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Critical thermal limits of Atlantic bluefin tuna (*Thunnus thynnus*) larvae

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ABSTRACT

There is a growing interest in understanding the thermal tolerance of ectotherms across life stages. Identifying the stages that are most sensitive can help develop more robust projections on the consequences of climate impacts to populations, as well as help guide management and conservation efforts. Here, we estimate upper and lower thermal tolerance (as Critical Thermal maximum, CTmax, and minimum, CTmin) of Atlantic bluefin tuna (*Thunnus thynnus*) larvae. This species is an iconic apex predator that exhibits regional endothermy during the adult stage, but thermal tolerance of larvae was unknown. CTmin and CTmax were estimated in larvae grown from wild eggs under laboratory conditions. The mean (±SE) CTmax and CTmin across all tested batches and developmental stages was 31.7 (±0.6) and 17.9 (±0.7)°C, respectively. Rate of temperature change (1.5, 3, 6, or 9 °C h^{-1}) had no effect on the thermal tolerance estimates. Similarly, CTmin and CTmax were consistent across preflexion, flexion, and postflexion larval stages. The observed high inter-individual variability in CTmin and CTmax (11-13 °C) likely reflects methodological challenges related to the extreme sensitivity of the species to handling stress and confinement. Present and future thermal safety margin (by 2060) for larvae in the Balearic Islands are 3.6 (±0.6 SE) °C and 1.8 (±0.6 SE)°C, respectively. Future research should continue exploring alternative methods for estimating thermal limits and incorporate experimental designs with multiple stressors such as exposing well- and poorly-fed larvae to heatwaves and/or different light levels.

1. Introduction

Recently, there has been a growing interest in evaluating thermal tolerance across different life stages in ectotherms to understand sensitivity to climate change (Dahlke et al., 2020; McKenzie et al., 2021; Ruthsatz et al., 2024). This information can be used to identify stages with the strictest temperature requirements, which may become a life cycle bottleneck. Conservation and management actions can greatly benefit from such assessments, as they can target this (these) critical life stage(s) (e.g. Howard et al., 2024; Komoroske et al., 2014). For example, species distribution models have now been developed and implemented for some management processes such as designing surveys for new populations or identifying priority locations for specific actions (Sofaer et al., 2019). Unfortunately, unprecedented rates of ocean warming and increased frequency and duration of extreme events associated to global climate change are generating conditions falling outside the historical range of observations (i.e. no analog conditions) in some regions, challenging the predictive capacity of these models (Payne et al., 2021; Rose et al., 2024). Estimates of thermal tolerance limits can support model parameterization outside the thermal conditions previously observed in the field, creating more mechanistic models and improving model performance (Muhling et al., 2020; Rose et al., 2024). While there have been some studies exploring general trends in thermal tolerance across fish life stages, these generally highlight a relatively limited amount of

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empirical (and comparable) data for all life stages (e.g. Dahlke et al., 2020; Dahms and Killen, 2023). This is even true for arguably one of the most studied species, Atlantic salmon (*Salmo salar)* (Mayer et al., 2024). Therefore, there is a need to advance the knowledge on thermal limits across life stages using comparable methods and metrics that allow to infer susceptibility under a changing ocean (McKenzie et al., 2021; Pottier et al., 2022).

Estimates of the Critical Thermal Maximum (CTmax) and Minimum (CTmin) are popular proxies for revealing the temperature tolerance window in fishes (Desforges et al., 2023; Nati et al., 2021). Initially developed within the field of ecotoxicology, these protocols consist of a stepwise ramping procedure using a fixed warming/cooling rate (e.g. 1 to 18 °C h^{-1}) (Lutterschmidt and Hutchison, 1997). The procedure stops when the fish reaches a given endpoint, generally loss of equilibrium but also onset of spams. While these estimates have been sometimes criticized for being oversimplistic, they prevail as an integrative, repeatable metric with comparable endpoints across individuals, populations and taxa (Desforges et al., 2023; Morgan et al., 2018). For example, CTmax has been related to biogeographic distribution of species (Payne et al., 2021) and can be particularly useful to assess vulnerability to climate change, e.g. through the estimation of the thermal safety margin (i.e. difference between CTmax and the maximum habitat temperature during summer) (Nati et al., 2021). Despite the long-term tradition of CTmin/CTmax measurements, there are still not standard protocols for comparing thermal tolerance across life stages (Pottier et al., 2022), although potential solutions are developing quickly (Cowan et al., 2023; Lechner et al., 2024; Raby et al., 2025). Rate of temperature change, choice of endpoint, and acclimation protocols are particularly important methodological aspects that differ and hinder comparability. Additionally, it is strongly recommended to use these estimates in combination with other indices to gain a more holistic understanding of thermal tolerance and performance in fish (Desforges et al., 2023; McKenzie et al., 2021).

Atlantic bluefin tuna (*Thunnus thynnus*) is an iconic apex predator playing a key role in pelagic waters of marine ecosystems. Adults have regional endothermy that allows them to maintain temperatures in certain regions of the body above the ambient water temperature by retaining the heat they produce (Dickson, 1994). This endothermy contributes to the ability of this species to migrate long distances and spend long periods of time in cold waters (Bernal et al., 2017). In Pacific bluefin tuna (*Thunnus orientalis*), endothermy begins when juveniles obtain lengths between 20 and 40 cm (Kitagawa et al., 2022; Kubo et al., 2008). Still, the timing when Atlantic bluefin tuna acquire endothermic capacity is unclear. Significant knowledge has been gained over the last decade on the thermal dependence of growth and metabolism for Atlantic bluefin tuna eggs (embryos) and larvae (Ortega et al., 2024; Reglero et al., 2018b). Moreover, field observations within the Balearic Islands (a main spawning ground for Atlantic bluefin tuna) have reported larvae to be within the upper 20-25 m of the water column, always above the thermocline with temperatures >20 °C (Reglero et al., 2018a). However, there is still very limited knowledge on the thermal tolerance limits of these early life stages. Estimating these limits is particularly important because the reproductive strategy of adults has been linked to the survival of eggs and larvae (Reglero et al., 2018b). While the onset of the spawning season is mainly determined by temperature and relatively well understood for Atlantic bluefin tuna, the duration of the season and its drivers remain uncertain. It is known that the timing of spawning coincides with temperatures warm enough to allow embryos to survive (>20 °C, Ortega et al., 2024) but cold enough to prevent metabolic meltdown of the larvae (<30 °C, Fiksen and Reglero, 2022). The spawning period coincides with a rapid warming of the surface layer (~10 °C per month), during which the thermocline remains very shallow. Under these conditions, adult tuna can move to deeper, cooler waters, whereas larvae are restricted to the upper mixed layer and therefore experience large thermal changes. In recent years, increased intensity and duration of marine heatwaves have been reported in recent years in the Balearic Islands, exceeding previous historical maxima (i.e. surface temperatures up to 28.5 °C, Juza and Tintoré, 2020), raising concerns about the potential impacts on larval survival and recruitment. Therefore, gaining further insights on thermal limits for larval stages can support a deeper understanding of tuna life history strategies and future challenges in the light of climate change, particularly how such extreme events may affect larval survival and, ultimately, recruitment success.

In the present study, we estimated the CTmax and CTmin of Atlantic bluefin tuna larvae as proxies for upper and lower thermal tolerance, respectively. First, the effect of the rate of temperature change (i.e. cooling or warming rate) on CTmin and CTmax was tested in young larvae. Then, CTmin and CTmax trials were conducted using larvae ranging from 3 to 17 mm using a common rate of temperature change. Estimates from this and other studies on tuna stages and species were compared and discussed in light of thermal safety margins at Atlantic spawning grounds.

2. Material and methods

2.1. Tuna larval rearing

Wild tuna eggs were collected next to bluefin tuna sea cage aquaculture facilities at El Gorguel, Cartagena (SE Spain), owned by Caladeros del Mediterráneo S.L. Several batches were used in these experiments, all collected between June 16th and July 7th’ 2017. Eggs were transported immediately to the Spanish Institute of Oceanography research station in Mazarrón (SE Spain). Once at the station, eggs were transferred into culture tanks of varying volumes (10 eggs L^{-1}), with each batch placed in a tank according to the number of eggs obtained (Table 1). Larvae hatched in these egg tanks and were reared at ambient temperature (24 to 26 °C) and a salinity of 38 psu (Table 1). The light regime was set to 14L:10D. Prey was offered *ad libitum*, consisting of a mix of i) enriched rotifers *Brachionus plicatilis* (2-16 dph, 5 rotifers mL^{-1} twice per day), ii) enriched *Artemia franciscana* instar II nauplii (AF, INVE AQUACULTURE, Belgium) (11-23 dph, 0.1-0.5 *Artemia* mL^{-1} twice a day), and iii) gilthead sea bream *Sparus aurata* yolk-sac larvae (YSL) (17-30 dph, 10-300 YSL per tuna larva twice a day). Tanks were also supplemented with the microalgae *Nannochloropsis gaditana* (0-16 dph) and *Chlorella* (Super fresh Chlorella SV-12, Chlorella Industry Co., Ltd., Japan) (after 16dph).

Larvae were collected from the different tanks at different developmental time points for the CTmin and CTmax trials (Table 2).

2.2. Critical temperature trials

The CTmax and CTmin of Atlantic bluefin tuna larvae were estimated following the protocol in Moyano et al. (2017). First, the effect of warming/cooling rate on CTmax and CTmin estimates was tested with Batch 1 (all preflexion larvae). In total, four rates (1.5, 3, 6 and 9 °C h^{-1}) were

Table 1
Details of batches and conditions used to rear Atlantic bluefin tuna larvae. “Rearing temperature” indicates the temperature range through the entire rearing period; “Rearing volume” refers to the rearing tank volume (in L); “Larval age” refers to the ages until batches were reared (days-post hatch, dph); “Growth rate” refers to the growth rate (in mm d^{-1}) for each of the batches during the entire larval age used (see Supp. Fig. 1).

Batch	Hatch date	Rearing temperature (°C)	Rearing volume (L)	Larval age (dph)	Growth rate (mm d^{-1})
1	June 16, 2017	24.5 ± 1.9	5000	0-12	0.349
2	June 16, 2017	25.4 ± 1.9	1500	0-8	0.517
3	June 17, 2017	23.5 ± 2.1	1500	0-26	0.197
4	July 07, 2017	26.3 ± 0.9	18 000	0-14	0.172
5	July 07, 2017	26.3 ± 1.3	50 000	0-17	0.334

Table 2

Details of the critical thermal maxima and minimum (CTmax and CTmin) trials conducted with Atlantic bluefin tuna larvae. “Age” refers to days-post hatch (dph); “Size” is the average length of all larvae used in each trial; “Rate Temp Change” indicates the warming or cooling rate used in the assays (°C h-1); “Acclimation temperature” refers to the temperature used across replicates during the acclimation period before starting the trials (similar to that of the corresponding rearing tank). Number of replicates per trial, replicate, replicate volume (i.e. beaker), and number of larvae per replicate is indicated. Total larvae tested (not including the controls) is indicated.

CT	Batch	Age (dph)	Size (mm, mean ± SE)	Rate Temp Change (°C h^{-1})	Acclimation temperature (°C ± range)	No. replicates per unit	Replicate volume (mL)	No. larvae per replicate	Total larvae tested
CTmax	1	5-6	4.1 ± 0.4	1.5,3,6,9	24.9 ± 0.2	9	250	1	36
	2	8	5.4 ± 0.3	3	24.9 ± 0.2	9	250	1	9
	1	11	6.0 ± 0.9	3	24.9 ± 0.2	2	2000	5	10
	3	26	8.5 ± 1.0	3	23.4 ± 0.3	2	2000	*5*	*10*
	4	14	6.6 ± 0.9	3	26.2 ± 0.2	2	2000	8	*16*
	5	17	11.6 ± 1.6	3	26.7 ± 0.3	2	2000	*3*	*6*
CTmin	1	6-7	3.9 ± 0.3	1.5,3,6,9	24.9 ± 0.2	9	250	1	36
	1	12	6.0 ± 0.6	3	24.9 ± 0.2	2	2000	5	10
	3	26	7.9 ± 0.6	3	23.4 ± 0.3	2	2000	5	10
	5	19	14.0 ± 1.5	3	26.7 ± 0.3	2	2000	*3*	*6*

tested. Thermal control units (Fisherbrand FBC 30, Fisher Scientific GmbH, Schwerte, Germany) were used, each containing nine 250-mL beakers (Supp. Fig. 2). One unit was used as a control and maintained at the starting temperature throughout the trial to evaluate the effect of handling. Warming rate treatments were randomly assigned to a thermal control unit in each trial. Individual larvae were randomly collected from the rearing tanks and gently transferred to a beaker (9 larvae per trial in total). Each beaker was aerated using a small pump (Tetra APS400, Spectrum Brands, VA, USA) with small bubbles produced using a fine glass pipette (Supp. Fig. 2). Larvae were allowed to acclimate in the beakers for 15 min before the start of the trial. Initial temperature in the beakers was close (within ±0.1 °C) to that in the corresponding rearing tanks (see Table 2). Once the warming/cooling protocol started, larvae were checked continuously, and the state of the larva and the temperature was recorded (P700, ±0.1 °C, Dostmann electronic, Wertheim-Reicholzheim, Germany). Only two warming rates were run at a time. The endpoint for CTmax and CTmin was defined as the loss of equilibrium, although note that larvae were not tracked for post-trial recovery. All trials were done with light, between 9:00 and 16:00. Once a larva had reached this endpoint, it was taken out of the beaker using a wide pipette, anesthetized with tricaine methanesulfonate (MS222, 0.1 g L^{-1}, Sigma-Aldrich, Germany). digitally photographed under a stereomicroscope (Leica MS5, camera EC3), and euthanized by an anesthetic overdose (MS222, 10 g L^{-1}). Body length (measured as notochord length for preflexion larvae and standard length for flexion and postflexion larvae) was measured using Leica Application Suite V4.3. Larvae were classified into one of three developmental stages (preflexion, flexion, postflexion) following Blanco et al. (2017) (Table S1).

Since no differences were observed across warming/cooling rates, one rate (3 °C h^{-1}) was used to estimate CTmax and CTmin in larvae from all batches at different developmental stages. This rate was chosen based on recommendation in Moyano et al. (2017). Trials on small larvae (<8 mm) were conducted in 250-mL beakers with one larva per beaker and nine beakers per unit as described above (Supp. Fig. 2). Preliminary tests suggested that these containers were not optimal for larger larvae, and thus 2-L beakers were used for larger larvae. In this case, two 2-L beakers were used per unit, each with 3-8 larvae (Table 2, Fig. S2).

CTmax and CTmin trials lasted up to 7.5 h during daylight conditions. No prey was added to the beakers at any point during a trial.

2.3. *Thermal safety margin*

Present and future thermal safety margins (TSM) were calculated for Atlantic bluefin tuna larvae in the Balearic Islands. Present TSM was estimated using equation (1) and future TSM using equation (2):

(Equation (1)) Present TSM = CTmax - maximum habitat temperatures in the Balearic Islands.

(Equation (2)) Future TSM = CTmax – (maximum habitat temperatures in the Balearic Islands + projected thermal increase by 2060)

where CTmax for each individual was used to account for the high-interindividual variability observed. For present TSM, maximum habitat temperatures in the Balearic Islands was 28.1 °C, based on thermal records from the TUNIBAL cruises (Table S2). These cruises survey the Balearic Islands during the spawning time of Atlantic bluefin tuna. Temperature at 10 m depth was used (rather than surface waters) to better represent the larval habitat. For the future TSM, the projected increase of 1.8 °C in surface waters in the Mediterranean Sea by 2060 under the IPCC Representative Concentration Pathway 8.5 was used (Kristiansen et al., 2024).

2.4. *Data analysis*

The effect of warming/cooling rate on CTmax and CTmin estimates was tested in Batch 1. As a second step, differences in CTmax and CTmin estimates across developmental stages (preflexion, flexion, postflexion) were tested in all batches using a common warming/cooling rate (3 °C h^{-1}). Developmental stages (rather than larval size) were chosen to have more representative sample sizes per group (Supp. Fig. 3). Note that not all developmental stages were represented in all batches (Supp. Fig. 3) and therefore “batch” could not be modeled as an independent factor. For both analyses, data were checked for normality and homogeneity of variance visually and running Shapiro-Wilks and Levene tests, respectively. The former was used due to its power with small to moderate sample sizes, while the second was chosen due to its robustness with non-normal data. Given the non-normality of the data, differences were then tested with a non-parametric test, Kruskal Wallis analysis of variance (KW-ANOVA).

All analyses were conducted at a significance level of $\alpha = 0.05$ with R version 4.2.2 (R Core Team, 2022).

3. Results

Different warming or cooling rate (1.5 to 9 °C h^{-1}) did not significantly impact CTmax (KW-ANOVA, $\chi^2(3) = 5.093$, $p = 0.165$) or CTmin estimates (KW-ANOVA, $\chi^2(3) = 5.020$, $p = 0.170$) in young Atlantic bluefin tuna (5-6 dph) (Fig. 1). Average CTmax ranged from 29.1 to 32.9 °C across warming rates, while CTmin was between 17.6 and 21.6 °C. Based on these results, all subsequent CTmax and CTmin trials were conducted using a rate of 3 °C h^{-1}, which has been previously suggested for marine fish larvae (Moyano et al., 2017).

Using a rate of temperature change of 3 °C h^{-1}, the mean(±SE) CTmax and CTmin across all batches and larval sizes was 31.7 (±0.6),

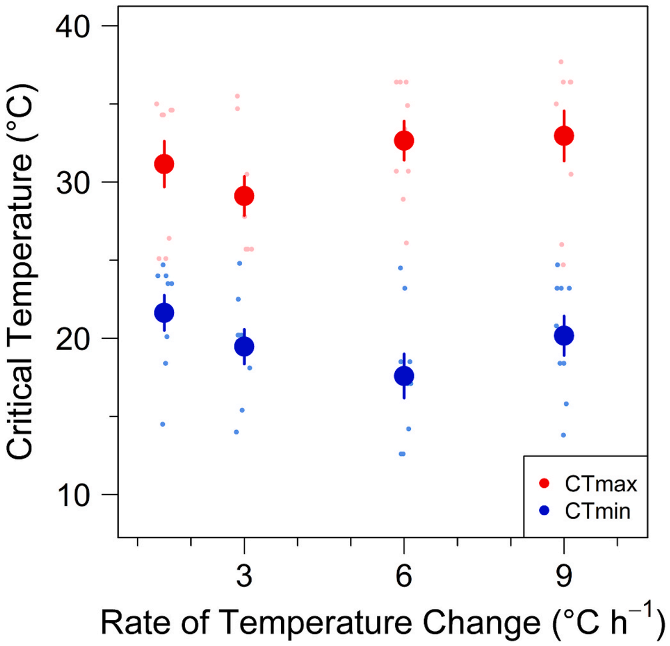

Fig. 1. Effect of rate of temperature change (i.e. warming or cooling rate) on the thermal tolerance of Atlantic bluefin tuna larvae (Batch 1). Mean (±SD) critical thermal maximum (CTmax, red) and minimum (CTmin, blue) are displayed at four cooling or warming rates (1.5, 3, 6, and 9 °C h^{-1}). Individual values are shown as small dots. Sample size (n) for CTmin and CTmax at each rate is 9. No significant effect of rate of temperature change was observed.

and 17.9 (±0.7) °C, respectively. CTmax was not significantly different across developmental stages (KW ANOVA, $\chi^2(2) = 2.020$, $p = 0.364$) nor was CTmin (KW ANOVA, $\chi^2(2) = 4.175$, $p = 0.124$) (Fig. 2). The inter-individual variability in CTmin and CTmax estimates was large, spanning a range of approx. 11-13 °C. The upper limit of CTmax (90% quantile) ranged between 36.3 °C and 37.3 °C for the three stages, while the lower limit of CTmin (10% quantile) ranged between 12.6 °C and 15 °C. It is important to note that larval growth rate differed across batches, ranging between 0.172 and 0.517 mm d^{-1} (Table 1). Also, thermal history experienced by the larvae before the CT tests was slightly different (average range 2.8 °C, Table 1). Larval survival in the controls was 100% for individuals older than 14 dph (batches 3-5, Table 1). However, younger larvae (5-12 dph) seemed more sensitive. A maximum of two larvae (out of the nine replicates in two trials with 5-7 dph larvae) had to be removed during the first 20 min of the test because they were unresponsive. Survival after those first 20 min was stable (typically 100%, except two dead larvae in CTmax with Batch 1 and one in CTmax with Batch 4).

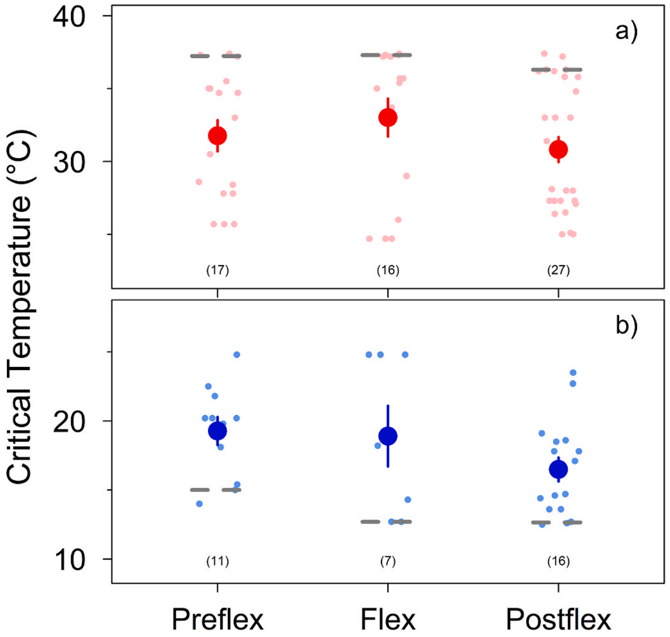

Fig. 2. Thermal tolerance range of bluefin tuna larvae across larval development: a) critical thermal maximum (CTmax, red), and b) minimum (CTmin, blue). Mean (±SD) estimates are displayed across three developmental stages (preflexion, flexion and postflexion). The 90% quantile for CTmax (panel a) and 10% quantile for CTmin (panel b) are displayed as dashed grey lines. Sample sizes are shown in parentheses. No significant effect of developmental stage on CTmin or CTmax was observed.

Present and future TSM (±SE) was 3.6 (±0.6) °C and 1.8 (±0.6)°C, respectively.

4. Discussion

While significant knowledge has been gained over the past years on the thermal ranges that support growth of Atlantic bluefin tuna eggs and larvae in the lab and the field (Ortega et al., 2024; Reglero et al., 2018b, Table 3), there is still very limited information on the upper and lower thermal tolerance for this species. The present study is the first to estimate the CTmax and CTmin of Atlantic bluefin tuna larvae. The obtained CTmax and CTmin were 31.7 °C (±0.6 SE) and 17.9 °C (±0.7 SE), respectively, for larvae 5-17 mm. These estimates were not impacted by the tested rates of temperature change (between 1.5 and 9 °C h^{-1}) nor by developmental stage. The high variance in the CT estimates highlights the methodological challenges encountered during the study mostly related to the intrinsic extreme sensitivity of this species to handling and confinement. Given the ecological, economic and cultural value of this iconic species, there is a need to continue exploring approaches and metrics to estimate thermal tolerance in this species.

The thermal tolerance range observed for larval stages in this study agrees well with that for embryos of this and other tuna species (Table 3). For Atlantic bluefin tuna, the small differences in thermal tolerance between embryos and larvae (e.g. thermal range of 15 °C and 13.8 °C, respectively) need to be interpreted with caution, as the methodology used was study-specific. Lower and upper tolerance in bluefin tuna embryos was estimated from the median lethal temperature (LT50), that is the temperature that lead to 50% survival at hatching (Ortega et al., 2024), while this study on larvae used a CTmin and CTmax protocol. The LT50 protocol uses constant temperatures over longer time periods (days) and the endpoint is death, whereas the CT protocols use changing temperatures and obtain estimates in only a few hours. Therefore, the estimates for embryos (LT50) and larvae (CT) could be considered as measures of medium-term and short-term thermal stress, respectively. Recent studies suggest that thermal tolerance estimates based on the time at which embryos stop moving could be a better proxy for acute thermal tolerance (Cowan et al., 2023), as well as changes in heart rate (e.g. Mauduit et al., 2023; Moyano et al., 2020). Recording additional behavioral metrics during the CTmax tests (e.g. agitation swimming) can also help in the understanding of thresholds that may have ecological relevance (Kochhann et al., 2021). This is particularly relevant because small fish are generally euthanized after CT tests, and recovery assessments are not frequently done as in larger fish (e.g. Auer et al., 2015; Illing et al., 2020; Strader et al., 2023). This is likely due to the challenge of individual tagging on those small sizes (<1.5 cm). The absence of a recovery period can raise questions on whether the reported estimates truly reflect sublethal thermal limits. Given the current emphasis on assessing life cycle thermal tolerance in fishes (including Atlantic bluefin tuna), future research should emphasize the need to combine different metrics (based on behavior, heart rate, etc.), as well as the development of clear standardized protocols that allow comparisons across life stages.

Table 3

Summary of studies reporting thermal tolerance of tuna and bonito species from laboratory experiments or temperatures at which they have been observed in the field. Species include Atlantic bluefin tuna (*Thunnus thynnus*), yellowfin tuna (*Thunnus albacares*), skipjack tuna (*Katsuwonus pelamis*), Pacific bluefin tuna (*Thunnus orientalis*) and Atlantic bonito (*Sarda sarda*). Only studies reporting estimates made over a wide range of temperatures are included.

Species	Stage	Field vs Lab	Tmin (°C)	Tmax (°C)	Trange (°C)	Method	Reference
Thunnus thynnus	Embryo	Lab	18	34	16	50% hatching success	Miyashita et al. (2000)
	Embryo	Lab	18	33	15	50% hatching success	Ortega et al. (2024)
	Larvae	Lab	21.9	29.8	7.9	Growth rate	Reglero et al. (2018)
	Larvae	Lab	17.9	31.7	13.8	CTmin/CTmax	This study
	Larvae	Field	24.7	28.5	3.8	Presence in field	Reglero et al. (2014)
	Adult	Field	2.8	31	28.2	Presence in field	Boyce et al. (2008)
Thunnus albacares	Embryo	Lab	19	35	16	50% hatching success	Wexler et al. (2011)
	Embryo	Lab	23	35	12	50% hatching success	Kim et al. (2015)
	Embryo	Lab	21.9	31.4	9.5	50% hatching success	Margulies et al. (2007)
	Embryo	Lab	22	32	10	50% hatching success	Guillen et al. (2014)
	Embryo	Lab	24	32	8	50% hatching success	Hutapea (2007)
	Larvae	Lab	21	33	12	Growth rate	Wexler et al. (2011)
	Larvae	Field	20.2	30.2	10.0	Presence in field	Reglero et al. (2014)
	Adult	Field	7	31	24.0	Presence in field	Boyce et al. (2008)
Katsuwonus pelamis	Embryo	Lab	21	33	12	50% hatching success	Fujioka et al. (2024)
	Larvae	Field	19.2	30.2	11.0	Presence in field	Reglero et al. (2014)
	Adult	Field	14.7	33	18.3	Presence in field	Boyce et al. (2008)
Sarda sarda	Embryo	Lab	16	28	12	50% hatching success	Ortega et al. (2024)
	Larvae	Lab	19	26.3	7.3	Growth rate	Reglero et al. (unpub.)
Thunnus orientalis	Larvae	Lab	20	29.5	9.5	Growth rate	Kimura et al. (2010)
	Larvae	Field	21.7	28.9	7.2	Presence in field	Reglero et al. (2014)
	Adult	Field	5	28.4	23.4	Presence in field	Boyce et al. (2008)

Inter-individual variability in CTmin and CTmax estimates for Atlantic bluefin tuna larvae (i.e. 11-13 °C) was higher than generally reported in fish, but within the range of other studies in larvae (e.g. 8-13 °C, Illing et al., 2020; Moyano et al., 2017) and embryos (10 °C, Lechner et al., 2024). Such high variability is arguably related to the low tolerance to handling stress and confinement of the larvae (De La Gándara et al., 2016; Ghysen et al., 2010). Larvae older than 14 dph were relatively robust and their survival in the controls was 100%. However, some younger larvae had to be removed from the controls because they were unresponsive around 20-30 min after transfer. This extreme sensitivity has been reported for both Pacific and Atlantic bluefin tuna larvae, including daily mortalities up to 40% after larvae were transported to a new tank (Blanco et al., 2018; Seoka et al., 2007). The large size of the cupula makes larval tuna neuromasts highly susceptible to shearing forces, which has been suggested to partially explain this sensitivity to handling. Other potential factors behind the observed inter-individual variability include larval batch, container size and number of larvae in the container. First, different batches had to be used in this study to obtain enough representation of the different larval sizes within a reasonable time frame that allowed for similar thermal histories (i.e. eggs were collected from the wild and temperatures can easily rise quickly within a week). While most batches displayed relatively similar growth rates (i.e. 0.35-0.50 mm d^{-1}), batch 3 and 4 had lower rates (0.20 and 0.17 mm d^{-1}, respectively). The thermal history of each batch was also slightly different, and this may have also contributed to the observed variability as it is widely accepted that acclimation to warmer temperatures generally leads to increased CTmax (McKenzie et al., 2021). Note, however, that the variability in temperatures within tanks was lower than the difference among the average temperatures. Second, container size had to be increased for larger larvae. While the CTmin and CTmax estimates for young larvae (5-7 mm) seemed comparable among methods (Supp. Fig. 3), the container effect cannot be discarded. Third, groups of three to five larvae were used in the large containers rather than the individuals used in the small containers. Recent research now suggests that social experience can influence how a fish perceives temperature, leading to longer exposures to critically warm water (Melanson et al., 2023). Moreover, the disturbance created by removing larvae from the groups may have impacted the remaining larvae. Therefore, the effect of the social context on the CT estimates cannot be excluded. Unfortunately, testing the potential effect of these four factors was not possible in our study due to limited access to large larvae and other logistical problems. Future research should focus on further developing the CT protocols for this particularly sensitive species. For example, testing the feasibility of running CT trials in large rearing tanks (e.g. 100 L) with large larval groups.

The effect of rate of temperature change on CTmin and CTmax estimates varies across species (Mora and Maya, 2006; Moyano et al., 2017; Vinagre et al., 2015). In this study, we did not find any effect of warming rate on CTmax estimates for Atlantic bluefin tuna larvae, but other studies have observed an increased CTmax or decreased CTmax at faster warming rates. These differences are arguably the result of inter-specific differences in the capacity and lag time in temperature acclimation (i.e. time for the internal body temperature to match the external water temperature) (Desforges et al., 2023). Acknowledging these differences is important when considering the ecological relevance of the thermal limits obtained. While some studies suggest using "ecologically relevant" warming rates to estimate thermal limits (Peck et al., 2009; Vinagre et al., 2015), larvae enduring longer trials (at slower ramping rates) would experience other types of stress that would impact estimates of CTmax. Slow ramping rates would be a particular challenge for fish larvae that have high growth rates and low starvation resistance (Moyano et al., 2017), particularly for Atlantic bluefin tuna that grow at 35 % d^{-1} at 28 °C and need to eat within 4 h (Blanco et al., 2017; Reglero et al., 2018b). In fact, a recent methodological guide for CTmax studies in ectotherms recommends using 0.3 °C min^{-1} (i.e. 18 °C h^{-1}) for small fish (Raby et al., 2025). This recommendation is based on classic work on freshwater fishes (Becker and Genoway, 1979). In this study we chose 3 °C h^{-1} following the recommendation in Moyano et al. (2017) tailored to small marine fish larvae (<1.5 cm). Given the need to find consistent protocols for CT estimates across life stages, future studies in Atlantic bluefin tuna should test a broader range of rates of temperature change that includes 18 °C h^{-1}, and stick to that one if changes across rates are not observed.

The thermal ranges that support growth of Atlantic bluefin tuna larvae in the laboratory and in the field are well within the observed responses to short- and medium-term thermal stress (Table 3). Combining CTmin and CTmax estimates with thermal tolerance estimates of other processes (e.g. growth) that account for acclimation potential and short-vs. long-term thermal sensitivity is highly advisable (Desforges et al., 2023; Moyano et al., 2017). Previous research has reported that Atlantic bluefin tuna in the laboratory can grow between 21.9 and 29.8 °C (Table 3, Reglero et al., 2018b). Above 30 °C, a key limitation for rearing larvae of this species is related to technical challenges, such as bacterial proliferation in the water (Patricia Reglero, personal observation). Therefore, it is possible that the 29.8 °C limit reported for laboratory growth underestimates the upper thermal limit for growth. Metabolic rates have only been measured at a constant temperature of 26 °C, and not at temperatures close to upper thermal limits (Blanco et al., 2020). Field observations indicate that bluefin tuna larvae are primarily found in relatively warm water, usually between 24.7 °C and 28.5 °C, although they can also be found in waters as cold as 20 °C (Reglero et al., 2014). These thermal ranges observed in larvae are clearly narrower than in adults (3-31 °C), when endothermy and other behavioral thermoregulation processes are well developed (Boyce et al., 2008).

To our knowledge, differences in thermal tolerance within Atlantic bluefin tuna populations have not been studied. Evidence suggests that there is a size-related shift in the migratory behavior of this species in the Mediterranean Sea, with smaller individuals tending to remain resident and larger individuals undertaking long-range migrations (Rouyer et al., 2022).This ontogenetic change, occurring around 140–200 cm, could influence thermal acclimation to spawning grounds, as residency or migration determines the thermal environment experienced prior to spawning. This is particularly relevant in the Mediterranean spawning areas, regions experiencing rapid warming, and especially in the Balearic spawning area, where long-distance migrants may join locally resident individuals. Moreover, the species also utilizes other spawning grounds, such as the Gulf of Mexico, where spawning takes place in slightly warmer waters and where the thermocline lies much deeper than in the Mediterranean (Muhling et al., 2013). These consistently high-temperature environments, despite contrasting vertical thermal structures, raise the possibility that spawning adults have adapted to local temperature regimes in each area, potentially influencing the thermal tolerance and survival of their larvae. In this sense, the present study tests larvae from different batches representing the first half of the spawning period in the NW Mediterranean (mid June to early July). We acknowledge that the sample size and single collection area precludes us from making general conclusions since it is unlikely that the genetic variability among our tested individuals represents that from the Mediterranean spawning population. It is worth noting, however, that some studies have highlighted that CTmax seems to be well conserved within populations, e.g. comparing fish kept in the laboratory for several generations and fish from wild populations (Morgan et al., 2019).

Tuna is often considered a climate change “winner” (Cavole et al., 2016). Large-scale, long-term trends in ocean warming could potentially improve the survival and recruitment of Atlantic bluefin tuna since larval growth increases with temperatures up to 30 °C, as long as food is plentiful (Fiksen and Reglero, 2022). These temperatures are still above maximum values recorded in the Balearic Islands during recent heatwaves in 2024 and 2025 and during oceanographic cruises during spawning time in the past decade (~28.5 °C, Table S2, Juza and Tintoré, 2020). The present TSM estimated here is 3.6 (±0.6 SE) °C, which is still well above the average warming of Mediterranean Sea surface waters projected to exceed 1.8 °C by 2060 under the IPCC Representative Concentration Pathway 8.5 (Kristiansen et al., 2024). It is worth noting two aspects in our TSM estimations. First, these TSM are estimated using field temperatures at 10 m depth, which should be representative of the conditions within the upper 20-25 m (where the larvae are observed), given the strong thermocline during the summer months. To our knowledge, the size at which Atlantic bluefin tuna start moving vertically in the water column (behavioral thermoregulation) has not been reported yet. Second, we include observed variability in CTmax estimates by providing reporting the variability around the mean (SE) of the present and future TSM. This conservative approach to presenting the TSM was taken to acknowledge the methodological challenges of making laboratory measurements in this species and the high inter-individual variability observed. Altogether, these estimates are a first step towards a better characterization of the upper thermal tolerance and TSM of Atlantic bluefin tuna. For example, they can inform models projecting impacts of climate change scenarios at non-analog temperatures (i.e. temperatures beyond those previously observed in the field) (Muhling et al., 2020; Rose et al., 2024). Nevertheless, it will be important to expand research beyond the short- and medium-term effects of temperature alone to understand better the processes that threaten the survival and life cycles of marine species in a future climate.

In conclusion, the present study provides novel results on the thermal limits of bluefin tuna larvae. Combined with previous estimates made on embryos, results suggest that both stages have a relatively similar lower and upper thermal tolerance, acknowledging that the different metrics were used for each stage. Using the obtained larval CTmax values (and its variability), present TSM for larvae in the Balearic Islands (a key spawning ground in the NW Mediterranean) is 3.6 (±0.6 SE) °C. This new knowledge contributes to advance our understanding of thermal tolerance of an iconic apex species, and more generally, to a general database on thermal limits for early life stages of fish. Moreover, we provide recommendations on fruitful pathways for future research on this species, given the methodological challenges encountered due to its extreme sensitivity to handling and confinement, and its small sizes.

CRediT authorship contribution statement

Marta Moyano: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Edurne Blanco:** Writing – review & editing, Methodology, Investigation. **Aurelio Ortega:** Writing – review & editing, Methodology, Investigation, Funding acquisition. **Fernando De la Gándara:** Writing – review & editing, Methodology, Investigation, Funding acquisition. **Laia Armengol:** Writing – review & editing, Visualization, Formal analysis, Data curation. **Myron A. Peck:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Patricia Reglero:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used Microsoft Copilot during the writing process to increase the readability of the manuscript. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

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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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2026.104410.

Data availability

Data are available at zenodo (10.5281/zenodo.18632811).

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