX_t}$$

where  $L_t$  is length at time  $t$ ,  $L_0$  is mean length-at-hatch,  $k$  is the mean instantaneous growth parameter, and  $X_t$  is age-at-time  $t$ . For overall and daily larval growth, all statistical comparisons were conducted using analysis of covariance (ANCOVA) with up to two primary covariates, surface water temperature and age, included to minimize their potential influence on growth. Although larvae were collected over 5 months in the summer and early fall having relatively similar surface (to 5 m depth) water temperatures that rarely varied substantially across the SOF (Fig. 2), we included temperature as a covariate because larval growth



**Fig. 2** Surface water temperature (5 m depth) measured during monthly MOCNESS tows at 17 stations distributed across the Straits of Florida. Billfish larvae were most abundant in surface waters during 5 months (June–October) for each of the two study years (2003–2004)

is strongly temperature dependent in poikilotherms. Photoperiod was not included as a covariate because it was not independent of temperature (positively correlated at  $P < 0.0001$ ). Differences in age distributions between regions could also bias growth estimates; therefore, larval age was included as a covariate. Non-significant covariates were removed from final analyses. Data were log-transformed where variance was heterogeneous and were excluded from analyses when tests for homogeneity of slopes failed.

For the comparison of daily growth for each species, mean otolith increment widths (MIW) at each day of larval life up to day 12 (i.e., as far as sample sizes allowed) were compared by region in separate ANCOVAs. Prior to our sampling, there was not likely much cross-SOF movement of larvae between regions due to the dominant northward-flowing FC, however, because all fish (ages 1–20 days) were collected at approximately the same latitudinal position in the SOF, comparison of daily growth at earlier days (e.g., day 7) of larval life may be confounded. For example, on day 7 of larval growth, an older fish (e.g., 18–20-day old at capture) may have been in an oceanographic region farther upstream of the collection location and, therefore, exposed to different environmental conditions affecting growth than younger fish (e.g., 7–9-day old at capture), which were likely closer to the collection region at the time of their day 7 growth. Therefore, to minimize the potential effect of differential physical location on early larval growth, we examined the recent growth during the last two complete days prior to capture for all larvae. Because otolith growth is age dependent (mean otolith increment widths and variances increase with age), we detrended the data following Baumann et al. (2003) and Robert et al. (2009) to

be able to compare recent growth of different aged larvae. A detrended growth index was computed using

$$DG_{ij} = (G_{ij} - G_j) SD_j^{-1}$$

where  $DG_{ij}$  is the detrended growth of individual  $i$  at age  $j$ ,  $G_{ij}$  is the otolith growth (increment width) for individual  $i$  at age  $j$ ,  $G_j$  is the mean of otolith growth (increment width) of all individuals at age  $j$ , and  $SD$  is the standard deviation of  $G$  (Robert et al. 2009). The detrended growth index was computed for the last two complete otolith increments (i.e., excluding the last marginal otolith increment) for all fish aged 3 days and older. We compared detrended recent growth (DRG) for each species from the two regions using ANCOVA with temperature as a covariate.

#### *Relationship between larval growth and prey consumption*

Diet composition changes substantially during early life for both blue marlin and sailfish. Smaller larvae consume primarily crustaceans, with copepods of the genus *Farranula* and cladocerans of the genus *Evadne* together composing 90% of prey items (Llopiz and Cowen 2008). Although most *Farranula* spp. were *F. gracilis* and most *Evadne* spp. were *E. tergestina*, we hereafter refer to these prey simply as the genera *Farranula* and *Evadne*. At ~5 mm SL, larvae become capable of piscivory (corresponding with flexion of the urostyle; Llopiz and Cowen 2008), and the proportion of fish prey in the diet increases progressively with increasing larval size. Approximately one-third of larvae 6–8 mm SL show evidence of recent piscivory, and larvae  $\geq 9$  mm SL are predominantly piscivorous, with  $>85\%$  having larval fish prey present in the guts (Llopiz and Cowen 2008). Thus, to examine whether the recent growth (DRG) was related to gut fullness and prey composition, we examined  $<9$  and  $\geq 9$  mm larvae separately. For  $<9$  mm larvae, we obtained gut fullness and numerical proportions of consumed *Farranula* and *Evadne* for a subset of aged blue marlin ( $n = 134$ ) and sailfish ( $n = 130$ ). We first examined whether DRG was related to overall gut fullness. To avoid variability due to different prey mixtures and to enable the precise calculation of prey biomass, only  $<9$  mm larvae that had consumed *Farranula* and/or *Evadne* were used in the analysis of the relationship between DRG and overall gut fullness (biomass). ANCOVAs were conducted between fish with guts  $<60\%$  full and  $\geq 60\%$  full since a high proportion of guts had  $>50\%$  fullness (sample sizes for the 60% split were blue marlin:  $n = 12, 24$  and sailfish:  $n = 21, 35$ ).

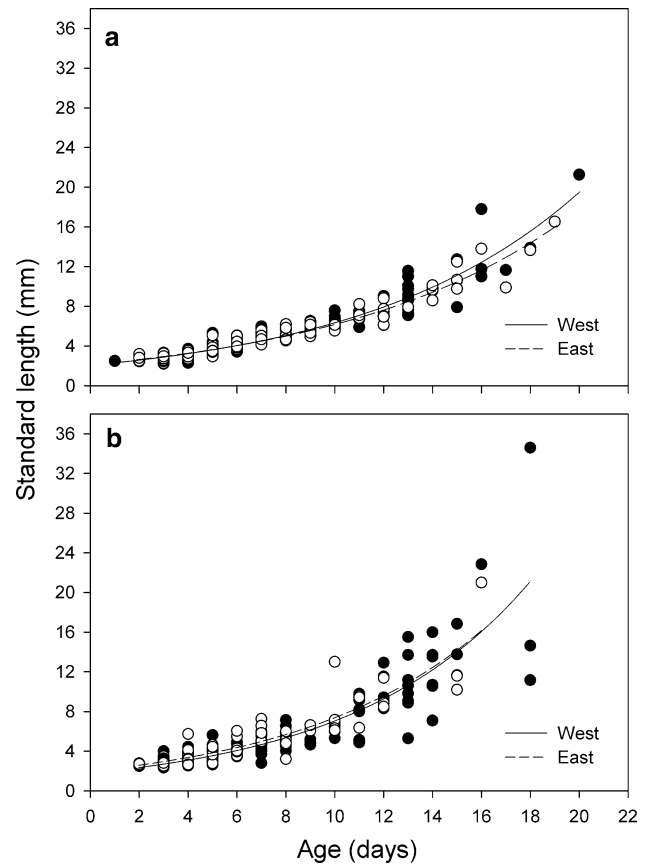
Secondly, we examined the relationship between DRG and prey composition in the guts of larvae. DRG was compared for  $<9$  mm larvae with  $<33.3$ ,  $33.3$ – $66.6$ , and  $>66.6\%$  of a given prey type (*Farranula* or *Evadne*) in

their guts. Thirdly, to determine whether the recent growth varied between larvae with different diet compositions (<9 mm vs.  $\geq$ 9 mm), DRG was compared between <9 and  $\geq$ 9 mm larvae using ANCOVA with covariates as before. To reduce the possibility of even small numbers of fish prey in the guts of <9 mm larvae influencing their growth, we included all larvae <6 mm and only those larvae  $\geq$ 6 mm that had no fish prey in their guts. Finally, separate tests were performed comparing mean daily growth (MIW) for each group (<9 mm vs.  $\geq$ 9 mm) on each day (having adequate sample sizes) during the first 12 days of larval life, using ANCOVA with only temperature as the covariate. To confirm growth-related findings, we also compared size (otolith radius) at days 11 and 12 between <9 and  $\geq$ 9 mm larvae.

## Results

Surface water temperatures did not differ substantially among months, and more importantly, they did not differ cross-Straits at the depths larvae were collected (Fig. 2). Cooler upwelled waters do reach shallower depths on the western side of the Straits, but typically not in the surface layer occupied by the majority of these neustonic larvae (~75% of billfish larvae were collected in the neuston net; 25% were collected in the 1–25 m MOCNESS; Llopiz and Cowen 2008).

For both blue marlin and sailfish, significant linear regressions of SL vs. otolith radius (blue marlin =  $P < 0.0001$ ;  $r^2 = 0.93$ ; sailfish:  $P < 0.0001$ ;  $r^2 = 0.79$ ), as well as significant regressions of otolith radius-at-age residuals vs. SL-at-age residuals (as per Hare and Cowen 1995), demonstrated that otolith increment data can be used to examine somatic growth. Overall growth obtained from exponential regressions of SL-at-age (Fig. 3; Table 1) did not vary between the western and eastern regions of the SOF for either species (homogeneity of slopes test:  $P > 0.05$ ). Instantaneous growth parameters ( $k$ ) were significantly higher for sailfish (overall  $k = 0.134$ ) than for blue marlin (overall  $k = 0.110$ ; homogeneity of slopes test:  $P < 0.0001$ ). Mean daily growth (MIW) during the first 12 days of larval life was not significantly different for larvae of either species collected from the western vs. the eastern region of the SOF with the only exception being blue marlin on day 9 (ANCOVA:  $P = 0.034$ ; for all other days, ANCOVA:  $P = 0.088$ – $0.980$ ; temperature covariate significant for sailfish day 1–7; age covariate significant for sailfish day 1–3; Fig. 4). Recent growth (DRG) of sailfish was not significantly different between regions (ANCOVA:  $P = 0.379$ ; temperature covariate significant); however, DRG of blue marlin larvae was significantly higher in the west (ANCOVA:  $P = 0.036$ ; Fig. 5).



**Fig. 3** Exponential regression of SL-at-age in larval **a** blue marlin and **b** sailfish collected along a transect across the Straits of Florida over 2 years (2003–2004). Individuals were sampled at western or eastern stations, and exponential regressions were fit to the raw data for each species. From the regressions, somatic instantaneous growth parameters ( $k$ ) were estimated for blue marlin (West:  $n = 107$ ,  $k = 0.112$ ; East:  $n = 145$ ,  $k = 0.106$ ) and sailfish (West:  $n = 132$ ,  $k = 0.137$ ; East:  $n = 83$ ,  $k = 0.131$ )

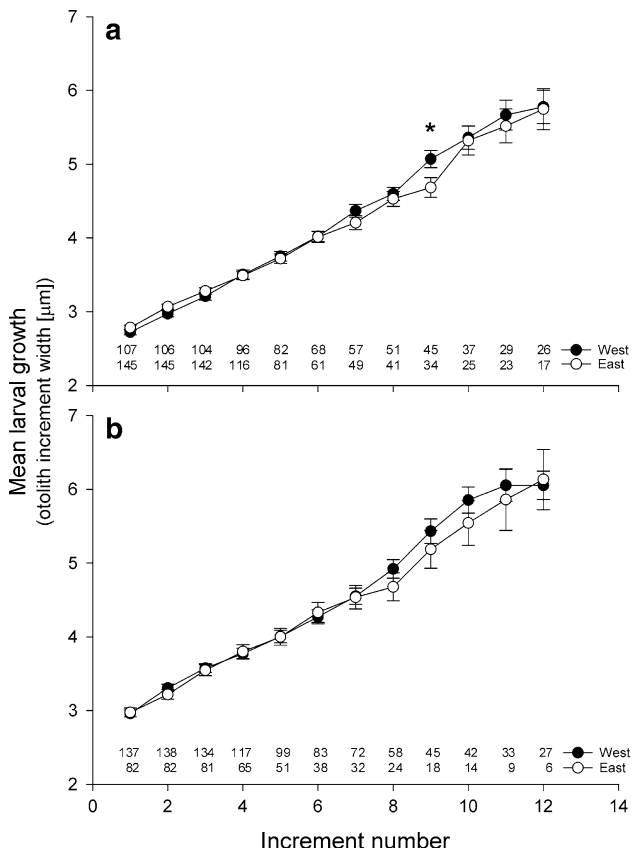
Detrended recent growth (DRG) was unrelated to relative gut fullness (ANCOVA: blue marlin:  $P = 0.703$ ; sailfish:  $P = 0.670$ ). For <9 mm blue marlin, DRG was significantly related to the proportion of *Farranula* in their gut: larvae with >66.6% *Farranula* in their guts exhibited significantly faster recent growth than those with <33.3% or 33.3–66.6% *Farranula* in their guts (ANCOVA:  $P = 0.002$ ; Bonferroni multiple comparison; Fig. 6). The opposite trend toward lower growth with higher proportions of *Evadne* in the gut was not significant for blue marlin (ANCOVA:  $P = 0.131$ ; Bonferroni multiple comparison; Fig. 5). There were no significant differences in DRG for <9 mm sailfish for either diet group (ANCOVA: *Evadne*:  $P = 0.242$ ; *Farranula*:  $P = 0.226$ ; temperature covariate significant for both).

Small (<9 mm) blue marlin from western stations consumed a higher proportion of *Farranula* copepods than larvae from eastern stations (Fig. 7), corresponding with significantly higher DRG in these larvae (ANCOVA:  $P = 0.048$ ; Fig. 8). There was no significant difference in

**Table 1** Exponential regression of standard length (SL) at age for Atlantic blue marlin and sailfish from the Straits of Florida, 2003–2004

Species	Region	<i>n</i>	<i>L<sub>t</sub></i> range (mm)	<i>L<sub>0</sub></i> (mm)	<i>k</i>	<i>X<sub>t</sub></i> range (days)	<i>r</i> <sup>2</sup>
Blue marlin	West	107	2.22–21.28	2.06 ± 0.091	0.112 ± 0.003	1–20	0.91
Blue marlin	East	145	2.28–16.53	2.14 ± 0.050	0.106 ± 0.002	2–19	0.94
Sailfish	West	132	2.35–34.60	1.79 ± 0.150	0.137 ± 0.006	2–18	0.77
Sailfish	East	83	2.40–21.00	2.00 ± 0.129	0.131 ± 0.006	2–16	0.81
Blue Marlin	All	252	2.22–21.28	2.10 ± 0.048	0.110 ± 0.002	1–20	0.92
Sailfish	All	215	2.35–34.60	1.87 ± 0.106	0.134 ± 0.004	2–18	0.78

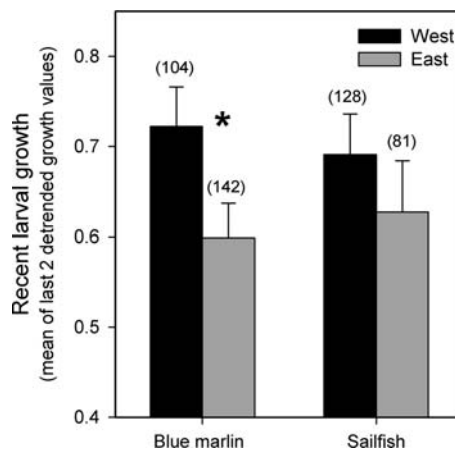
The equation fit to the data was  $L_t = L_0 e^{kX_t}$ , where  $L_t$  is length at time  $t$ ,  $L_0$  is mean (±SE) length-at-hatch,  $k$  is the mean (±SE) instantaneous growth parameter, and  $X_t$  is age-at-time  $t$



**Fig. 4** Daily growth (mean [±SE]) of otolith increment width [MIW] for larval **a** blue marlin and **b** sailfish collected at western or eastern stations during monthly cruises across the Straits of Florida over 2 years (2003–2004). Increment width values were truncated at 12 days due to small sample sizes of older fishes. Separate ANCOVA comparisons of MIW between regions were made for each day of larval life. All days of growth tested were non-significant (ANCOVA:  $P > 0.05$ ), except where indicated (asterisk  $P = 0.034$ ). Sample sizes for each increment are indicated at the bottom of each plot

DRG between regions for  $\geq 9$  mm blue marlin larvae (ANCOVA:  $P = 0.839$ ) or for either group ( $< 9$  or  $\geq 9$  mm) of sailfish larvae (ANCOVA:  $< 9$  mm:  $P = 0.525$ ;  $\geq 9$  mm:  $P = 0.293$ ; both with significant temperature covariates).

Comparison of daily growth (MIW) between  $< 9$  and  $\geq 9$  mm larvae revealed significant size-specific

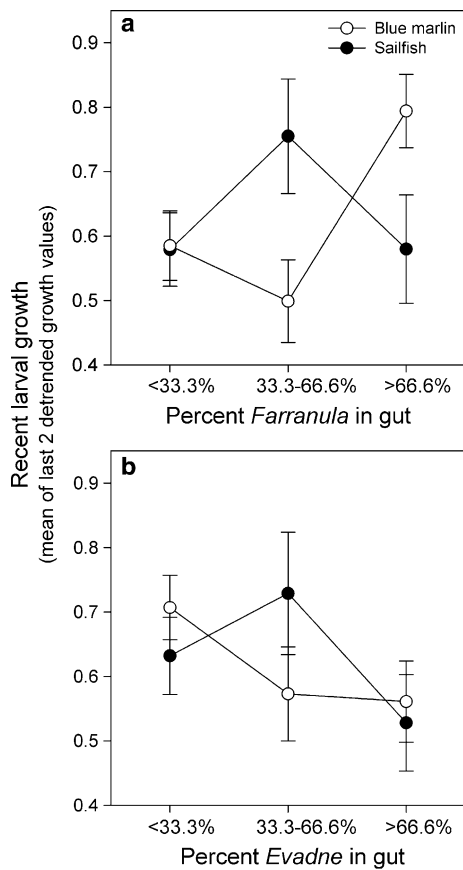


**Fig. 5** Detrended recent growth (DRG) during the last two complete days prior to collection for all blue marlin and sailfish larvae  $\geq 3$ -days old collected at western or eastern stations. Asterisk indicates differences significant at  $P = 0.036$

patterns after the first week of larval life for both species. MIW was not significantly different between size groups during the first week of life, but began diverging at day 7 (sailfish) and 9 (blue marlin), with  $\geq 9$  mm larvae generally exhibiting significantly faster daily growth than  $< 9$  mm larvae (Fig. 9). This faster growth led to significantly larger sizes of  $\geq 9$  mm larvae at day 12 in blue marlin (ANCOVA:  $P = 0.007$ ) and at day 11 in sailfish (ANCOVA:  $P = 0.029$ ; low sample sizes for  $\geq 9$  mm larvae at day 12 likely resulted in the non-significant [ $P = 0.271$ ] difference for this day). We repeated this comparison of growth between size groups for each region separately, but while overall patterns (i.e., location of growth divergence) were similar to the overall combined region analysis, low sample sizes precluded statistical comparisons.

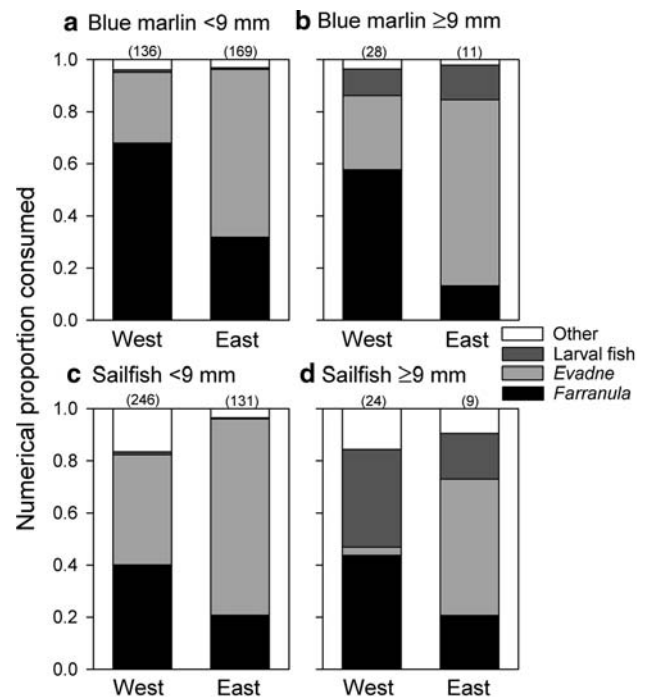
**Discussion**

On a population scale, early larval growth of blue marlin and sailfish varied little across the Straits of Florida (SOF).



**Fig. 6** Detrended recent growth (DRG) during the last two complete days prior to collection of blue marlin ( $n = 134$ ) and sailfish ( $n = 130$ ) larvae  $<9$  mm SL according to percentage of prey type in gut. Prey types were **a** copepods in the genus *Farranula* and **b** cladocerans in the genus *Evadne*. Blue marlin with  $>66.6\%$  *Farranula* in their guts grew faster than larvae with  $<33.3$  and  $33.3\text{--}66.6\%$  *Farranula* in their guts (ANCOVA:  $P = 0.002$ ; Bonferroni multiple comparison). No other comparisons were significant

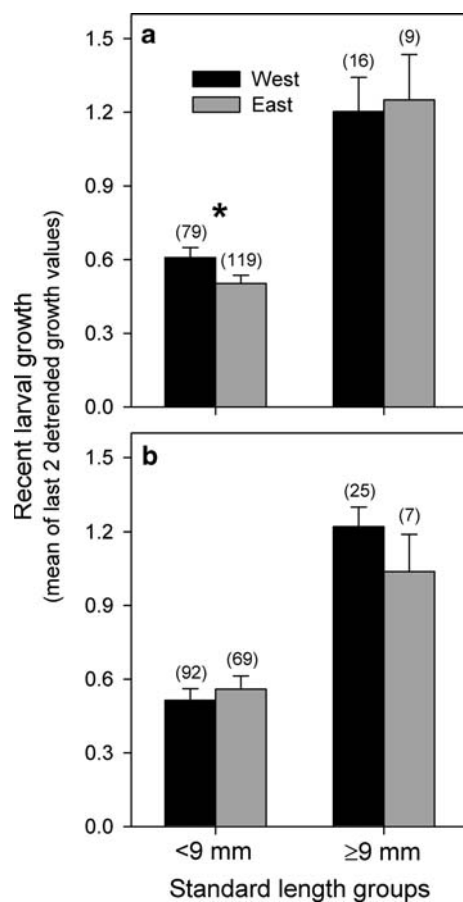
Once variation in age (both species) and surface temperature (sailfish) were factored out, there were no significant differences in the SL-age relationship between the western and eastern regions for either species. This was echoed in the lack of significant differences in the daily growth of each species from each region. Both billfish species are pelagic and spawn throughout the SOF (Richardson et al. 2009a), consequently, their larvae may be sourced from different areas of the SOF. The nature of our monthly sampling over a single transect across the SOF contributes to some uncertainty regarding the specific location of larvae earlier in their life. All larvae we collected were moving meridionally (south–north) through the SOF. Although the dominant northward-flowing FC reduces the likelihood of substantial cross-SOF (between-region) movement of larvae, and thus the regions can be considered large north–south zones, the specific earlier upstream location of larvae is unknown. Therefore, to minimize this



**Fig. 7** Numerical proportions of prey types consumed by small ( $<9$  mm SL) and large ( $\geq 9$  mm SL) larval **a, b** blue marlin and **c, d** sailfish from the western and eastern regions of the Straits of Florida. Data are from all larvae that were inspected (not only those that were aged) and are from the same individuals analyzed in Llopiz and Cowen (2008). Number of larvae inspected indicated above each bar

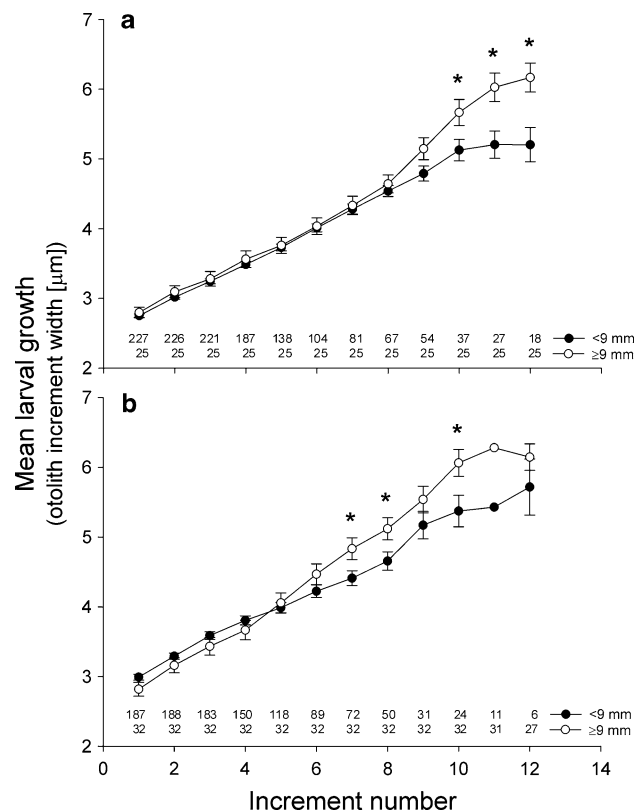
element of uncertainty, we also examined the recent larval growth (detrended for age effects) during the last two full days prior to collection for each individual. Recent growth did not differ significantly between regions for sailfish, but blue marlin larvae grew significantly faster in the western region of the SOF. We therefore divided larvae into two size groups that reflected distinct diet differences (driven by a shift to piscivory) and compared growth with diet composition, within and between groups.

Small ( $<9$  mm) zooplanktivorous blue marlin larvae grew significantly faster in the west than they did in the east. For a common reef fish, *Thalassoma bifasciatum*, larval growth was consistently higher at western stations along the same SOF transect, and high growth was directly associated with fuller larval guts and higher levels of prey availability (*Farranula*, harpacticoid, and *Oncaea* copepods) in the west (Sponaugle et al. 2009). For the two billfish species considered in the present study, however, variation in larval growth of these small larvae was unrelated to gut fullness; thus, prey availability does not appear to underlie growth variation. Instead, higher larval growth was associated with specific prey composition in one of the species. For blue marlin, larvae with higher proportions of *Farranula* in their guts had the highest recent growth. Recent growth of sailfish was not associated with distinct



**Fig. 8** Detrended recent growth (DRG) during the last two full days prior to collection for **a** blue marlin and **b** sailfish larvae  $\geq 3$ -days old, divided into two size groups (<9 and  $\geq 9$  mm SL). DRG of blue marlin <9 mm SL was significantly higher at western stations than at eastern stations (ANCOVA:  $P = 0.034$ )

differences in prey composition. Llopiz and Cowen (2008) demonstrated that sailfish and blue marlin (considered together) consume greater proportions of *Evadne* and *Farranula* than their availability in the environment would suggest (with *Evadne* selected for over *Farranula*). They hypothesized that billfishes may select these prey due to their greater profitability or that these proportions may be the result of differential capture success (prey occurrence, detection, or handling). Our findings for blue marlin suggest that recent larval consumption of higher proportions of *Farranula* confers higher growth to small, zooplanktivorous larvae; a trend toward lower growth with higher proportions of *Evadne* consumed was not significant. Both billfish species consumed larger proportions of *Farranula* in the west, and this heavier reliance on *Farranula* was associated with significantly higher recent growth of zooplanktivorous blue marlin larvae in the west. Note that due to the temporal mismatch between gut contents and somatic and otolith growth, these results are conservative. More direct cause and effect relationships would likely be



**Fig. 9** Daily growth (adjusted mean  $\pm$  SE) of otolith increment width [MIW] of **a** blue marlin and **b** sailfish larvae collected from stations across the Straits of Florida. Larvae were divided into two size groups: <9 and  $\geq 9$  mm SL. MIW values were truncated at 12 days due to small sample sizes for older fishes and adjusted for differences with temperature when this covariate was significant (sailfish). MIW values for sailfish, day 11 are unadjusted means and were not analyzed because they failed the homogeneity of slopes test. Separate ANCOVA comparisons of MIW between size groups were made for each day of larval life. All days of growth tested were non-significant (ANCOVA:  $P > 0.05$ ), except where indicated (asterisk blue marlin: day 10–12,  $P = 0.005$ – $0.030$ ; sailfish: day 7–8 and 10,  $P = 0.024$ – $0.029$ ; temperature covariate significant for sailfish day 1–3, 5–7, 11). Sample sizes for each increment are indicated at the bottom of each plot

evident where closer functional linkages could be examined.

Our results indicate that the prey composition may limit the growth of young blue marlin larvae, whereas neither prey composition nor availability appear to limit sailfish larval growth. Relative to blue marlin, sailfish may be more versatile and less constrained to the specific type of crustacean prey they consume during the first week of life (sailfish had higher proportions of “other” prey in their guts than blue marlin, largely consisting of *Corycaeus* copepods and *Limacina* pteropods). While studies of other species and systems have found correlations between prey availability and larval growth (Govoni et al. 1985; Wexler et al. 2007; Shoji and Tanaka 2004, 2007; Dower et al. 2009), there is

less evidence of links between prey type or composition and patterns of growth of marine larvae in the field. Laboratory experiments with yellow perch larvae fed different prey demonstrated that growth and survival of larvae  $\leq 12$  mm was greatest when they were fed adult copepods and copepod nauplii, whereas growth and survival of larvae  $> 12$  mm was greatest when they consumed adult copepods and cladoceraans (Graeb et al. 2004). Subsequent experiments revealed that larval perch prey selection tracked these trends in growth and survival (Graeb et al. 2004).

There were no significant spatial differences in the recent growth of larger ( $\geq 9$  mm) piscivorous larvae of either species. Similar to copepods, larval fish prey are typically more abundant at the most western SOF stations (Llopiz et al. 2009). The overall distribution of sailfish larvae mirrors this pattern in that they were consistently more abundant in the far western stations. Blue marlin larvae from the western region were collected primarily at stations closer to the central region of the transect, where larval fish prey were less abundant than at the far western stations and more similar to that of the eastern stations (Llopiz and Cowen 2008). This difference in the spatial co-occurrence of billfish larvae and their fish prey underlies the observed numerical dominance of fish prey in the guts of piscivorous sailfish larvae from the west and the roughly similar proportions of fish prey in the guts of western and eastern blue marlin larvae. The remainder of the gut contents of these piscivorous blue marlin larvae consisted of *Farranula* and *Evadne* in roughly similar proportions as in the guts of the smaller larvae. Note, however, that these are numerical proportions and since individual fish larvae have a substantially higher biomass than individual zooplankton prey, biomass, and energetic contributions of fish prey likely dominate by this point. Piscivorous sailfish larvae that consumed substantial proportions of fish larvae in the west tended to have higher recent growth than those in the east, but this was not significant, perhaps reflecting a still versatile diet and a high efficiency at capturing prey regardless of their availability.

The transition to feeding on fish prey is associated with a sharp increase in the growth rates of both species of billfish. This is evident in the exponential relationship between length and age as well as in the measurements of recent growth and is afforded by not only the ability to capture and consume such large prey but also the ability to digest the high protein content of other fish larvae (Govoni et al. 1986). Govoni et al. (2003) demonstrated that the slope of the growth curve of swordfish larvae increases sharply as larvae switch from copepods and chaetognaths to fish prey, and a similar change in growth has been shown for tuna larvae (Jenkins and Davis 1990). Growth increases sharply for young-of-the-year bluefish (*Pomatomus saltatrix*) when they enter estuaries and switch to piscivory (Juanes and

Conover 1994). Sailfish larvae in the SOF consumed primarily reef-associated goatfishes (Mullidae) and coastal pelagics such as halfbeaks (Hemiramphidae), flying fishes (Exocoetidae), and jacks (Carangidae; Llopiz and Cowen 2008). Blue marlin larvae, being distributed farther offshore, consumed pelagics such as tunas (Scombridae) and snake mackerels (Gempylidae; Llopiz and Cowen 2008). For predators with high growth rates, early transition to feeding on high caloric food such as fish prey is essential.

The time when billfish larvae become capable of feeding on other larval fish prey appears to be a pivotal period in early life. For both species (regions combined), daily growth of large ( $\geq 9$  mm) piscivorous larvae and smaller ( $< 9$  mm) zooplanktivorous larvae was similar for the first week of life, but at about day 7 in sailfish and after day 9 in blue marlin, growth trajectories began to diverge. Larvae  $\geq 9$  mm grew faster after day 7–9 than  $< 9$  mm larvae, and this faster growth led to significantly larger larval sizes by days 11 and 12. The ages where growth rates diverged correspond to  $\sim 5$  mm SL in both species, the size at which larvae become functionally capable of piscivory (Llopiz and Cowen 2008). We do not have direct evidence that these differences in early growth were due to prey composition, but our results indicate that the older survivors (who were piscivorous at the time of collection) had faster growth than younger fish (mostly zooplanktivorous) with a lower likelihood of survival. Our analysis of selection is cross-sectional in that larvae of different ages were not part of the same cohort that was tracked over time (e.g., Hawn et al. 2005), rather we are averaging growth over many cohorts, so only recurring, common processes will emerge. If we assume that mortality schedules did not change appreciatively through time, older fish can be thought of as the portion of the population with higher survival rates than the portion comprised of smaller, younger larvae. Thus, blue marlin and sailfish survivors in both regions had faster growth beginning  $\sim 5$  mm SL, around the time piscivory commences, suggesting that an early switch to piscivory may confer a survival advantage to individuals. Fitzhugh et al. (1996) suggested that a bifurcation in the growth curve of juvenile southern flounder (*Paralichthys lethostigma*) was due to variation in the onset of piscivory. Most longitudinal studies of selective mortality in larvae have found that survivors are those with higher growth rates and/or larger sizes-at-age (Meekan and Fortier 1996; Hare and Cowen 1997; Takasuka et al. 2003; Nielson and Munk 2004; Tanaka et al. 2006). Shoji and Tanaka (2006) showed that the strength of selection for fast growth in piscivorous larvae was further dependent on prey availability. In Atlantic mackerel, high larval growth rate was related to abundant nauplii and warm water temperatures (Robert et al. 2009), and the combination of high growth and weak selection for high growth contributed to an exceptional year class (Robert et al. 2007).

Our cross-sectional approach to examine selective mortality is somewhat constrained in this oceanographically dynamic region because all of the collections were made from stations along a single transect across a major ocean current. Thus, older larvae were upstream of the transect in early larval life, whereas younger larvae were in closer proximity to the transect. This spatial aliasing means that it is possible that the environment occupied by the older larvae when they were young was a more favorable growth environment, leading to the observed difference in the growth trajectories between smaller/younger larvae and larger/older larvae. Two lines of evidence are inconsistent with this possibility. The first is that growth during the first week of life was similar across size groups, reflecting potentially similar growth environments in the different locations of early growth. Secondly, both sailfish and blue marlin exhibit this divergence in growth during the second week of life despite the fact their peak abundances across the SOF differ. The difference in their distribution would result in different back-calculated upstream environments—sailfish along and upstream of the Keys and blue marlin potentially from closer to the Bahamas Bank or Cuba (Richardson et al. 2009a). Disparate upstream environments would not likely underlie these similar patterns of high growth.

In summary, variation in the earliest growth of blue marlin larvae is related to the composition of their zooplankton prey, and results in distinct regional differences in recent growth of blue marlin larvae consuming crustaceans. However, once larvae switch to piscivory after the first week, these spatial patterns begin to disappear such that cumulative growth over the first three weeks of larval life is similar between regions. Sailfish larvae do not have such tight coupling to prey composition and appear to have a more versatile diet. For both of these fast-growing species, early onset of piscivory is likely to be critical to survival.

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