

1 **Original research paper**

2 Sub-annual cohort representation among young-of-the-year recruits of the western stock of
3 Atlantic bluefin tuna

4 Kohma Arai^{1*}, John E. Graves², David H. Secor¹

5 ¹Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science,
6 Solomons, MD 20688, USA

7 ²Virginia Institute of Marine Science, William & Mary, P.O. Box 1346, Gloucester Point, VA
8 23062, USA

9

10 *Corresponding author

11 Kohma Arai

12 Email: karai@umces.edu

13

14 E-mail addresses:

15 John E. Graves: graves@vims.edu

16 David H. Secor: secor@umces.edu

17

18 **Abstract**

19 The western stock of Atlantic bluefin tuna receives recruits principally from spawning habitats in
20 the Gulf of Mexico although the recent discovery of bluefin tuna larvae in the western North
21 Atlantic Slope Sea calls into question whether there is another key source of recruits to the
22 western stock. We tested whether age-0 juveniles occurring in the US Mid-Atlantic Bight during
23 the late summer might originate from Slope Sea spawning by estimating the hatch date
24 distribution based on otolith microstructural analysis given larval production occurs
25 approximately two months later in the Slope Sea (late June to early August) than in the Gulf of
26 Mexico (early April to mid-June). Following a review of the literature on ageing methodology
27 for Thunnini species, we attempted trials on both sectioned and whole un-sectioned otoliths, and
28 adopted the latter based on higher precision levels. Estimated ages ranged from 122 to 175 (days
29 post hatch) for fish ranging 23.2 to 36.3 cm fork length. Hatch dates ranged 20 March to 12 May
30 2010, exhibiting a unimodal distribution. Hatch dates mainly occurred in early-April 2010,
31 which corresponded to the spawning and larval production period for the Gulf of Mexico.
32 Estimated growth rate (size-at-age) was 1.1 mm d⁻¹. Thus, we failed to observe evidence for
33 recruitment from the newfound Slope Sea spawning region, albeit our sample represents only a
34 single year and region. More conclusive inferences on recruitment from the Slope Sea spawning

35 will depend on a greater sample of age-0 juveniles sampled across years or molecular approaches
36 that can identify recruits in older juveniles and adults.

37

38 **Key words**

39 Atlantic bluefin tuna, hatch date analysis, otolith microstructure, pulsed recruitment, growth

40

41 **1. Introduction**

42 Pulsed production of sub-annual cohorts, which can result from protracted spawning or from
43 different spawning components, is a common attribute for marine fishes, including Atlantic
44 herring, Pacific salmon, Atlantic sturgeon, and bluefish (Harden Jones, 1968; Balazik and
45 Musick, 2015; Callihan et al., 2008). Intra-annual cohorts that are split at multiple
46 spatio-temporal scales dampens overall recruitment variability by encountering different
47 environmental conditions and spreading the risk of poor survival (Secor, 2007).

48 Temporally and spatially segregated spawning was recently reported for the western stock
49 of Atlantic bluefin tuna (*Thunnus thynnus*; ABFT) (Richardson et al., 2016), a valuable species
50 harvested throughout the North Atlantic and marketed and consumed around the globe
51 (Fromentin and Powers, 2005). ABFT is currently managed by the member nations of the
52 International Commission for the Conservation of Atlantic Tunas (ICCAT) as two distinct stocks:
53 the eastern stock that spawns in the Mediterranean Sea, and the western stock that spawns
54 primarily in the Gulf of Mexico. The current assessment models assume no mixing of the two
55 stocks that are spatially divided with the 45° W international management boundary (SCRS,
56 2017); however, studies using conventional (Fromentin, 2001) and electronic tagging (Block et
57 al., 2005), organochlorine pollutants (Dickhut et al., 2009; Graves et al., 2015), and otolith
58 chemistry (Rooker et al., 2008, 2014) have suggested extensive trans-Atlantic migration across

59 the 45° W management boundary, with the eastern stock significantly contributing to the US
60 ABFT fishery in some years (Siskey et al., 2016).

61 The discovery of ABFT larvae in the Northwest Atlantic Slope Sea (the region between the
62 Gulf Stream and the northeast US continental shelf; Csanady and Hamilton, 1988; Fig. 1) during
63 summer 2013 (Richardson et al., 2016) challenged a long-held premise that spawning by the
64 western stock occurred only in the Gulf of Mexico and northwestern Caribbean Sea (Rooker et
65 al., 2007). The collection of larvae in the Slope Sea demonstrated that larval production occurred
66 outside the Gulf of Mexico, but population-level implications of these findings depend upon the
67 magnitude of recruitment from this newly discovered spawning region. Consequently, Walter et
68 al. (2016) emphasized the need for additional research to further confirm the importance of the
69 Slope Sea to the population.

70 Hatch date estimation based on otolith microstructural analysis has been used widely to
71 identify the presence of sub-annual cohorts in marine fishes (Limburg, 2002). Hatch dates are
72 estimated through daily age determination, and the presence of multiple cohorts is characterized
73 by a multi-modal pattern in the hatch date distributions. Hatch date analysis is also a powerful
74 tool to identify different natal regions of cohorts when the spawning periods among regions are
75 discrete, and the cohorts subsequently mix in the sampling region (Callihan et al., 2008). Hatch
76 date analysis is based on a key assumption that otolith micro-increments are deposited at daily

77 intervals. While formal daily age validation is currently lacking for ABFT, daily deposition of
78 micro-increments has been suggested for this species (Brothers et. al., 1983; Radtke, 1984).
79 Laboratory rearing and oxytetracycline hydrochloride (OTC)-marking experiments for the
80 congeneric Pacific bluefin tuna (*Thunnus orientalis*) larvae and juveniles (Foreman, 1996; Itoh et
81 al., 2000), as well as marginal increment analysis of southern bluefin tuna (*Thunnus maccoyii*)
82 larvae (Jenkins and Davis, 1990) have confirmed daily formation of micro-increments, further
83 supporting the assumption that micro-increments of ABFT are deposited at a daily basis.

84 Atlantic bluefin tuna larvae in the Slope Sea were collected between late-June to
85 early-August (Richardson et al., 2016). This is approximately two months later than the larval
86 collection period in the Gulf of Mexico, where decades of ichthyoplankton survey demonstrate
87 high incidence of larvae to occur between late-April to late-May (Muhling et al., 2010). The
88 small size (≤ 3.0 mm standard length) and young age (≤ 6 days post hatch) of Slope Sea-collected
89 larvae, together with oceanographic studies based on satellite-tracked drifters, provide further
90 support that larvae collected in the Slope Sea were not advected individuals spawned in the Gulf
91 of Mexico (Richardson et al., 2016). Electronic tagging studies have indicated adult ABFT
92 exiting the breeding grounds in the Gulf of Mexico by the end of June (Block et al., 2005; Teo et
93 al., 2007; Wilson et al., 2015), with peak utilization of the region occurring from April to May
94 (Wilson et al., 2015). Temporally discrete spawning between the Gulf of Mexico and Slope Sea

95 is further supported by the temperature regimes of the two regions in respect to the thermal
96 preference of larval bluefin tuna. Peak larval collection in the Gulf of Mexico occurs at sea
97 surface temperature between 25 and 28°C (Muhling et al., 2010). This optimal thermal range for
98 ABFT larvae occurs between early April to mid-June in the Gulf of Mexico, but only occurs in
99 the Slope Sea region between late June to early August (Richardson et al., 2016). Hatch date
100 distributions between the Gulf of Mexico and the Slope Sea should therefore be discrete. While
101 historical annual catch-at-size data from the North American purse seine fishery (1970–1976)
102 showed no apparent bimodal pattern within the length distribution of age 1 fish (Restrepo et al.,
103 2010), hatch date analysis could be a powerful tool to identify the presence of sub-annual cohorts
104 in the western stock of ABFT.

105 We evaluated whether pulsed recruitment might be evident for a sample of age-0 juvenile
106 ABFT collected from a principal nursery area, near-shelf waters of the US Mid-Atlantic Bight.
107 We evaluated whether hatch date distributions of age-0 juveniles represented those expected
108 from natal origins from the Gulf of Mexico, Slope Sea, or both regions. Because otoliths of age-0
109 western ABFT have rarely been examined for daily increments, we undertook a literature review
110 of approaches used to age juvenile Thunnini species to inform the selection of a feasible
111 methodology for otolith microstructure analysis. Recreational and commercial fishers only rarely

112 encounter age-0 juveniles, but in 2010 sufficient samples (25 fish) were collected to test for
113 discrete hatch date distributions. Growth rate was also estimated from size-at-age for this sample.

114

115 **2. Materials and methods**

116 *2.1 Sample collection*

117 A total of 25 age-0 Atlantic bluefin tuna were collected approximately 100 km off Virginia Beach,
118 VA on 30 August and 11 September 2010 using hook and line under an Exempted Fishing Permit
119 (Fig. 1). Collected samples were frozen until later dissection in the laboratory. Fork lengths (FL)
120 were measured to the nearest 1 mm, and sagittal otoliths were extracted.

121

122 *2.2 Literature review on otolith microstructural analysis*

123 A literature review reporting techniques for observing daily increments in otolith structure of
124 *Thunnus* and *Katsuwonus* species was undertaken using Google Scholar. Three query terms,
125 “tuna”, “age”, and “otolith”, were used in the search procedure, with no restriction on the publish
126 date. The coefficient of variation (CV) was compared between studies to evaluate the precision
127 of different ageing techniques. Where average percent error was reported, conversion to CV
128 followed the regression equation reported by Campana (2001). A total of 44 studies undertaking
129 otolith microstructural analysis on *Thunnus* and *Katsuwonus* species were identified (Table 1).

130 Studies comprised investigations of all eight species of *Thunnus* and the one species of
131 *Katsuwonus*, with most studies focusing on yellowfin (*Thunnus albacares*; $n = 14$), skipjack
132 (*Katsuwonus pelamis*; $n = 11$), and bigeye (*Thunnus obesus*; $n = 8$) tunas. A total of 12 studies
133 focused on the three bluefin tuna species including five studies each on Atlantic bluefin tuna (*T.*
134 *thynnus*) and Pacific bluefin tuna (*T. orientalis*), and two on southern bluefin tuna (*T. maccoyii*).
135 The majority of studies analyzed a broad size range of individuals, rather than focusing
136 exclusively on the juvenile stage. Transverse sectioning was the most common method used to
137 expose otolith daily increments for tuna species. However, for the three bluefin tuna species,
138 daily increments were frequently observed through whole un-sectioned otoliths (Fig. 2a).
139 Chemical treatment (i.e., EDTA and HCL etching, and oil immersion) were often applied to both
140 sectioned and un-sectioned whole otoliths to facilitate the observation of daily increments (Table
141 1).

142 Comparison of CV among preparation methods indicated highest precision (i.e., lowest
143 CV) for whole un-sectioned otoliths, with the transverse section providing the lowest precision
144 (i.e., highest CV) among the three observation techniques (Fig. 2b). On the basis of the literature
145 review and initial comparisons between sectioned and whole un-sectioned otoliths, we opted for
146 the latter approach.

147

148 *2.3 Otolith microstructural analysis*

149 Otoliths were placed in immersion oil to improve readability of daily increments, and digital
150 images were taken under a compound microscope at high magnification ($\times 200$) using
151 transmitted light. The number of discontinuous zones (Secor et al., 1991) that appears dark under
152 transmitted light were counted as daily increments. Images were captured using an Olympus
153 Camedia C-5050 digital camera (5 megapixel resolution). A single blind daily ring count (i.e., no
154 prior information on fork length [FL] and collection date of fish) was made from the core to the
155 post-rostrum in the lateral face of the otolith by an experienced principal reader using annotated
156 micrographs from Adobe Photoshop CS2 Version 9.0 (Fig. 3). An additional count was
157 conducted by a second reader to evaluate the consistency of daily increment counts. Both readers
158 had received training prior to the exercise and were experienced in reading daily increments in
159 otolith structure of *Thunnus* species. Ageing error can affect both accuracy and precision, where
160 accuracy represents the closeness to the true age, and precision measures the reproducibility of
161 repeated age counts (Kalish et al., 1995). While none of the age interpretations of age-0 juvenile
162 ABFT was validated, we assumed that micro-increments are deposited at a daily basis, and
163 considered our ageing method to be accurate given previous studies for congeneric Pacific and
164 southern bluefin tuna have confirmed daily formation of micro-increments (Jenkins and Davis,
165 1990; Foreman, 1996; Itoh et al., 2000). Systematic difference in matched pairs of ages between

166 the two readers was evaluated using a paired *t*-test and was graphically assessed by producing
167 age-bias plots (Campana et al., 1995). Precision between the two readers was measured as the
168 mean coefficient of variation (CV) following the method by Chang (1982).

169

170 *2.4 Data analysis*

171 Estimated age was obtained by adding 4 days to the raw increment count assuming the first
172 increment is deposited 4 days after hatching as has been observed for Pacific bluefin tuna (Itoh et
173 al., 2000). Hatch date distributions were determined by subtracting estimated ages from the
174 collection date. Because we were principally concerned about the presence of certain hatch date
175 intervals rather than their relative representation, we did not correct hatch dates for cumulative
176 mortality effects (Callihan et al., 2008). Mean growth rate of juveniles within a given size stanza
177 was estimated by fitting a linear regression of FL against age by ordinary least squares
178 minimization. A size-at-estimated age relationship was obtained from 24 individuals since the FL
179 information was not available for one individual.

180

181 **3. Results**

182 *3.1 Ageing bias and precision*

183 Micro-increment count estimates from the two readers, in general, followed the identity line (i.e.,

184 replicate estimated ages are equal) in the age-bias plot, although reader 1 produced higher counts
185 on average (Fig. 4). Application of the paired *t*-test suggested significant differences in matched
186 pairs of ages between the two readers ($p < 0.05$). Ageing precision between the two readers
187 measured in the form of CV was 4.0%, indicating moderately high precision in comparison to
188 reported values (Campana, 2001).

189

190 *3.2 Hatch date estimation*

191 Estimated ages ranged between 122 and 175 days post hatch (mean \pm SD = 152 \pm 12 days) for
192 juvenile bluefin tuna ranging from 23.2 to 36.3 cm FL (mean \pm SD = 28.9 \pm 3.5 cm). A positive
193 relationship, although not statistically significant, was observed between fork length and
194 estimated age ($r = 0.39$; $p = 0.057$), with large positive residuals occurring for large individuals
195 (FL > 33 cm). The relationship was described by the following equation:

$$196 \quad FL \text{ (cm)} = 11.97 + 0.11 \text{ Age (days)}$$

197 The linear slope of size-at-estimated age indicated a growth rate of 1.1 mm d⁻¹ for this size
198 stanza (Fig. 5).

199 Estimated hatch dates ranged from 20 March to 12 May 2010, with the majority occurring
200 in early-April 2010 (Fig. 6). No apparent multi-modal pattern was observed in the hatch date
201 distribution, and collection dates (i.e., 30 August and 11 September) were not associated with

202 estimated hatch dates. The larval collection period in the Slope Sea which occurred late-June to
203 early-August (Richardson et al. 2016) fell out of the range of the mean and 95% confidence
204 intervals for the estimated hatch dates (Fig. S1).

205

206 **4. Discussion**

207 We employed hatch date estimation based on otolith microstructural analysis to evaluate whether
208 young-of-the-year Atlantic bluefin tuna recruiting to the US Mid-Atlantic Bight might originate
209 from the newfound Slope Sea spawning region. Estimated hatch dates for age-0 juveniles
210 collected off Virginia Beach in 2010 ranged from 20 March to 12 May, with majority of hatch
211 dates occurring in early-April. These hatch dates overlap with periods in the Gulf of Mexico
212 when the optimal thermal range for ABFT larvae (SST of 25–28°C; Muhling et al., 2010) occur
213 between early April to mid-June (Richardson et al., 2016), as well as with periods when peak
214 utilization by adults occur in this region during April to May (Wilson et al., 2015). While using
215 counts from reader 2 would better match the expected larval production period in the Gulf of
216 Mexico, we have no reason to reject the alternative that hatch dates may reflect differential
217 survival or representation in our age-0 sample. Recruitment from the recently reported spawning
218 of ABFT in the Slope Sea region to the Virginia Beach juvenile sample was not evident given the
219 expectation of late-June to early-August hatch date for that region (Richardson et al., 2016).

220 A key assumption to the hatch date analysis is that otolith micro-increments are deposited
221 daily, which is supported for congeneric Pacific and southern bluefin tuna larvae and juveniles
222 (Jenkins and Davis, 1990; Foreman, 1996; Itoh et al., 2000). While some systematic differences
223 occurred between matched pairs of age estimates between the two readers, age differences were
224 within 20 d for all samples analyzed. The two-month difference in the larval production period
225 between the two observed spawning regions (i.e., Gulf of Mexico and Slope Sea), together with
226 high ageing precision (CV = 4.0%) indicate that the conclusions derived from this study are
227 robust to ageing bias.

228 Given past emphasis on sectioning techniques in the analysis of daily micro-increments
229 (Secor et al., 1991; Campana, 1992), we expected that such methods would be best applied to
230 scombrids yet observed in our own trials and in the literature, that whole otolith observations
231 resulted in comparable or better precision levels. Bluefin tuna otoliths are likely unusual in their
232 early growth, which occurs along three primary axes, which could contribute to less growth
233 overburden on early formed increments along certain axes as we observed in this study (Fig. 3).

234 Hatch date estimation provided no evidence of pulsed recruitment for juveniles collected in
235 a principal nursery area in the US Mid-Atlantic Bight. It is likely that these age-0 juveniles
236 migrated northward from the Gulf of Mexico through initial larval transport via the Loop Current
237 and larval and juvenile movement along the Gulf Stream to the nursery ground off Virginia

238 Beach (Mather et al., 1995; Muhling et al., 2017). Because young-of-the-year bluefin tuna are
239 rarely encountered by recreational and commercial fishers, both the collection site and sampling
240 period were restricted in this study. Given that ABFT juveniles utilize a wide range of habitat
241 across temperate latitudes off the US coast in summer (Galuardi and Lutcavage, 2012; Druon et
242 al., 2016), Slope Sea spawned individuals could be recruiting to other nursery regions, although
243 the sampling site off Virginia Beach is in much closer proximity with the Slope Sea spawning
244 region relative to the Gulf of Mexico.

245 Few studies have examined the growth rate of juvenile ABFT given the difficulties in
246 sampling and ageing (Brothers et al., 1983; La Mesa et al., 2005; Megalofonou, 2006). The
247 age-length relationship in this study supported a mean growth rate of 1.1 mm d^{-1} within the size
248 stanza for juveniles collected in the Mid-Atlantic Bight in 2010. The estimated growth rate for
249 YOY ABFT off Virginia Beach was similar, albeit slightly lower, than values reported in the
250 literature for this species, with the exception of Megalofonau (2006), who indicated a growth rate
251 of 4.7 mm d^{-1} for fish collected in the Mediterranean Sea (Fig. 7). The inconsistency could be
252 due to the wider distribution of sizes that Megalofonau (2006) analyzed, which included either
253 very small ($<20 \text{ cm FL}$) or large ($>35 \text{ cm FL}$) juveniles. Variation in growth rates could also be
254 due to the difference in the sampling period, where strong interannual variation in growth was
255 observed for ABFT larvae sampled in the Mediterranean (García et al., 2013). Juvenile growth

256 rates of ABFT would be important to assess to inform important early survival bottlenecks
257 (age-length keys and hatch date analysis), and regional differences in nursery production (growth
258 rate comparison between nursery habitats), as differences in early growth rates among the two
259 spawning regions has been reported for Pacific bluefin tuna (Watai et al., 2018; Ishihara et al.,
260 2019).

261 While formal daily age validation is still lacking for ABFT, this study provides
262 methodology for identifying the hatch date distribution and, by inference, the implied birth
263 locations for the western stock of Atlantic bluefin. Pulsed production of sub-annual cohorts that
264 result from multiple spawning components could possibly dampen overall recruitment variability
265 by “bet-hedging” against environmental stochasticity (Secor, 2007). Similarly, bet-hedging could
266 buffer the population against climatic changes predicted to alter the spawning suitability of the
267 Gulf of Mexico (Muhling et al., 2011, 2015). Through the analysis of electronic tagging data,
268 Richardson et al. (2016) suggested that the western stock could exhibit a size-structured
269 spawning migration, where larger fish spawn in the Gulf of Mexico and smaller fish spawn in the
270 Slope Sea, similar to the size-structured spawning partitioning that occurs for Pacific bluefin tuna
271 (Itoh, 2006; Shiao et al., 2017; Ohshimo et al., 2018). Given strong age truncation evident for the
272 western stock of the ABFT (Siskey et al., 2016), recruitment contribution from the Slope Sea
273 could be important should Richardson et al.’s speculation prove true.

274 A recent genetic study on larvae collected from the Slope Sea showed this small sample (n
275 = 7) comprised individuals of two stocks: four samples assigned to the Gulf of Mexico stock,
276 with two samples originating from the Mediterranean stock (one unassigned; Rodríguez-Ezpeleta
277 et al., 2019). Small sample size precludes strong inferences on whether larvae of the Slope Sea
278 are from mixed origins. As age-0 juveniles are only encountered fortuitously by anglers and have
279 not been the target of commercial fisheries, future efforts should focus on interacting with
280 anglers and charter vessel captains to collect a broad size range of age-0 samples across time and
281 space, as well as developing a genetic marker specific to recruits from the Slope Sea to answer
282 the question of the relative magnitude of recruitment from the Slope Sea compared to the Gulf of
283 Mexico, and to further uncover the complex spawning migration of Atlantic bluefin tuna.

284

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
565 IPTP, Colombo, Sri Lanka.

566

567 **Table 1** Summary of otolith microstructure analyses of *Thunnus* and *Katsuwonus* species.

568 Values in parentheses for fork length range indicate size range in the form of standard length

Species	Study region	Fork length range (cm)	Observation method	Chemical treatment	Reference
Atlantic bluefin	Northwest Atlantic	30.6–41.3	Other	Oil immersion	Brothers et al. 1983
		216–275	Transverse	Etching	Radtke 1984
	Mediterranean	34–53	Transverse	Etching	Radtke and Morales-Nin 1989
		19.5–40.0	Whole	Oil immersion	La Mesa et al. 2005
Pacific bluefin	Northwest Pacific	8.5–55.5	Transverse	No	Megalofonou 2006
		2.8	Whole	Etching	Itoh et al. 2000
		16.7–31.9	Whole	Etching	Tanaka et al. 2006
		10.8–28.0	Whole	Etching	Tanaka et al. 2007
		17–93 (2.4–24.8)	Whole Other	Etching No	Itoh 2009 Watai et al. 2017
Southern bluefin	West Australia	24.7–82.0	Whole	Etching	Itoh and Tsuji 1996
Yellowfin	Indian and South Australia	40–199	Transverse/Frontal	Etching	Williams et al. 2013
Yellowfin	Western central Pacific	7–93.0	Whole	Etching	Uchiyama and Struhsaker 1981
		25–40	Frontal	Etching/Oil immersion	Yamanaka 1990
		20–145	Transverse	No	Lehodey and Leroy 1999
		40–139	Transverse/Frontal	Etching	Williams et al. 2013
	Eastern Pacific	40–110	Whole	Etching	Wild and Foreman 1980
		30–170	Whole	Etching	Wild 1986
		40–148	Whole	Etching	Wild et al. 1995
	Indian	19–115	Transverse	Etching	Morize et al. 2008
		19–146.5	Transverse	Etching	Dortel et al. 2013
		66–165	Frontal	Etching	Shih et al. 2014
	Western Indian	47.9–135.4	Transverse	Etching	Sardenne et al. 2015
		28–154	Transverse	Etching	Stéquert et al. 1996
	Atlantic	5.2–179	Transverse	No	Shuford et al. 2007
	Northwest Atlantic	<68	Transverse	No	Lang et al. 2017
Bigeye	Western central Pacific	33.4–57.9	Whole	Etching	Matsumoto 1998
		25–157	Transverse	No	Lehodey et al. 1999

		50–179	Transverse/Frontal	Etching	Williams et al. 2013
	Indian	46–105.3	Transverse	Etching	Morize et al. 2008
		46–141.6	Transverse	Etching	Sardenne et al. 2015
	Western Indian	–	Transverse	No	Stéguert and Conand 2000
	Eastern Atlantic	29–190	Transverse	Etching	Hallier et al. 2005
	Australia	81–120	Transverse	Etching	Farley et al. 2006
Albacore	Western central Pacific	40–119	Transverse/Frontal	Etching	Williams et al. 2013
	Northeast Pacific	51–97	Whole	Oil immersion	Laurs et al. 1985
		50.5–79.6	Transverse	No	Renck et al. 2014
	South Pacific	45–49	Transverse	No	Leroy and Lehodey 2004
		43–56	Transverse	No	Farley et al. 2013
	North Pacific	55.5–61.5	Transverse	No	Wells et al. 2013
Blackfin	Northwest Atlantic	20–68	Transverse	Etching	Doray et al. 2004
Longtail	Central Indo-Pacific	23.8–62.2	Transverse	Oil immersion	Griffiths et al. 2010
Skipjack	Western central Pacific	3–80	Whole	Etching	Uchiyama and Struhsaker 1981
		30–61	Transverse	Etching	Leroy 2000
		(1.3–4.0)	Whole	No	Tanabe et al. 2003
		24.4–34.1	Whole	No	Kayama et al. 2007
		(11.4–54.8)	Whole	No	Ashida et al. 2018
	Eastern Pacific	42–64	Whole	Etching	Wild and Foreman 1980
		42–64	Whole	Etching	Wild et al. 1995
	Indian	48.0–56.6	Transverse	Etching	Adam et al. 1996
		48.5–60.2	Transverse	Etching	Sardenne et al. 2015
	East Indian	42.8–66.2	Whole	Etching	Kayama et al. 2004
		39.5–63.4	Whole	Etching	Kanaji et al. 2012

569

570

571 **Figure captions**

572 **Fig. 1** Map of the western Atlantic Ocean illustrating two known spawning regions for Atlantic
573 bluefin tuna in the Gulf of Mexico and the Slope Sea. The sampling region for young-of-the-year
574 juveniles off Virginia Beach is denoted with the *solid circle*

575

576 **Fig. 2** (a) Frequency of methods used to expose otolith daily increments for tuna species in a
577 total of 44 studies. Bars represent the frequency of whole un-sectioned observation, transverse
578 and frontal sectioning, and other observation techniques. (b) Comparison of CV between three
579 observation techniques. In the boxplots, *midlines* indicate median, *boxes* represent 0.25 and 0.75
580 quartiles, *whiskers* extend to $1.5\times$ of the interquartile range, and *solid circles* indicate outliers

581

582 **Fig. 3** Micrograph of a whole un-sectioned sagittal otolith of juvenile Atlantic bluefin tuna with
583 annotated daily increments (*solid circles*). Daily increment counts were made from the core to
584 the post-rostrum (*dashed arrow*)

585

586 **Fig. 4** Age-bias plot illustrating matched pairs of estimated ages between two readers.
587 Deviations from the identity line (*solid diagonal line*) indicates the degree of systematic
588 difference in matched pairs of age counts between the two readers

589

590 **Fig. 5** Size-at-estimated age relationship of 24 juvenile Atlantic bluefin tuna. The *solid line*
591 indicates the linear regression line fitted to the data

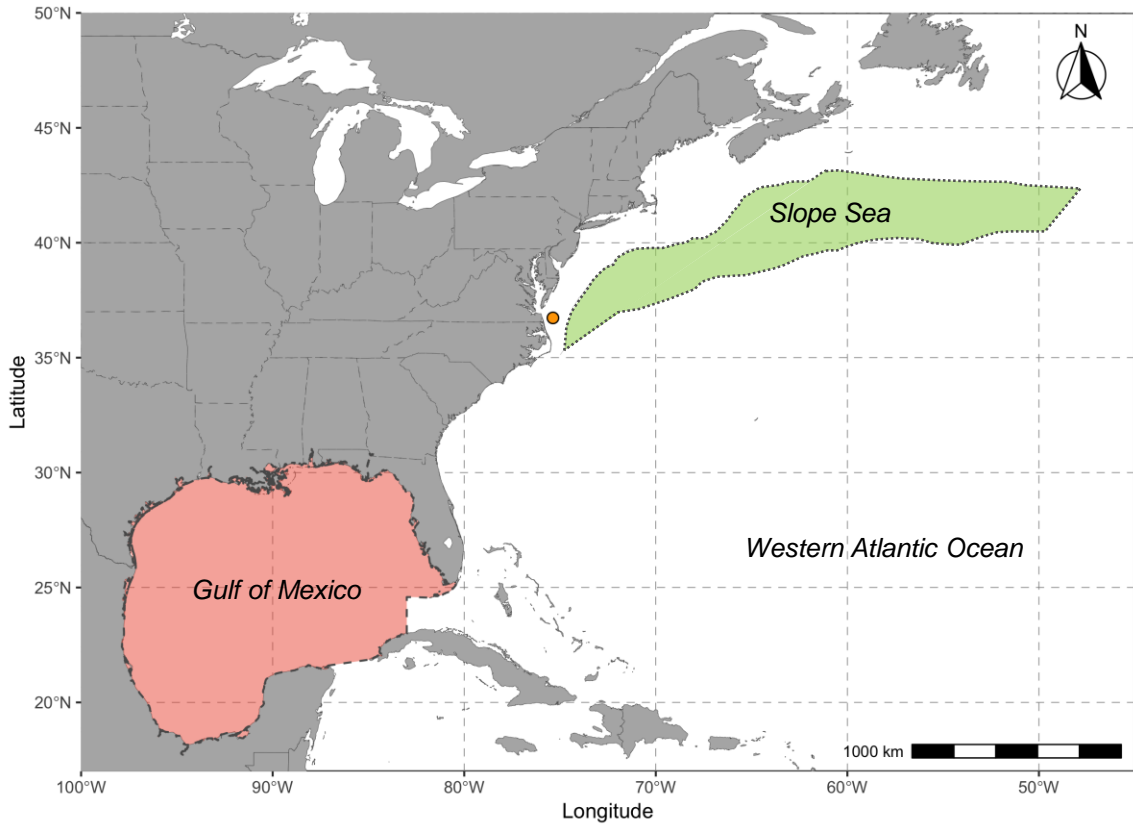
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593 **Fig. 6** Estimated hatch date distribution of 25 juvenile Atlantic bluefin tuna collected on 30
594 August (*dark grey*) and 11 September (*light grey*) 2010

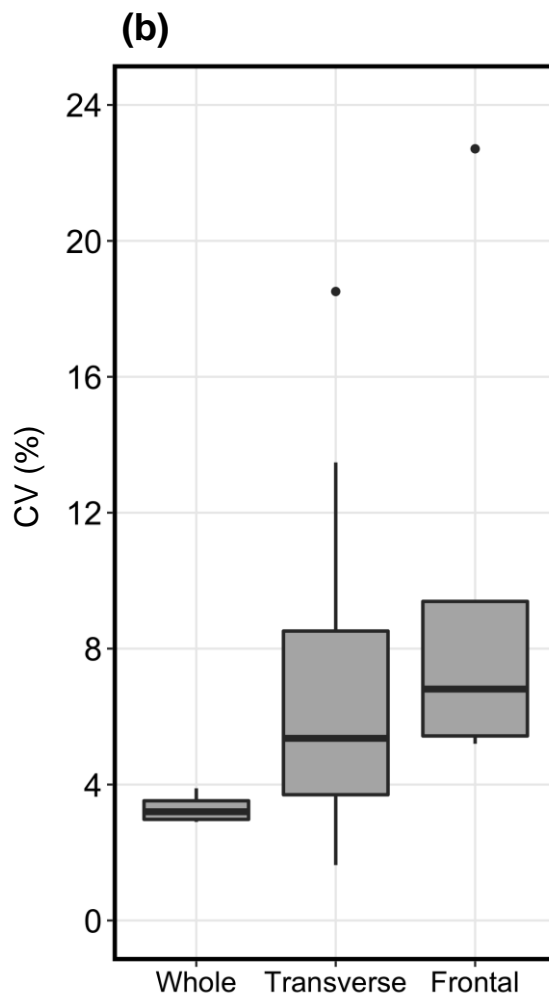
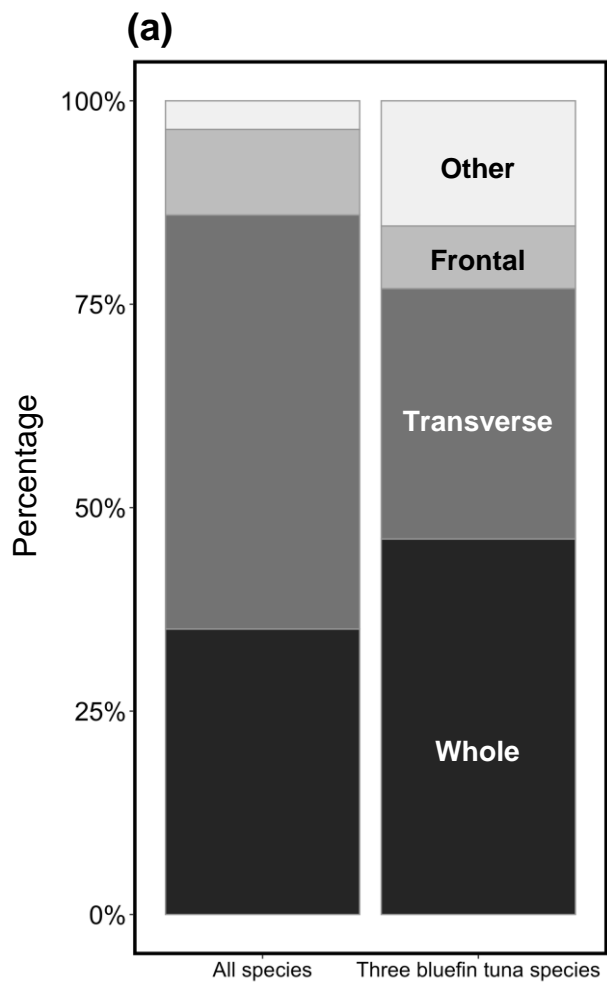
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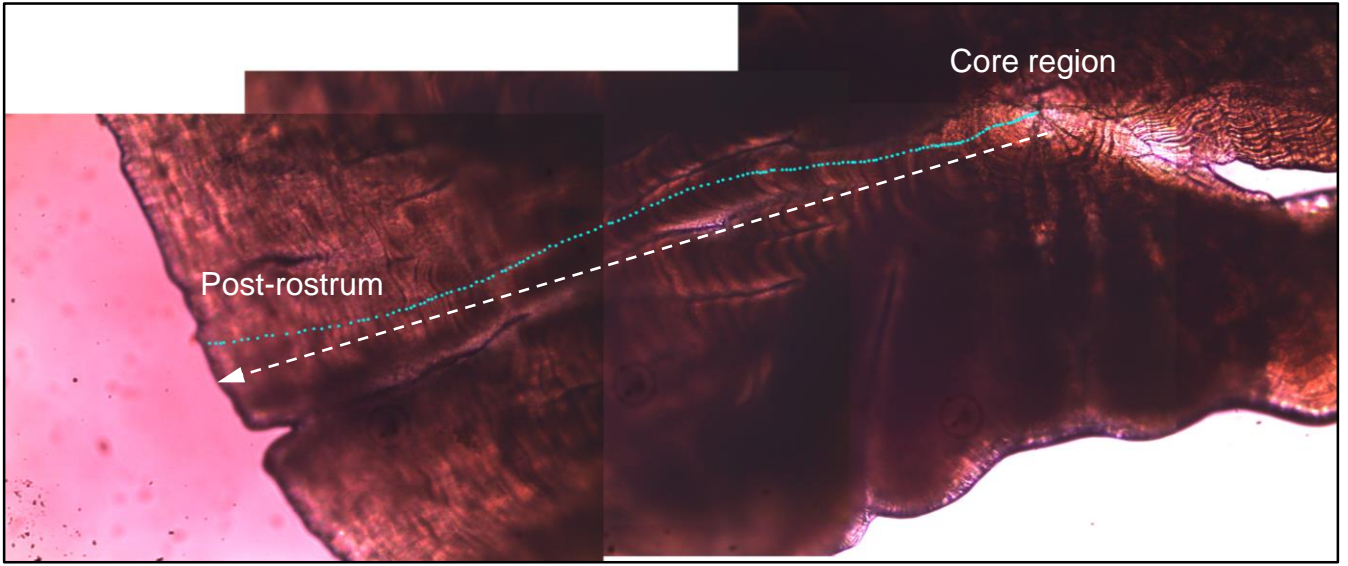
596 **Fig. 7** Comparison of the size-at-estimated age relationship determined in this study for
597 juvenile ABFT with values reported in the literature. Mean growth rates estimated from the linear
598 slope of size on age are denoted in parentheses

599

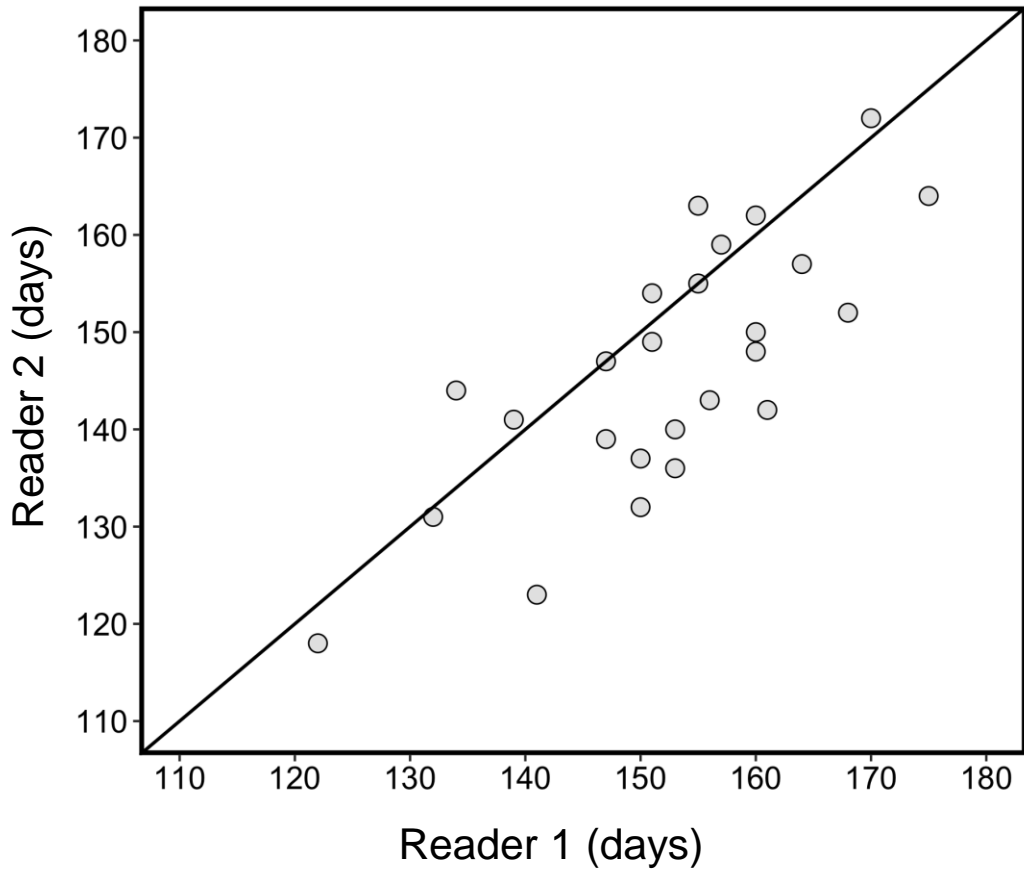


Arai et al. **Figure 1**

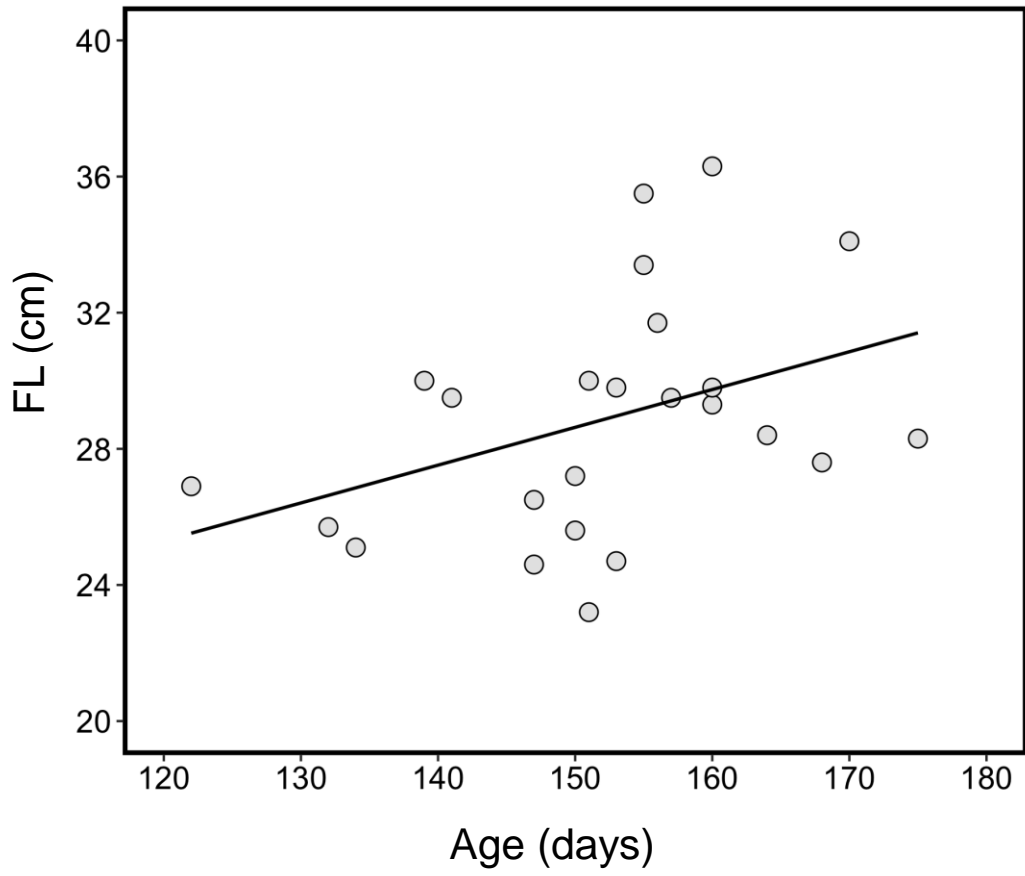




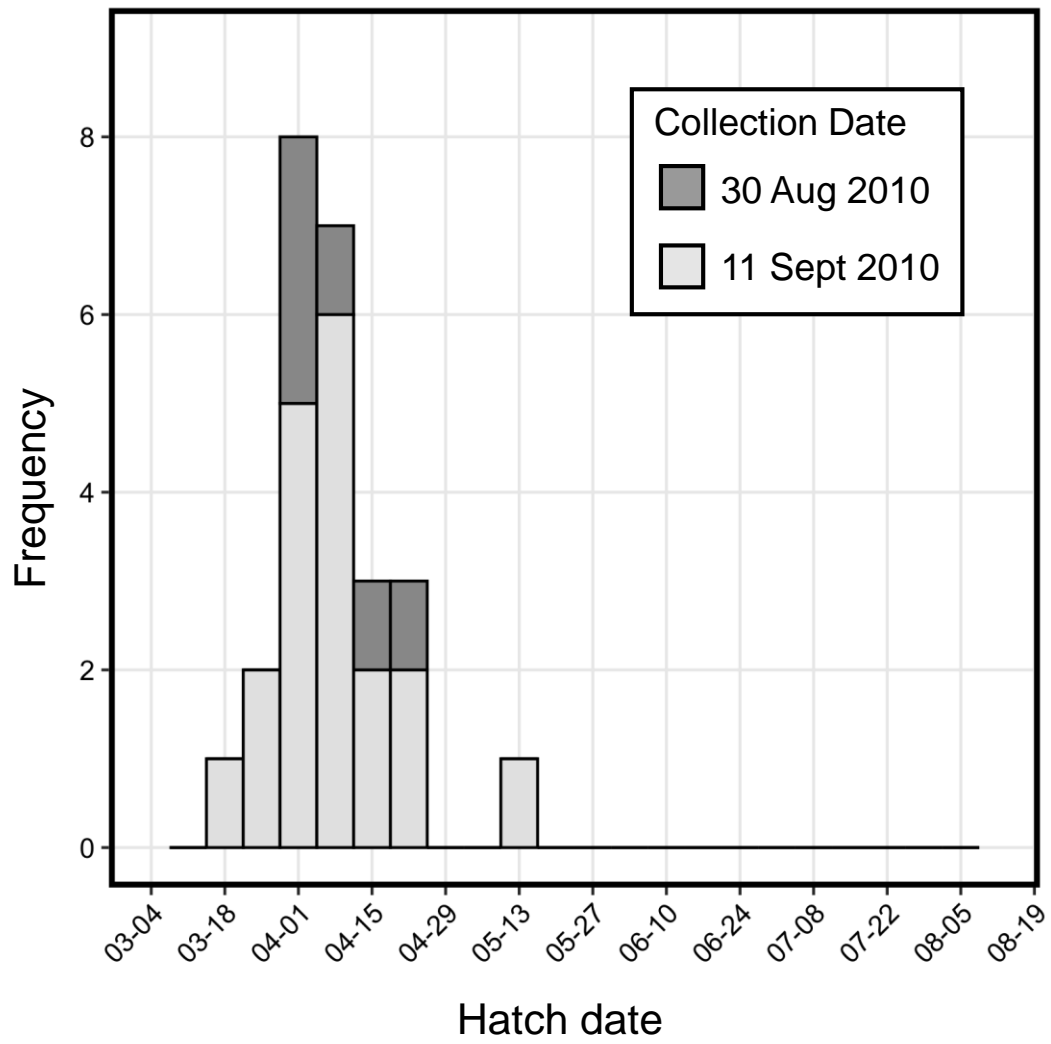
Arai et al. **Figure 3**



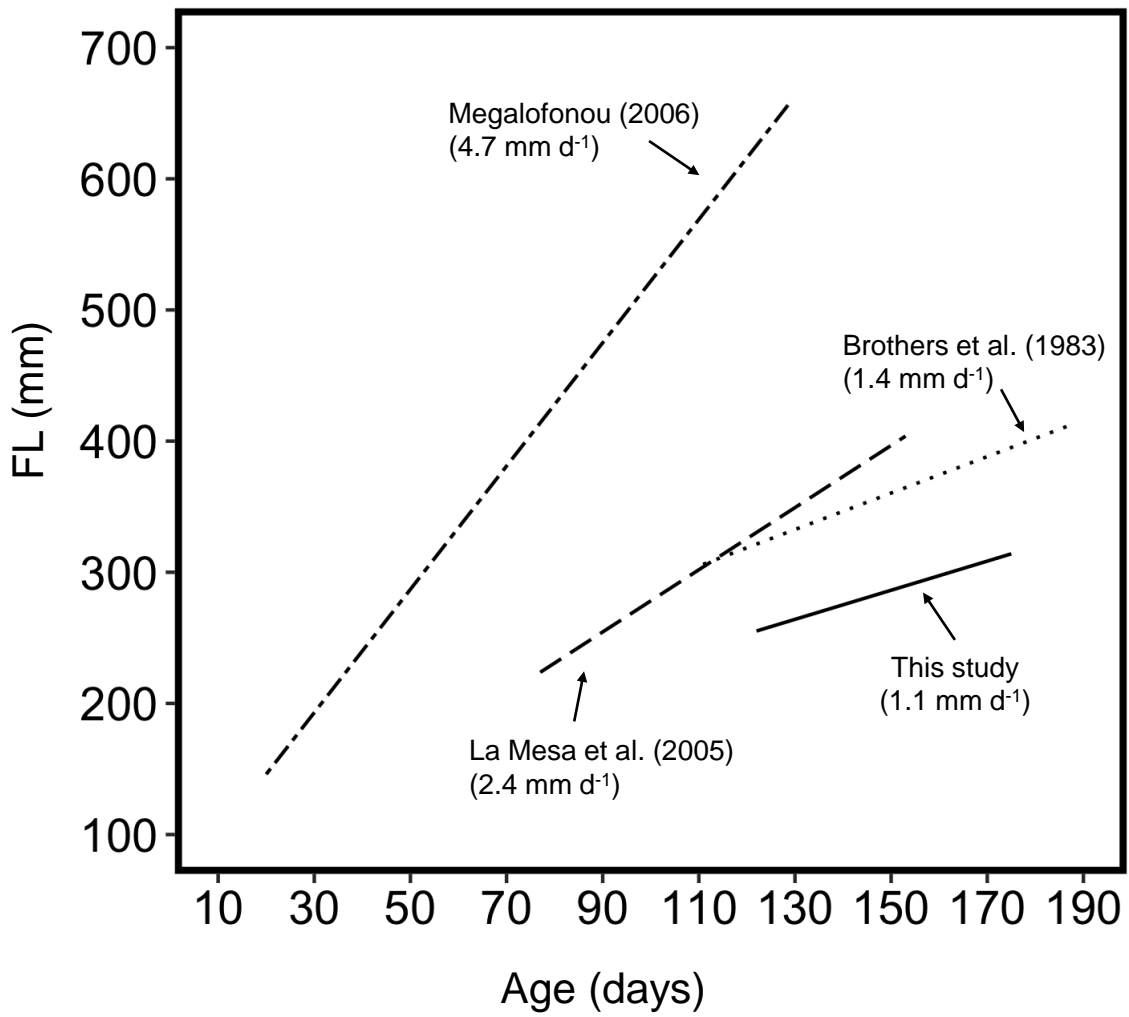
Arai et al. **Figure 4**



Arai et al. **Figure 5**



Arai et al. **Figure 6**



Arai et al. **Figure 7**