Evidence of isotopic maternal transmission influence on bluefin tuna (*Thunnus thynnus*) larval growth

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ABSTRACT

Pre-flexion stages of Atlantic bluefin tuna (*Thunnus thynnus*) larvae were collected in 2014 during the peak of spawning in the two main spawning areas: Gulf of Mexico (GOM) and Mediterranean Sea (MED). We examined daily growth, otolith biometry, and stable isotopes and found that the GOM grew at a faster rate, had larger otoliths, wider daily increments, and significantly lower values of $\delta^{15}N$ when compared to the MED. In addition, an intra-population comparative analysis between slow- and fast-growing individuals (deficient vs. optimal growth groups, respectively) showed that optimal growth groups had significantly lower $\delta^{15}N$ within each spawning area, implying a direct relationship between growth potential, development, and maternal transmission of isotopic signatures. A third pre-flexion larval group that was aquaculture-reared also exhibited the same pattern to the wild larval groups. In addition, for the first time, we estimated the maternal trophic niches using models developed with field-captured pre-flexion larvae. The estimated maternal trophic niches for the GOM were narrower than the MED, implying differences in the maternal trophodynamics from each nursery area. Overall, the inter-population (GOM vs. MED) and intra-population growth groups (deficient vs. optimal) grew faster and had narrower maternal niches. This study shows the advantages that larval SIA research can aid in the understanding of the trophodynamics of their breeders by examining the trophic relationship of a spawning stock jointly with the development of growth potential in offspring within the same breeding season.

1. Introduction

Atlantic bluefin tuna, *Thunnus thynnus* (Linnaeus, 1758, ABFT) is a migrating top predator, an important fishery resource worldwide, and a key species in pelagic ecosystem (Bakun and Broad 2003; Bakun 2006). ABFT exerts top down control on the lower trophic levels of the food web and is distributed throughout the Atlantic Ocean from cold waters off Norway and Canada to tropical equatorial regions (Muhling et al., 2017).

ABFT is managed by the International Commission for Conservation of Atlantic Tunas (ICCAT) as two stocks. Stocks have been mainly defined and separated for management purposes at 45°W (Rooker et al., 2007) corresponding to the eastern and western populations. This division is a consequence of broad biological differences related with reproduction areas, age at first maturation and feeding distribution patterns. However, recent genetic studies (Johnstone et al., 2021; Puncher et al., 2022; Diaz-Arce et al., 2023) have revealed uncertain

degree of mixing is occurring between both stocks. The eastern stock spawns in the Mediterranean (MED) and the western stock spawns mainly in the Gulf of Mexico (GOM). Starting in 2010 onwards, evidence of the eastern stock's expansion of ABFT are evidenced, as the extension of the western MED spawning grounds towards peninsular coastal waters off Spanish Levantine waters (García et al., 2013a). With regards to the western stock, in 2013, new spawning grounds were reported along the Slope Sea in North America's northeast continental slope (Richardson et al., 2016; Hernández et al., 2022).

ABFT spawn in warm (23–28 °C) oligotrophic ecosystems (Alemany et al., 2010; Muhling et al., 2017). where low concentrations of predators and prey occur (Reglero et al., 2014). This spawning strategy appears to enhance larval survival by reducing predation-induced mortality (Bakun 2013; Muhling et al., 2017). When spawning ceases, ABFT re-initiate a trophic migration. The eastern stock mainly feeds in the MED and in the northeastern Atlantic, while the western stock principally feeds in the northwestern Atlantic (ICCAT 2019). However,

recent studies have pointed out that both stocks share common feeding grounds in the North Atlantic Ocean (Deshpande et al., 2016; Druon et al., 2016; Puncher et al., 2022) and that some individuals are capable of trans-Atlantic migrations (Rooker et al., 2014). The migration to and from spawning regions to feeding grounds implies energy consumption costs throughout the ABFT life cycle (Shimose and Farley 2016).

Energy allocation for migrating (to and from spawning grounds) and the subsequent metabolic costs of reproduction is highly dependent on the success of feeding while in their foraging grounds (Golet et al., 2007; Chapman et al., 2011). Currently, stable isotope analysis (SIA) is commonly implemented to assess the trophodynamics in many species (Fredriksen, 2003). The $\delta^{15}N$ levels indicate the position of consumers in the trophic web which is a function of its enrichment in relation to prey consumed (Post, 2002), while $\delta^{13}C$ is linked to primary production sources and reflects the origin of the prey consumed (Pinnegar and Polunin 2000). Thus, from the trophic standpoint, each feeding ground will imprint a respective isotopic trophic signature incorporated from their respective diet in foraging grounds.

Maternal investment is an association between a mother and her offspring that simultaneously carries an energetic or fitness cost for the mother and a fitness benefit for the offspring (Clutton-Brock 1991). Maternal effect influences size at first hatch, growth rates, and larval survival (Chambers and Leggett 1996; Letcher et al., 1996; Starrs et al., 2014). Thus, maternally transmitted qualities are determinant for larval development and provided the necessary nutritional and immunological conditions for larval survival (Swain and Nayak 2009; Perez and Fuiman 2015). Reproductive females have faster growth rates, produce larger eggs (Green and McCormick 2005), and can enhance larval growth by the provision of yolk-reserves (Bernardo 1996) during the earliest developmental stages of life (pre-flexion phases). For example, Pacific bluefin tuna (*Thunnus orientalis*, PBT) females had better nutritional condition and not only shed more eggs, but they were of higher quality (Ohshimo et al., 2018a). Characterizing the isotopic patterns provides insight into the breeder-offspring isotopic relationship (i.e. isotopic heritance). This is particularly interesting for a capital breeder such as ABFT (Laiz-Carrión et al., 2019) whose isotopic signatures (of eggs and offspring) display considerable changes across the breeding season (Uriarte et al., 2016; Planas et al., 2020). The key transition from lecitotrophic larvae with high metabolic rates to pre-flexion stages is directly dependent on maternal factors (Conover and Schultz 1997) because the egg quantity and quality influences the overall survival rates of newly hatched larvae (Ohshimo et al., 2018a, Hiraoka et al., 2019). However, the ABFT maternal isotopic influence has not been characterized yet from wild-specimens in their respective spawning grounds. Faster growing fish populations ultimately yield larger sizes in shorter temporal windows (Takasuka et al., 2003; Palomera et al., 2007) which result in greater predatory evasion (Miller et al., 1988; Chick and Van Den Avyle 2000) and improve feeding opportunities (Pitchford and Brindley 2001), thus increasing survivorship (Folkvord and Hunter 1986). The growth mortality assumption (Anderson 1988) has also been the focus in bluefin tuna populations, as examined for PBT (Tanaka et al. 2006, 2014, 2017; Satoh et al., 2013; Watai et al., 2017), southern bluefin tuna (Jenkins and Davis 1990), and also for yellowfin tuna (Wexler et al., 2007). Scombrids are top predators and they base their survival strategy on fast larval growth, allowing larvae to become an active predator earlier than other larval fishes by benefiting from a precocious piscivourous diet that avoids predatory pressure from other species (Tanaka et al., 1996) or shifting to cannibalistic habits (Llopiz et al., 2015; Uriarte et al., 2019). Survival of the youngest PBT larvae (∼6–13 days) has been attributed to faster larval growth rates (Tanaka et al., 2006) in addition to reaching the juvenile stage earlier, while the slower growing larvae were not able reach the juvenile phase (Watai et al., 2017). These findings support the role of larval growth for survival to reach the juvenile and young of the year (YOY) stages.

Ambient temperature and food availability have been shown to be the major environmental factors influencing larval fish growth (Takahashi and Watanabe 2004), including for tuna species (Tanaka et al., 2006; Wexler et al., 2007; García et al., 2013b; Satoh et al., 2013; Gleiber et al., 2020). However, some field studies have reported that environmental variables account for less than 40% of observed growth variability (Wilson and Meekan 2002; Caldarone et al., 2003) suggesting the importance of other factors, where the quality of the breeding population may be essential.

Generally, the maternal contribution is considered more important for larval fish survival than the paternal (Green and McCormick 2005), principally because it is directly linked to the provision of yolk to eggs (Bernardo 1996; Tanaka et al., 2014). Maternal inheritance is more influential and it is easier to track during earliest stages of development (egg to yolk absorption, pre-flexion, to the notochord flexion) (Heath and Blouw 1998). While maternal investment in larvae is high (Green and McCormick 2005), its effects become mitigated as larvae develop (Green 2008; Donelson et al., 2009; Moore et al., 2019). The isotopic values recorded from eggs and pre-flexion larvae would reflect maternal diet and the differences observed between these two may point towards a differential transfer of essential amino acids or changes in proportion of lipids allocated as lipo-glyco-protein reserves. Understanding these sources of variation can improve isotopic data analysis and interpretation. Moreover, this approach may lay the groundwork to assess the maternal influence and to infer the different feeding strategies (capital vs. income) of the breeders (Laiz-Carrión et al., 2019).

Maternal stable isotope transmission has been traced in perciforms to offspring (Starrs et al., 2014). Few studies have applied stable isotopes to investigate the effects of maternal nutrition on offspring quality (Kouwenberg et al., 2013). Uriarte et al. (2016) showed in a rearing experiment that eggs and pre-flexion larvae of eastern ABFT larvae reflected to the adult female isotopic signatures. Subsequently, Uriarte et al. (2016) developed a model for estimating maternal isotopic signatures utilizing the SIA of N and C of pre-flexion ABFT larvae. This finding paves the way to estimate the trophodynamics of the adult stock and enable to define the trophic niche for wild bluefin stocks without having to sample mature female ABFT. Furthermore, SIA can define isotopic niche and niche overlap with other species competing for food resources using Bayesian inference models (SIBER, Jackson et al., 2011) which are measures of dietary diversity (Bearhop et al., 2004; Newsome et al., 2007; Syväranta et al., 2013).

Although the isotopic niche mostly corresponds to a portion of the ecological niche of organisms, isotopic data reflect patterns of resource and habitat use (Rader et al., 2017) and can be used to define niche hypervolumes and assess overlap in resource requirements (Newsome et al., 2007).

This study undertakes a comparative approach to unravel early larval growth characteristics based on two field-collected pre-flexion larval tuna cohorts originating from the GOM and MED spawning grounds, and compares these results with aquaculture-reared specimens of known age. We analyze somatic and otolith growth variables jointly with corresponding individual $\delta^{15}N$ and $\delta^{13}C$ signatures. Furthermore, we estimated the maternal isotopic signatures ($\delta^{15}N_{maternal}$, $\delta^{13}C_{maternal}$) and their corresponding trophic niches to infer feeding strategies of the females from each spawning ecosystem. Consequently, the main objective of this study focuses on analyzing the impact of maternally inherited trophic signatures on the growth of early stages of bluefin larvae.

2. Material and methods

Ichthyoplankton samples correspond to two hydrographic and plankton surveys conducted during the ABFT spawning season of 2014. The first survey carried out 74 stations on board the R/V F.G. Walton Smith from 28 April to 25 May in the northern GOM. The second survey sampled 98 stations on board the R/V SOCIB from 17 June to 3 July in the Balearic Sea in the western MED basin (Fig. 1).
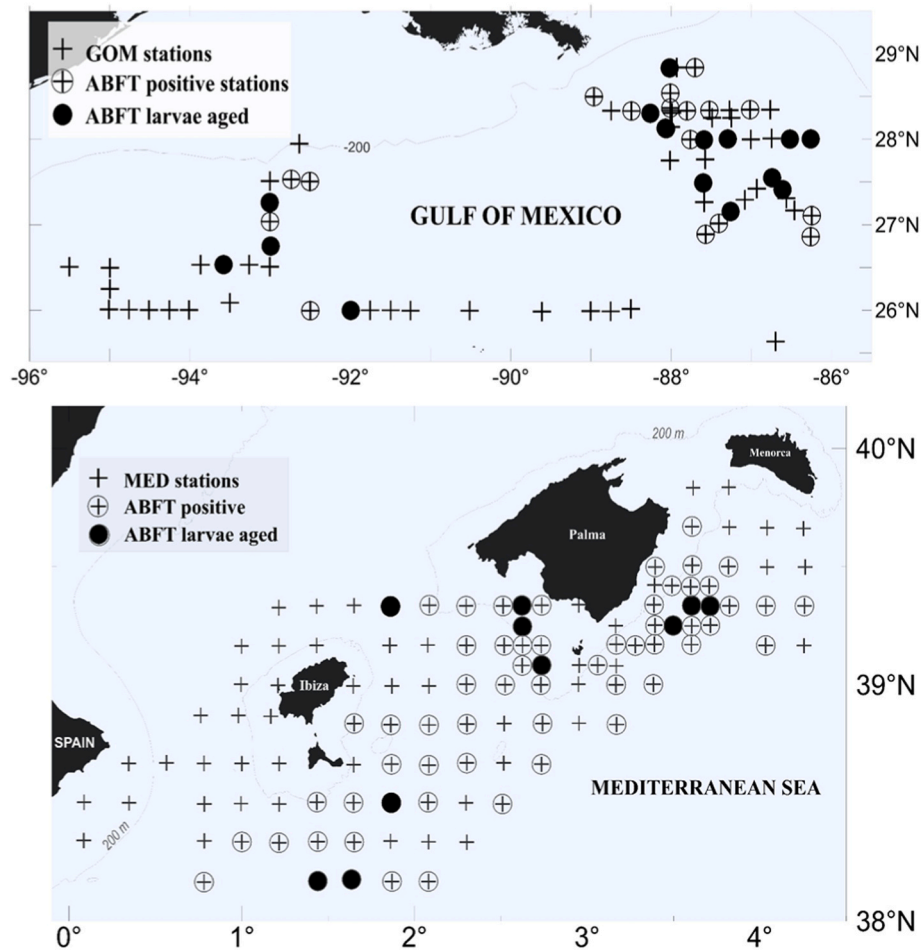
Fig. 1. Geographical location of larval tuna sampling (+), positive stations for ABFT (⊕) and stations where ABFT larvae aged included in this study were captured (●) for the Gulf of Mexico (GOM) in the top panel, and Mediterranean (MED) in bottom panel.

2.1. Field larval sampling

Both cruises used similar sampling methods for field collection of scombrid fish larvae as previously described in Laiz-Carrión et al. (2015). Larvae were sorted onboard, placed in cryogenic vials and stored in liquid nitrogen until further analysis in the laboratory of the Málaga Oceanographic Center from the Spanish Institute of Oceanography (IEO-CSIC).

2.2. Aquaculture eggs and larval sampling

Fertilized eggs of ABFT from open sea caged ABFT were obtained in the western MED on 24 June 2013 and were transported to aquaculture tanks and reared until reaching pre-flexion stage (12 days after hatch) as described in Uriarte et al. (2016). The subsequent larval rearing followed the methodology described by Ortega et al. (2011) and De la Gándara et al. (2012). The experiment was performed according to Spanish law 6/2013 complying with the European Union directive on animal welfare (Directive, 2010/63/EU) on the protection of animals used for scientific purposes.

2.3. Larval handling for growth and isotope analysis

2.3.1. Field samples

Individual larvae that were prepared for growth analysis were also processed for SIA in a two-step procedure. In the first step, for daily growth analysis, only pre-flexion larvae were selected based on the degree of notochord flexion observed on a digitized and calibrated image of each larva. A total of 66 and 54 ABFT larvae were selected from the GOM and MED spawning grounds, respectively, within a common standard length (SL, mm) range (3–6 mm). In the laboratory, ABFT larvae were measured with Image J 1.44a software (USA National Institute of Health) and dry weighed (DW, mg) with a precision balance of 1 mg after dry-freezing for 24 h. Subsequently, otoliths (sagittae) were removed and mounted following García et al. (2003). All otoliths were digitized using Leica DM6 B microscope at 1000 magnification along with Leica Application Suite X (LAS ×2.0.0) software. Otolith radius (OR, μm), daily increments (AGE, days) and mean increment widths (MIW, μm) were also measured using the LASX Leica software. Age estimates were done by two experts on otolith microstructure of ABFT larvae to carry out an intercalibration exercise. In this exercise, the readings of both experts were used first to compare age estimates between left and right sagittae from the same fishand second to verify that the precision of reads generated by both readers was ~5% coefficient of variation (Malca 2022). After otolith extraction, the stomach was removed and larvae were packed in tin vials (0.03 ml) for SIA.

2.3.2. Aquaculture samples

Isotopic values from ABFT eggs (n = 10 pooled) and measurements of SL, DW followed a similar protocol described for field larvae. AGE (days post-hatch in captivity) and isotopic signatures of pre-flexion stages (n = 55) from the aquaculture (AQU) rearing experiment (Uriarte et al., 2016) were selected for comparison with wild ABFT.

2.4. Stable isotope analysis

In the second step of larval handling, natural abundances of N (δ^{15}N) and C (δ^{13}C) were measured using an isotope-ratio spectrometer (Thermo-Finnigan Delta-plus) coupled to an elemental analyzer (FlashEA1112 Thermo-Finnigan) at the Instrumental Unit of Analysis of the University of A Coruña. Ratios of ^{15}N/^{14}N and ^{12}C/^{13}C were expressed in conventional delta notation (δ), relative to the international standard, Atmospheric Air (N_2) and Pee-Dee Belemnite (PDB) respectively, using acetanilide as standard. The analyses precision for δ^{15}N and δ^{13}C were 0.10‰ and 0.14‰, respectively, based on the standard deviation of internal references (repeatability of duplicates). An initial chemical extraction for lipid correction was not possible to carry out due to the low amount of available sample. Nevertheless, a posterior lipid content correction of the δ^{13}C values was conducted following Logan et al. (2008) in which we selected the best model for predicting lipid correction. For ABFT larvae, four equations for all fish tissues (liver, muscle, gonad, whole body) (Logan et al., 2008) were considered to obtain a mean value (0.69‰ SD = 0.01) used for lipid correction of ABFT larvae. This procedure has been previously described by Laiz-Carrión et al. (2013, 2015, 2019).

2.5. Estimation of isotopic maternal signatures

We estimated the δ^{15}N$_{maternal}$ values following the model proposed by Uriarte et al. (2016):

$$\delta^{15}N_{maternal} = \delta^{15}N_{larva} + (\delta^{15}N_{egg} - \delta^{15}N_{larva}) = \delta^{15}N_{larva} + (a + b*AGE)$$

$$\delta^{13}C_{maternal} = \delta^{13}C_{larva} + (\delta^{13}C_{egg} - \delta^{13}C_{larva}) = \delta^{13}C_{larva} + (a + b*AGE)$$

$\delta^{15}N_{larva}$ and $\delta^{13}C_{larva}$ represent the individual's bulk stable isotope values. However, for the calculation of factor ($\delta^{15}N_{egg} - \delta^{15}N_{larva}$) and ($\delta^{13}C_{egg} - \delta^{13}C_{larva}$), two different protocols were followed based on the linear relationship with age:

1. First, we used the least squares linear regression equation to estimate the pre-flexion δ^{15}N and δ^{13}C values from the rearing experiment (AQU) and use it to estimate δ^{15}N and δ^{13}C values in wild ABFT larvae from each spawning site (AQU, Table 1).
2. We developed a specific model of this relationship for each population of wild pre-flexion larvae for each study area (GOM and MED, Table 1).

In both protocols, a and b are coefficients and AGE is days after hatching of larvae.

2.6. Maternal isotopic niche width and trophic overlap

Maternal isotopic niches were calculated using the estimated maternal δ^{15}N$_{maternal}$ and δ^{13}C$_{maternal}$ from the isotopic variables of pre-flexion wild larvae from each corresponding spawning ground. Isotopic niche widths were estimated by standard Bayesian ellipses areas and associated credible interval adjusted for small sample size (SEAc)

Table 1
Maternal isotopic signature equations derived from larvae reared in aquaculture facilities (AQU) and larvae captured in the field (GOM and MED).

Population	n	Maternal isotopic signature estimation equation	p	r^2 (%)
AQU	54	($\delta^{15}N_{egg}$ - $\delta^{15}N_{larva}$) = (−2.813 + 0.875 * AGE)	**	88
		($\delta^{13}C_{egg}$ - $\delta^{13}C_{larva}$) = (2.279–0.557 * AGE)	**	87
GOM	66	($\delta^{15}N_{egg}$ - $\delta^{15}N_{larva}$) = (5.301 + 0.2232 * AGE)	**	16
		($\delta^{13}C_{egg}$ - $\delta^{13}C_{larva}$) = (2.327–0.1088 * AGE)	**	20
MED	54	($\delta^{15}N_{egg}$ - $\delta^{15}N_{larva}$) = (4.756 + 0.2087 * AGE)	**	25
		($\delta^{13}C_{egg}$ - $\delta^{13}C_{larva}$) = (1.704–0.0492 * AGE)	*	10

* p < 0.05; ** p < 0.01.

(Jackson et al., 2011, 2012). Isotopic niche widths and overlap analyses were conducted using the R package SIBER (Stable Isotope Bayesian Ellipses in R) v.3.3.0 (Jackson et al., 2011, R Development Core Team, 2012). The standard ellipse from the bivariate data was calculated from the variance and 40% covariance of the data following Laiz-Carrión et al. (2019). SEAC overlaps between groups were calculated as the proportion of the overlapping area relative to the non-overlapping area (i.e., overlapping area divided by the sum of each group area minus the overlapping area).

2.7. Statistical analysis

Analysis of covariance (ANCOVA) were run for growth differences, isotopic signatures and otolith metrics for each GOM and MED larval groups using AGE as covariate. Variables were log-transformed (LOG) prior to statistical analysis when necessary to obtain linearity and variance homogeneity (Sokal and Rohlf 1979).

Estimated SIA maternal signatures were analyzed for inter- and intra-population comparisons by applying non-parametric Mann-Whitney U test as variables did not fulfill parametric assumptions.

Least squares linear regression (y = a+x*b) for LogSL and LogDW vs AGE were fitted to define the daily growth pattern of each larval population. Residuals were calculated for each larval group, and groups were assigned following Quintanilla et al. (2015). according to their residual values. Briefly, these groups were included as factors of a grouping variable in ANCOVA analysis with AGE as covariate to compare intra-population differences. The GOM and MED population was divided into four groups according to their residual values of length (SL) and weight (DW) controlled by AGE. Larger and heavier than expected by the model (GOM+ and MED+ with positive residuals for both fits), while smaller and lighter than expected (GOM- and MED- with negative residuals for both fits), with two intermediate groups (shorter SL but heavier and vice versa). The AQU larvae were also grouped according to their residual values (AQU+, AQU-). In summary, this residual differentiation method distinguishes between optimal and deficient growth patterns that an individual larva is having with respect to the whole population. This approach allows comparisons between trophic variables and otoliths measurements between the most contrasting growth groups.

Statistical analyses were undertaken using the STATISTICAL 7.0 package (Statsoft Inc.) and significance level for analysis were set at $\alpha = 0.05$.

3. Results

3.1. Larval growth and SIA analysis

Both populations, GOM (n = 66) and MED (n = 54) showed differences between their pre-flexion stages between their common size frequency distribution, however, age distribution was similar (Table 2).

The inter-population comparison (GOM vs. MED) growth patterns determined significant differences between both populations where larvae from GOM showed significantly greater growth in SL and DW by AGE (Table 3).

Table 2
Results of Mann-Whitney U test (mean ± SE, number of larvae, Z adjusted and p) between areas (GOM and MED) for SL and AGE. *p < 0.05; **p < 0.01; NS: no significant differences.

	GOM vs. MED					
	GOM		MED		MW - U test	
	Mean ± SE	n	Mean ± SE	n	Z adjusted	p
SL (mm)	5.052 ± 0.06	66	4.628 ± 0.07	54	3.919	**
AGE (days)	7.712 ± 0.27	66	8.574 ± 0.30	54	0.011	NS

Table 3

ANCOVA for ABFT larvae (mean ± SE, number of larvae, F and p) with AGE as covariate between areas (GOM and MED) for somatic (LogSL, LogDW), trophic ($\delta^{15}N$, $\delta^{13}C$) and otolith biometric (LogOR, MIW) variables. *p < 0.05; **p < 0.01; MS: marginally significant; NS: no significant differences.

	GOM vs. MED					
	GOM		MED		ANCOVA	
	Mean ± SE	n	Mean ± SE	n	F	p
LOG SL	0.702 ± 0.01	66	0.662 ± 0.01	54	$F_{(1,117)}$=53.44	**
LOG DW	−0.678 ± 0.02	66	−1.542 ± 0.08	54	$F_{(1,117)}$ = 231.87	**
LOG OR	1.273 ± 0.01	66	1.282 ± 0.01	66	$F_{(1,117)}$ = 6.44	*
MIW	1.404 ± 0.03	60	1.344 ± 0.04	51	$F_{(1,108)}$ = 3.00	MS
$\delta^{15}N$	5.377 ± 0.22	54	5.798 ± 0.21	54	$F_{(1,105)}$=13.06	**
$\delta^{13}C$	−19.454 ± 0.04	54	−19.201 ± 0.06	54	$F_{(1,105)}$=10.25	**

Larval $\delta^{15}N$ were consistently significant and had a negative linear relationship with AGE for both populations (Fig. 2), whereas the MED population had higher $\delta^{15}N$ values and $\delta^{13}C$ values than the GOM (Table 3).

The biometrics of OR measurements rendered significant populations differences and OR in the GOM was greater. Moreover, marginally significant (p < 0.08) higher MIW in GOM were also detected (Table 3).

The linear regressions for daily larval growth of SL and DW for pre-flexion stages of each population and residual analysis for the GOM population showed 44% of the individuals in the positive residual population (GOM+) and 38% of the total population in the negative residual population (GOM-). In the MED, larval population showed an equal (37%) of the total larval population corresponding to the MED+ and MED-.

The SIA of the intra-population comparisons showed that the positive residual groups (GOM+ and MED+) were significantly lower in $\delta^{15}N$ (Fig. 3). No differences in $\delta^{13}C$ between residuals groups were detected in any population (Table 3).

With regards to the intra-population differences in the otoliths' biometrics, the analysis of the positive residuals of the GOM+ and MED + groups showed significantly larger otoliths and wider MIW than GOM- and MED- groups, respectively (Table 4).

Similarly, residual analysis for pre-flexion larvae obtained from the aquaculture rearing experiment (n = 55) was also applied and the optimal group (33%, AQU+) showed higher growth in SL and DW than the deficient group (25%, AQU-) (Table 5). In addition, AQU + group

presented significant lower values of $\delta^{15}N$ with higher values of $\delta^{13}C$ (Fig. 3, Table 5).

3.2. Estimated maternal isotopic signatures

Table 1 indicates the maternal isotopic signatures from the AQU, as well as from the field-based models of the sampled larval populations (GOM, and MED) proposed for this study (Table 1). In AQU, the isotopic values were obtained from newly spawned eggs and lecitotrophic larvae (n = 20 pooled). The mean values ± SD of $\delta^{15}N$ and $\delta^{13}C$ were 12.31 ± 0.32 and −18.06 ± 0.31, respectively. For wild ABFT larvae, the isotopic values of eggs were calculated using a random variable originating from the mean and standard deviation of the egg and lecitotrophic larvae obtained in the rearing experiment. Both in the wild population estimates (Table 6), as well as those obtained from the residual analysis groups (Table 7), the estimates of $\delta^{15}N_{maternal}$ and $\delta^{13}C_{maternal}$ were always greater in the field-estimated equations compared with the experimental rearing values. The only significant differences in the estimated $\delta^{15}N_{maternal}$ values between populations occurred when using the model from the aquaculture rearing experiment, in which the GOM signatures were significantly lower (Table 6).

On the other hand, the comparison between the established optimal vs deficient growth groups (GOM + vs GOM-, MED + vs MED-) showed differences in estimated $\delta^{15}N_{maternal}$ (Table 7), whereby the maternal signatures of $\delta^{15}N_{maternal}$ were always lower in the optimal growth group. No differences were observed for estimated $\delta^{13}C_{maternal}$.

The inter-population comparison of the estimated maternal isotopic niches showed centered ellipse areas (SEAc, Fig. 4a) enclosing the GOM population within the MED population. The GOM trophic niche was narrower and totally overlapped with the MED, meanwhile the MED overlaps 23% with the GOM (Fig. 4b, Table 8). The comparison of residual groups (Fig. 5a) showed that faster growth (GOM+, MED+) is related to narrower maternal niches in both populations (Fig. 5b, Table 8). Maternal isotopic niche overlap intra-population comparison (Fig. 5a) reveals a higher overlap area between optimal vs deficient in the GOM region with global smaller niches, than in the MED with wider niches (Table 8).

4. Discussion

It is widely accepted that population dynamics of fish species are determined during the early life stages. During this critical stage, larvae undergo acute developmental processes that intertwine with hydrophysical forces (Cowen and Sponaugle 2009, Pepin et al., 2015), thereby influencing survival and recruitment variability of fish populations (Houde 2008). Faster bluefin tuna growth has influenced the variability of the fishery resources (Satoh et al., 2013; Tanaka et al. 2014, 2017; Watai et al., 2017) by shortening larval developmental stages (Pepin 1991), and decreasing predation pressure (Takasuka et al., 2003, Sponaugle et al., 2011). Larval growth rates play a critical role in species recruitment (Tanaka et al., 2006; Satoh et al., 2013) and the referenced framework responds to the growth-dependent hypothesis of survival (Meekan and Fortier 1996; Robert et al., 2007; Sponaugle et al., 2011) in which pre-flexion larvae are especially vulnerable to mortality (Fortier and Leggett 1985).

Larval growth is influenced by ambient variables, temperature being the most crucial factor (Gleiber et al., 2020). In our particular case, the sea surface temperature (SST) from shipboard measurements (Seabird SBE 9/11 Plus CTD profiler) are less than 1 °C on average between the two study areas. The SST measurements indicated that the GOM was slightly warmer than the MED (on average, 0.61 °C) during the corresponding ABFT collections at each spawning grounds. When comparing SST, year 2014 was relatively cooler in the GOM (SST 24.30 °C ± 0.67) and only after the first week of May, did temperatures increase beyond 23.5 °C. The SST observed in the MED was within average conditions (23.72 ± 0.62). (Malca et al., 2023). Despite these differences in
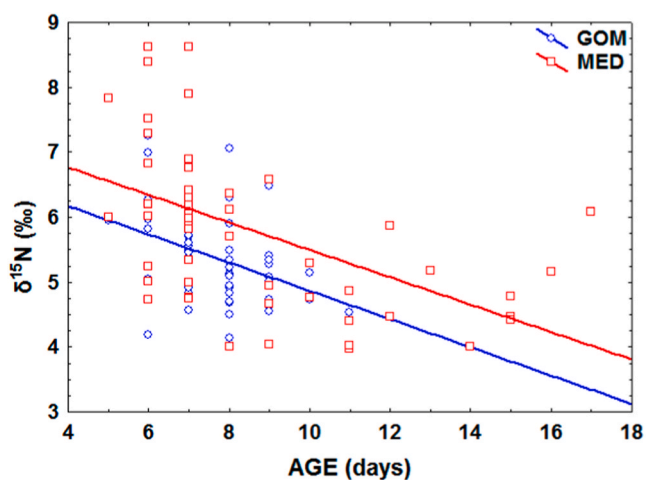

Fig. 2. Relationship between $\delta^{15}N$ and AGE (days) for ABFT pre-flexion larvae from GOM (○) and MED (□) populations.
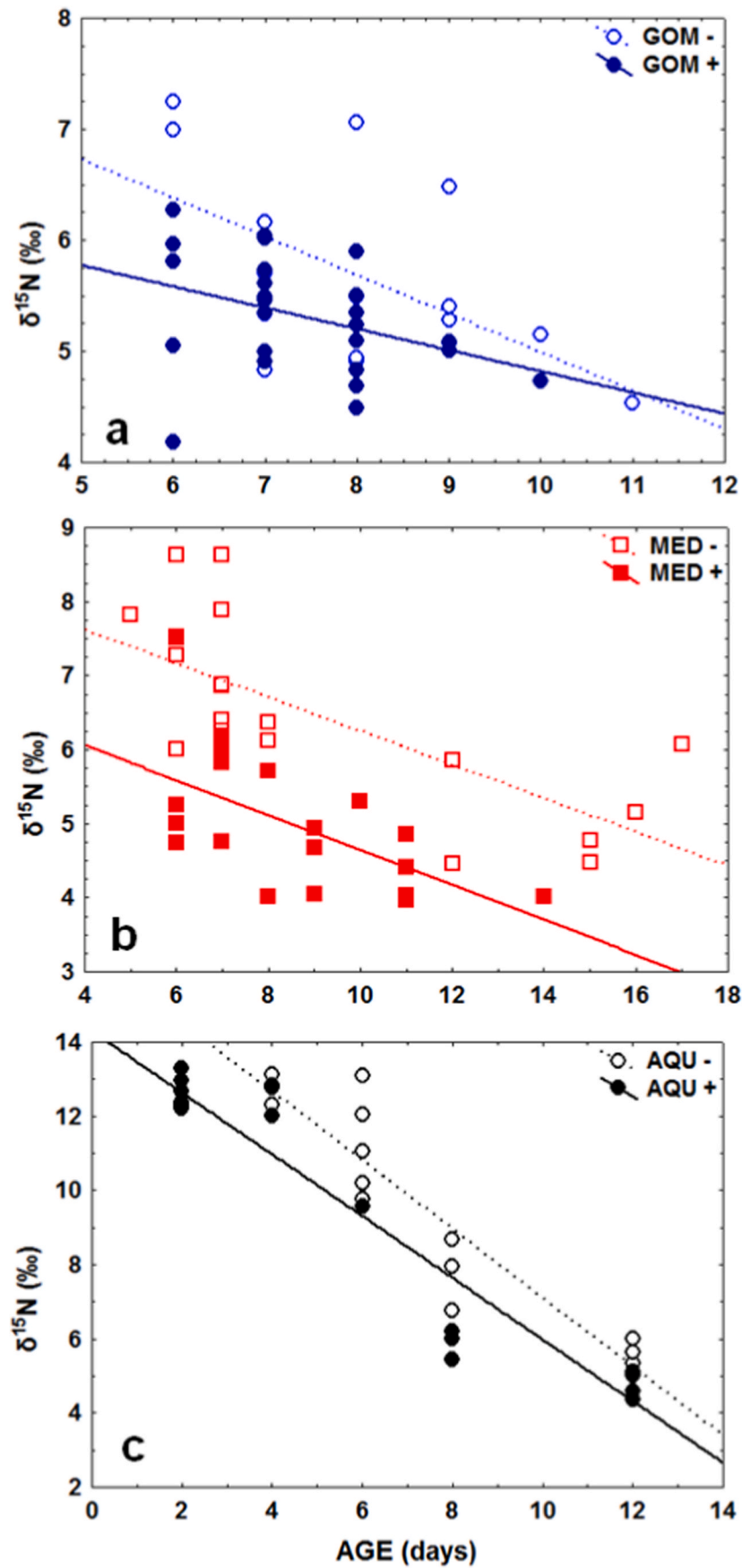
Fig. 3. Isotopic signature of Nitrogen ($\delta^{15}N$) and AGE (days) for ABFT pre-flexion larvae in the four groups established by the residuals of length and weight related to age for GOM (a; GOM + vs GOM-), MED (b; MED + vs MED-) and for aquaculture facilities (c; AQU + vs AQU-).

Table 4

Residuals ANCOVA analysis (mean ± SE, number of larvae, F and p) with AGE as covariant within each area (GOM and MED) in the groups established by the residuals of length and weight related to age for somatic (LogSL, LogDW), trophic (δ^{15}N, δ^{13}C) and otolith biometric (LogOR, MIW) variables. *p < 0.05; **p < 0.01; NS: non-significant differences.

	GOM + vs. GOM –						MED + vs. MED –					
	GOM +		GOM –		ANCOVA		MED +		MED –		ANCOVA	
	Mean ± SE	n	Mean ± SE	n	F	p	Mean ± SE	n	Mean ± SE	n	F	p
LOG SL	0.725 ± 0.005	29	0.672 ± 0.01	25	$F_{(1,51)} = 110.58$	**	0.699 ± 0.01	20	0.629 ± 0.02	20	$F_{(1,37)} = 88.46$	**
LOG DW	-0.585 ± 0.02	29	-0.772 ± 0.03	25	$F_{(1,51)} = 80.64$	**	-1.144 ± 0.09	20	-1.905 ± 0.14	20	$F_{(1,37)} = 68.89$	**
LOG OR	1.291 ± 0.01	29	1.256 ± 0.01	25	$F_{(1,51)} = 24.76$	**	1.322 ± 0.02	20	1.263 ± 0.03	20	$F_{(1,37)} = 31.06$	**
MIW	1.476 ± 0.04	26	1.304 ± 0.03	22	$F_{(1,45)} = 11.42$	*	1.526 ± 0.07	18	1.198 ± 0.04	19	$F_{(1,34)} = 23.38$	**
δ^{15}N	5.317 ± 0.22	26	5.662 ± 0.21	16	$F_{(1,39)} = 7.23$	*	4.910 ± 0.20	20	6.469 ± 0.28	20	$F_{(1,37)} = 38.00$	**
δ^{13}C	-19.500 ± 0.04	26	-19.410 ± 0.05	16	$F_{(1,39)} = 0.66$	NS	-19.252 ± 0.06	20	-19.082 ± 0.14	20	$F_{(1,37)} = 0.99$	NS

Table 5

ANCOVA analysis (mean ± SE, number of larvae, F and p) with AGE as covariant in the groups established by the residuals of length and weight related to age in aquaculture larvae for somatic (LOG SL, LOG DW) and trophic (δ^{15}N, δ^{13}C) variables. *p < 0.05; **p < 0.01.

	AQU + vs. AQU –					
	AQU +		AQU –		ANCOVA	
	Mean ± SE	n	Mean ± SE	n	F	p
LOG SL	1.493 ± 0.05	18	1.395 ± 0.04	14	$F_{(1,29)} = 76.71$	**
LOG DW	−1.881 ± 0.21	18	−2.213 ± 0.16	14	$F_{(1,29)} = 54.36$	**
δ^{15}N	9.128 ± 0.87	18	9.630 ± 0.77	14	$F_{(1,29)} = 13.58$	**
δ^{13}C	−16.717 ± 0.50	18	−16.204 ± 0.59	14	$F_{(1,29)} = 32.69$	**

Table 6

Summary of Mann-Whitney *U* test (mean ± SE, number of larvae, Z adjusted and p values between the GOM and MED for maternal isotopic signatures (δ^{15}N$_{maternal}$, δ^{13}C$_{maternal}$) estimated by equations based on aquaculture (AQU $_{estimated}$) and field (WILD $_{estimated}$) samples.*p < 0.05; **p < 0.01; NS: no significant differences.

	GOM vs. MED					
	GOM		MED		MW - *U* test	
	Mean ± SE	n	Mean ± SE	n	Z adjusted	p
δ^{15}N$_{maternal\ (AQU\ estimated)}$	9.26 ± 0.24	54	10.49 ± 0.24	54	−3.109	**
δ^{13}C$_{maternal\ (AQU\ estimated)}$	−21.43 ± 0.16	54	−21.70 ± 0.16	54	−0.627	NS
δ^{15}N$_{maternal\ (WILD\ estimated)}$	12.38 ± 0.12	54	12.34 ± 0.12	54	0.602	NS
δ^{13}C$_{maternal\ (WILD\ estimated)}$	−17.96 ± 0.04	54	−17.91 ± 0.04	54	0.154	NS

temperature, less than 1 °C in temperature did not appear to cause great statistically distinguishable differences in growth. Previously in bluefin spawning habitats, strong interannual changes in temperature have been observed (as much as 3 °C) resulting in strong between-year differences in larval growth. In contrast, populations of ABFT larvae from years with 1.09° of difference on average (23.87 ± 0.313 vs. 24.96 ± 0.83) did not show any difference in their growth patterns of length (SL vs AGE) or weight (DRY WEIGHT vs AGE) (García et al., 2013b). Nonetheless, maternal condition impacts offspring development as manifested by spawning relatively larger sizes of eggs (Green and McCormick 2005), providing greater or more nutritious yolk to offspring (Tanaka et al., 2014), and where maternal genes can also affect quality of broodstock (Høie et al., 1999).

We observed higher growth for pre-flexion ABFT larvae from the GOM when compared to the MED as observed from somatic and otolith biometric variables (Table 2). These observations are in agreement with Malca et al. (2017) which compared ABFT GOM and MED larval growth models. Moreover, growth differences between and within populations are evident after the lecitotrophic stage (Tanaka et al., 2010) and faster growing individuals were quicker in reaching post-flexion stages (Tanaka et al., 2006; Satoh et al., 2013; Watai et al., 2017, 2018). Consequently, GOM larvae showed significantly larger SL at pre-flexion (Table 2), thus corroborating their greater growth potential in the early stages of development and reaching successive larval stages of development earlier (Tanaka et al., 2006; Malca et al., 2017).

4.1. Isotopic maternal influence on ABFT larvae growth

Maternal effects have been shown to affect the nutritional and immunological condition of larvae (Swain and Nayak 2009; Perez and Fuiman 2015). The maternal effect influences size at hatch and its subsequent growth (Bernardo 1996), thereby increasing larval viability and decreasing larval mortality (Chambers and Leggett 1996; Letcher et al., 1996; Starrs et al., 2014). With respect to bluefin tuna, Ohshimo et al. (2018a) demonstrated that PBT females with better nutritional condition shed more eggs and showed greater egg viability. Despite its importance, the influence of maternal transmission has not been sufficiently highlighted in field observations and studies for ABFT.
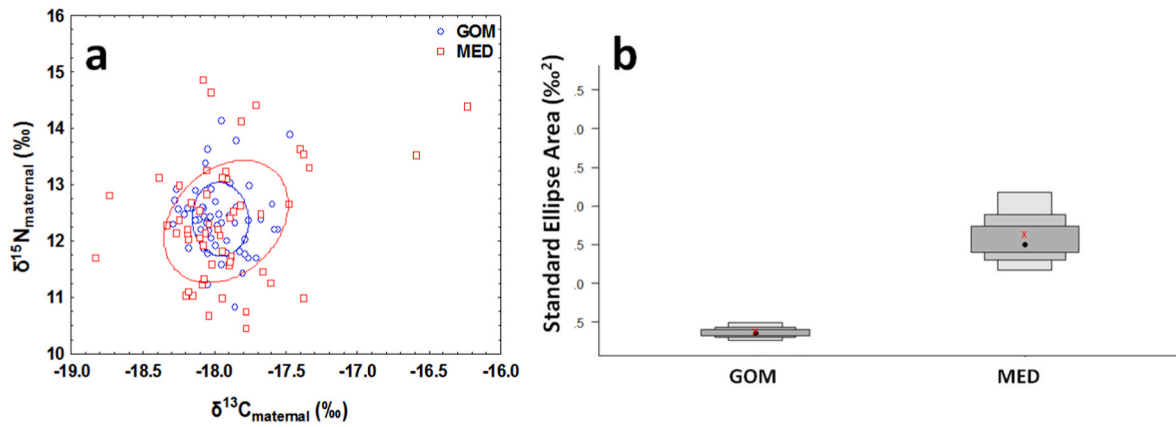
Table 7

Summary of Mann-Whitney *U* test (mean ± SE, number of larvae, Z adjusted and p) within each area (GOM and MED) in the four groups established from the residuals of length and weight related to age for maternal isotopic signatures (δ^{15}N$_{maternal}$, δ^{13}C$_{maternal}$) estimated by equations based on aquaculture (AQU estimated) and field (WILD estimated) samples. *p < 0.05; **p < 0.01; MS: marginally significant; NS: no significant differences.

	GOM + vs. GOM –						MED + vs. MED –					
	GOM +		GOM –		MW - *U* test		MED +		MED –		MW - *U* test	
	Mean ± SE	n	Mean ± SE	n	Z adjusted	p	Mean ± SE	n	Mean ± SE	n	Z adjusted	p
δ^{15}N$_{maternal}$ (AQU $_{estimated}$)	8.97 ± 0.18	26	9.90 ± 0.23	16	2.771	**	9.62 ± 0.50	20	11.57 ± 0.50	20	2.461	*
δ^{13}C$_{maternal}$ (AQU $_{estimated}$)	−21.33 ± 0.12	26	−21.62 ± 0.15	16	−1.321	NS	−21.71 ± 0.38	20	−21.84 ± 0.38	20	0.216	NS
δ^{15}N$_{maternal}$ (WILD $_{estimated}$)	12.27 ± 0.12	26	12.77 ± 0.15	16	1.942	MS (0.053)	11.53 ± 0.18	20	13.11 ± 0.18	20	4.571	**
δ^{13}C$_{maternal}$ (WILD $_{estimated}$)	−17.97 ± 0.04	26	−17.96 ± 0.05	16	0.00	NS	−17.97 ± 0.10	20	−17.82 ± 0.10	20	0.460	NS

Fig. 4. a) $\delta^{13}C$ vs $\delta^{15}N$ biplot of estimated maternal niches for the GOM and MED estimated by models based on wild collected samples. b) Standard ellipse area estimated as maternal trophic niche width by SIBER (Stable Isotope Bayesian Ellipses in R) analysis. The dark, intermediate and light grey boxes are the 50%, 75% and 95% credibility intervals, respectively. The red symbol (x) is the standard ellipse area calculated using correction for small sample size (SEAc).

Table 8
Standard ellipse area (SEAc) estimated as maternal trophic niche width by SIBER (Stable Isotope Bayesian Ellipses in R) analysis, overlapped area between maternal trophic niches and % of overlapped areas between maternal trophic niches corresponding to its size.

	SEAc	% SEAc Overlap	SEAc Overlap
GOM	0.378	100	0.378
MED	1.635	23.1	
GOM+	0.223	77.5	0.173
GOM-	0.590	29.3	
MED+	0.799	1.12	0.009
MED-	1.533	0.58	

This study's low $\delta^{15}N$ values for pre-flexion larval values vs. age for both populations (Fig. 2) agree with the results of a larval rearing experiment (Uriarte et al., 2016) and with different field studies (García et al., 2017; Laiz-Carrión et al., 2019) where higher $\delta^{15}N$ values of the earliest larval stages correspond to the maternal transmission of stable isotopes which gradually decline with larval ontogenic development.

The inter-population analysis revealed that faster growth relates to significantly lower $\delta^{15}N$ (GOM, Table 3). Moreover, based on our intra-population growth approach (optimal vs deficient), larval populations showed differences in the linear relationships of $\delta^{15}N$ values vs. age in the different GOM, MED and AQU groups (Fig. 3 a-c). Optimal growing larvae always showed significantly lower $\delta^{15}N$ values (Table 4 and 5).

Several authors have determined that stable isotopes values are influenced by growth (Suzuki et al., 2005; Watanabe et al., 2005) and that there is a close relationship between feeding behavior determined by SIA and growth potential in early life stages (Laiz-Carrión et al., 2011, 2013; Quintanilla et al., 2015, 2020). Thus, we can infer from this study that both the intra- and interpopulation comparison showed that faster growing larvae had significantly lower $\delta^{15}N$.

Maternal effect regulates various traits of offspring (Moore et al., 2019) strongly reducing the risk of predation/starvation, and by lowering the negative effects of adverse environmental by increasing the rate of development (Marshall et al., 2008). Maternal contribution to growth during the earliest life stages can vary depending of the age structure of a breeding population and the quality of the food consumed before reproduction. The maternal diet prior to spawning affects reproductive traits, such as the gonadosomatic index (Belgrad and Griffen 2016), as well, as size at hatch (Marshall et al., 2008; Reznick and Yang 1993) and in particular, the biochemical composition of eggs (Yoshida et al., 2011; Schlotz et al., 2013). Therefore, to understand why lower values of $\delta^{15}N$ in pre-flexion larvae can enhance growth, three possible hypothesis can be laid out.

1. *Age of breeders:* $\delta^{15}N$ increases with age in ABFT (Sará and Sará 2007) whereby indicating that larger/older mothers provide their offspring with a greater degree of growth potential in pre-flexion stages (Sakai and Harada 2001). Moreover, these older females are also more
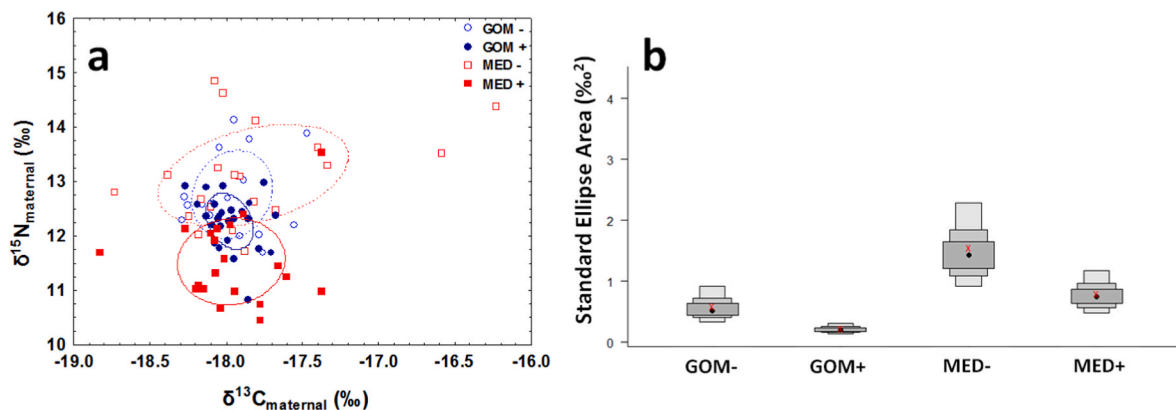

Fig. 5. a) $\delta^{13}C$ vs $\delta^{15}N$ biplot of estimated maternal niches for four groups: GOM+ (solid blue), GOM- (dashed blue), MED + (solid red), MED- (dashed red) from wild collected samples. b) Standard ellipse area estimated as maternal trophic niche width by SIBER (Stable Isotope Bayesian Ellipses in R) analysis. The dark, intermediate and light grey boxes are the 50%, 75% and 95% credibility intervals, respectively. The red symbol (x) is the standard ellipse area calculated using correction for small sample size (SEAc).

fecund (McGinley et al., 1987). However, Ohshimo et al. (2018b) observed that younger PBT females had greater spawning batch frequency and batch fecundity in comparison to older females. In this sense, Marshall et al. (2010) suggests that there is little theoretical justification or evidence that older mothers produce offspring with higher per capita fitness than younger mothers.

2. *Nutritional status of the breeders:* starvation increases the ratios of $\delta^{15}N$ (Doi et al., 2017; Varela et al., 2017) leading to preferentially expel the lighter isotope of N (^{14}N) in comparison to its heavier (^{15}N) that if not compensated by trophic consumption would increase $^{15}N/^{14}N$ ratios. This hypothesis could explain how lower ^{15}N ratios are related to likely better nutritional condition of females and consequently enhance growth in pre-flexion stages. Bluefin tunas are highly migratory species and have a capital breeding strategy (Laiz-Carrión et al., 2019). Thus, the probability of undergoing starvation during migration can influence the nutritional status of breeders leading to body reserve depletion via intensification of catabolic activity that cause ^{15}N enrichment. (Fleming et al., 2018; Hammerschlag et al., 2018).

3. *Quality variance among/within batches*: the high variability and unpredictability of egg quality depends on several factors, such as the timing of the spawning cycle, genetic factors and intrinsic properties of the egg itself (Ienaga et al., 2021). Some small pelagic species as anchovy (*Engraulis encrasicolus*) and sardinella (*Sardinella aurita*) spawn larger eggs during the beginning of the spawning season and gradually decline in size as the spawning season wanes (Mandic and Regner, 2014). Also, eggs spawned at the beginning of the spawning period have a higher concentration of protein which influences the acceleration of development (Riveiro et al., 2000). In tuna species, experimental rearing in captivity showed that the diameter of fertilized eggs from the broodstock has a negative relationship with onset of the spawning season (Tanaka et al., 2017). A similar experiment in captive ABFT (Bridges et al., 2020) demonstrated that strong variability between batches occur during the same spawning season. Arnold et al. (2017) found that offspring provisioning is a function of both maternal age and the timing of offspring release, with older perch (*Sebastes alutus*) females exhibiting increased provisioning over younger females throughout the spawning season despite an overall decrease in provisioning across all maternal ages as the season progressed. These results indicate great variation in offspring viability resulting from different spawned batches during the same spawning season. Furthermore, individual variability originating from one batch cannot be disregarded (Bobe 2015), as not all the eggs spawned have the same survival outcome.

4.2. Maternal influence validation

The larval rearing experiment confirmed that faster-growing larvae showed lower $\delta^{15}N$ inherited from spontaneous spawning of captive mothers (Fig. 3 c; Table 5) confirming the reliability of the pattern observed from the field samples. Moreover, this approach would eliminate sources errors as age assignment from microstructure analysis interpretation and different broodstock ambient conditions prior to reproduction. In this sense, $\delta^{13}C$ differences observed for AQU+ and AQU- (Table 5) cannot be attributed to external feeding factors, but should be more related with internal physiological or genetical conditions.

Maternal signatures estimations were calculated applying the model of Uriarte et al. (2016) based on age and using eggs and lecitotrophic larvae. Two complementary methods were applied: first, we obtained the equations from the experimental rearing data to apply them of the field collected larvae (AQU, Table 1). On the other hand, we were able to obtain the equations of isotopic values with age in our field-collected larvae, and thus, elaborate a specific model for each larval population (GOM and MED, Table 1). These estimates have the inconvenience of using eggs of the experimental rearing for the field-collected larval

populations, since collecting and determining ABFT tuna eggs in the wild is hardly feasible.

Through aquaculture-derived equations, $\delta^{15}N_{maternal}$ values were notably lower while the estimates of $\delta^{13}C_{maternal}$ presented more negative and wider ranges of values than the estimates derived from the field larvae (Table 6). Contrastingly, the same maternal estimates from field-derived equations were comparable to other studies applying SIA from muscle of adult ABFT (Sará and Sará 2007; Logan et al., 2011; Butler et al., 2015; Sorell et al., 2017; Varela et al. 2018, 2020) for both maternal $\delta^{15}N$ and $\delta^{13}C$. Thus, it further corroborates the validity of using field-collected larvae for maternal estimates of the $\delta^{15}N$ and $\delta^{13}C$. The differences between both methodological approaches can be originated from the prey's isotopic signatures for aquaculture adults which were artificially fed in comparison to the natural food sources of the two marine ecosystems (Planas et al., 2020) contrasted in this study. Therefore, we found that equations from field-collected larvae are more precise and biologically more realistic, and we conclude that they appropriately estimate maternal trophodynamics using the trophic niches' approach (Table 6).

Considering the residual groups, optimal growth groups showed lower values of $\delta^{15}N_{maternal}$ estimations for both populations (Table 7) that could be attributed to maternal diet differences or distinct feeding behavior among breeders within each population.

4.3. Maternal isotopic niche comparison

ABFT is an opportunistic and generalist predator (Varela et al. 2011, 2014, 2018, 2020; Logan et al., 2011; Butler et al., 2015; Sorell et al., 2017) that feeds on a wide range of available prey ranging from fishes, cephalopods, and crustaceans (Karakulak et al., 2009; Battaglia et al., 2013; Olafsdottir et al., 2016). Diet is affected by distinctive ecosystem food resources, and feeding grounds, For ABFT, these factors influence spatial and/or temporal changes affecting prey distribution and availability of different prey sizes. A comparison between ABFT diets of eastern and western YOY ABFT showed variability in consumed prey from each region dependent on the temporal availability, as anchovy, where diet shifts may be found between spatial and temporal feeding grounds (Logan et al., 2011). The maternal isotopic niches can be interpreted as trophic niches representing the trophic sources of mothers allowing to infer on diet differences and to provide of quantitative insight as niche width and overlap by examining their comparative trophic ecology under an inter- and intra-population standpoint.

The eastern stocks mainly feed in the MED and northeastern Atlantic waters (ICCAT 2019), while the western stock principally feeds off the New England's continental shelf (Chase 2002; Rooker et al., 2007; Logan et al., 2011; Varela et al., 2020). ABFT populations mix extensively outside of the spawning season and form large feeding aggregations in the western Atlantic Ocean, particularly in the waters of the Mid-Atlantic Bright, New England and Atlantic Canada (Rooker et al., 2008; Galuardi et al., 2010; Wilson et al., 2011). In any of these cases, the feeding ground's isotopic characteristics of the breeder's diet should be represented in their larvae via maternal transmission. The GOM and MED larval populations analyzed (Fig. 1a) had overlapping trophic niches between them (Table 8), which may be interpreted as breeders having similar trophic niches. Although our results do not necessarily indicate geographical coincidence of these trophic niches, it seems to fulfill the common feeding grounds hypothesis or, that at least, breeders of both stocks feed on preys with similar isotopic signatures.

If we consider the common feeding grounds hypothesis, higher $\delta^{15}N$ values in larvae from MED population (Fig. 2, Table 3) could be explained by the longer migrations distances covered by the breeders from the feeding grounds to the spawning areas. The energetic cost associated to this migration would reduce the availability of resources to invest in reproductive processes in comparison with GOM breeders and, hence, originating lower growth pre-flexion larvae of the MED larvae (Table 3).

Despite the similarity among trophic niches among both populations, we found smaller trophic niche size areas for GOM larvae (Fig. 4 a & b, Table 8) which may be related to females feeding in a different (potentially more productive) ecosystem in comparison to MED larvae. The size of the niche space is inherently plastic and changes in response to available food sources (Lesser et al., 2020) and should vary along gradients associated with the productivity of an ecosystem (MacArthur and Pianka 1966, O'Farrel et al., 2014) as consumers must adapt their foraging strategy to meet their metabolic demand as productivity changes. At high levels of productivity, mean niche size would decline as more individuals with similar specialized niche range can thrive. Increased reliance on fewer resources becomes a viable strategy at high productivity due to greater overall resource. On the other hand, as ecosystem productivity declines, resource production is not sufficient to support strategies focused on few resources. Thus, strategies that incorporate resources over a range of channels are favored, and niche sizes tend to increase (Lesser et al., 2020). In this context, GOM would represent a more productive habitat that allow predators to meet energy requirements by selectively feeding (stenophagous feeding behavior) on a lesser number of prey species (MacArthur and Pianka 1966) in a narrower trophic niche. In contrast, MED would represent a more oligotrophic habitat that lead predators to search food sources over larger areas contributing to a more diverse diet and a larger maternal trophic niche (Fig. 4 a & b, Table 8) associated to a more euryphagous feeding behavior.

Although the trophic niche of the GOM population was smaller, this result does not imply a direct relationship between range and size of maternal niche with larval growth. To test this hypothesis, the results from the intra-population approach indicate a similar pattern, where greater larval growth was observed when maternal niches were smaller and less disperse (Fig. 5 a & b, Table 8). Maternal diet is a major contributor towards chemical composition of eggs (Yoshida et al., 2011; Schlotz et al., 2013) and the fact that individual variation in diet within a population is common (Bolnick et al., 2002; Griffen 2014) may lead to intraspecific variations in egg size and offspring reserves, that will directly affect larval growth. This reasoning implies that pre-flexion larval faster growth is associated to stenophagous feeding behavior and, therefore, a direct relationship between larval growth potential and foraging strategy by breeders in both populations of ABFT.

The availability of trophic resources also influences the segregation or overlap of the trophic niches of the breeders within each population. In this sense, the smaller maternal niches found in the GOM would imply a higher overlap between their residual groups associated with a more productive habitats. On the other hand, larger maternal niches in the MED would represent higher oligotrophic areas where overlap would be lower between contrasting groups of breeders. Higher overlap (%) corresponds to groups with smaller maternal trophic niches in every comparison considered, precisely due to their smaller sizes (Table 8).

5. Conclusions

Our study documents the presence of maternal effect on larval growth in a long distance migratory teleost. This study shows the advantages that larval SIA research can aid in the understanding of the trophodynamics of their breeders by examining the trophic relationship of a spawning stock jointly with the development of growth potential in offspring within the same breeding season. As early growth patterns are strongly linked to survival, this approach can undoubtedly help understand recruitment variability in the light of trophic variations. However, regarding the paradox of maternal effects on larval growth via isotopic signatures, we can assert that:

1. There is direct relationship between the development of growth potential and $\delta^{15}N$ signatures for ABFT during the pre-flexion stages, where larger and heavier larvae show significantly lower $\delta^{15}N$ values

both from field population comparisons (GOM and MED) as well as from aquaculture reared specimens.
2. We estimated maternal ABFT isotopic signatures using the isotopic signatures of size at age of pre-flexion larvae. The estimated values are consistent with previous SIA studies that also utilized muscle tissue of adult females, and furthermore on the size and extent of adult trophic niche.
3. The inter- and intra-population analysis of the maternal trophic niches warrants us to infer on the feeding behaviour of adult females by determining isotopic changes where stenophagous feeding habits have narrower trophic niches that yield optimal growth in comparison to euryphagous feeding behaviour.

Author statement

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Estrella Malca: Methodology, Formal analysis, Investigation, Resources, Writing - Original Draft, Writing - Review & Editing, Visualization.

John Lamkin: Writing - Review & Editing, Project administrator, Funding acquisition.

Alberto García: Conceptualization, Writing - Original Draft, Writing - Review & Editing.

Raúl Laiz-Carrión: Conceptualization, Formal analysis, Investigation, Writing - Review & Editing, Visualization. Supervision, Project administrator, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

I have sahed my data on a DRYAD folder: https://doi.org/10.5061/dryad.ns1rn8pzg

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