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Atlantic bluefin tuna spawn early to avoid metabolic meltdown in larvae

Øyvind Fiksen [ID][1,3] and Patricia Reglero[2]

[1]*Department of Biological Sciences, University of Bergen, 5020 Bergen, Norway*
[2]*Centro Oceanográfico de Baleares, Instituto Español de Oceanografía (IEO, CSIC), 07015 Palma de Mallorca, Spain*

Abstract. To predict shifts in phenology and distribution of organisms we need to understand how survival through early life stages depends on environmental conditions. Here, we present a mechanistic model of development, feeding and bioenergetics of early life stages in bluefin tuna and predict the optimal time of the year for them to be born. We find that the availability of prey, particularly nauplii, is sufficient for fast growth in tuna larvae while temperature is moderate during midsummer, but not when temperatures increase later in summer. High temperatures benefit egg and yolk-sac stages, but the metabolic needs of feeding larvae are hard to sustain during the warmest periods. Heatwaves, such as the one in 2003, increase larval survival potential, but shorten the viable part of the season for the larvae. Atlantic bluefin tuna is a large, highly migratory marine top predator that spawns while temperatures are rising, but before the heat leads to a metabolic meltdown in larvae. This means that food resources modulate how temperature change shifts optimal phenology.

Key words: annual routine; bioenergetics; foraging model; match–mismatch; oligotrophic ocean; phenology; spawning migration; temperature-dependence.

Introduction

Phenology emerges from natural selection in temporal cycles of predation risk and resource availability (Varpe 2017, Shima et al. 2020). These routines, such as timing of breeding or dormancy, can shift rapidly with environmental change, and are early responses to global warming (Yang and Rudolf 2010, Scranton and Amarasekare 2017). Marine heatwaves may also change biogeography and biodiversity (Oliver 2018) and challenge the physiological limits of organisms. To predict change in diversity, distributions and phenologies, we need reliable quantitative models that includes individual, mechanistic physiology (Frölicher and Laufkötter 2018, Lefevre and Wang 2021).

Mechanistic studies of phenology often use temperature as the single driver (e.g. Scranton and Amarasekare 2017), but how temperature changes growth rates depends on availability of food (Brett 1979, Huey and Kingsolver 2019, Gleiber and Sponaugle 2020).

Combining two or more environmental drivers of phenology is complex and requires careful implementation of ecological and the physiological processes through focused, localized and mechanistic studies (Yang and Rudolf 2010, Chmura et al. 2019).

Simple or not, the importance of seasonal peaks in food availability and the 'critical period' or 'match–mismatch' hypotheses remain a key link between environmental cycles and potential temperature-mediated trophic or phenological asynchrony (Visser and Gienapp 2019). Early life stages suffer high mortality rates (Bailey and Houde 1989), and growth and stage duration depend on sufficient prey resources. Therefore, seasonal cycles in prey availability and temperature interact to determine optimal spawning phenology.

Many large, migratory fishes spawn in oligotrophic seas where temperatures are high, while prey and predators are few (Reglero et al. 2014). We know little about how temperature and prey cycles combine to limit their potential spawning areas, or how their fast-growing larvae can find enough food here. For instance, Atlantic bluefin tuna (*Thunnus thynnus*, ABFT) migrate thousands of kilometers from their feeding areas to spawn in some of the most oligotrophic, desert-like parts of the

[3] E-mail: oyvind.fiksen@uib.no

Mediterranean Sea. Their larvae first feed on the early stages of copepods (nauplii) near the surface and, as they grow larger, they select for larger zooplankton (Catalan et al. 2011, Landry and Beckley 2019), particularly Cladocera, which have a peak of abundance in the summer (Atienza et al. 2016). After metamorphosis, at a body length of only 7–9 mm, they turn piscivorous and cannibalistic. The larvae only thrive in water above 20°C, which means that zooplankton associated with the deep chlorophyll maximum below the thermocline are inaccessible (Fig. 1a).

Here, we present a detailed mechanistic model of feeding and growth in the early life stages of ABFT, with seasonal temperature and food availability cycles as main explanatory drivers. Our aim is to explain their time of spawning, which, in the Balearic Sea takes place at temperatures just high enough for the eggs to hatch but lower than their physiological optimum for growth and development (Reglero, 2018b). Our hypothesis is that food limitation in the larvae plays a major role in their reproductive phenology. To test this hypothesis, we have developed a detailed and carefully parameterized individual-based model of the feeding process and larval capacities, including ontogeny of visual acuity, seasonal day–night light cycles, gut dynamics and constraints, visual prey detection, and prey field over the year (Fig. 1b).

MODEL AND METHODS

Overview of the model (see Appendix S1 for details and equations)

The model includes empirical temperature-dependencies of egg hatching, development, and metabolism (Fig. 1c), while foraging and growth processes are mechanistic functions of body size, temperature, prey abundance and day length. We follow an individual tuna egg from birth until metamorphosis to the post-flexion larval stage at c. 7.5 mm body length and find the probability of survival to this stage from every possible day of spawning as a proxy for fitness of an egg spawned at different days of the year. The simulation experiments predict how variation in prey densities and temperature affect the fitness of eggs born at different days, and find the optimal spawning phenology.

ABFT hatching success peaks at temperatures c. 25°C, egg developmental time decreases continuously with temperature from 19°C up to 32°C, and larvae grow faster in warmer water (temperature range 22–28°C) if given surplus food (Fig. 1c) (Reglero et al. 2018b). The duration of the yolk-sac stage (Yúfera et al. 2014, see Appendix S1) and the routine metabolic rate have only been measured at 25°C and 26°C, respectively (Blanco et al. 2020, see Appendix S1), and we assume Q10 equal to 2 for both these rates (Peck and Moyano 2016, Fig. 1c).

We model the flow of energy through an individual as a function of temperature and food ingestion, include the gut as a state variable which constrain ingestion as it

fills up, or growth rate if it is empty. The larvae do not find food in darkness and therefore the gut empties during the night. At first feeding their prey is mainly small copepod nauplii, then gradually they include Cladocera with larger body sizes (Catalan et al. 2011); we assume a linear increase from 0 to 1 in capture probability of Cladocera as larvae grow from first feeding to metamorphosis. We model the foraging process from Holling disk mechanics, where a key factor is the prey detection distance, based on data from a study of eye development and visual acuity in southern bluefin tuna larvae (Hilder et al. 2019). The model links prey availability with the energy budget of individual larvae and predicts how temperature and prey modulate growth over the diel and seasonal cycle (see Appendix S1: Eqs. S1–S6).

In addition, survival (egg fitness) ultimately depends on predation mortality, which may be in the order of 0.6/day in early life stages of tuna (Davis and Lyne 1991), leading to severe consequences of delayed development and increased stage duration (Bailey and Houde 1989). We define fitness of an egg as the accrued survival probability from its birthday, through all hurdles of hatching, growing, finding enough food, and surviving. The model is coded in Python 3.7, and the source code is available (see *Open Research* and Data S1: Figures-forPaper.py).

Field data

The larval data are from field sampling of ABFT larvae during spring and summer from 2001 to 2017 in the Balearic Sea, Western Mediterranean (see Appendix S1). We use sea surface temperatures from the NOAA Coast-Watch Program and NASA's Goddard Space Flight Center (https://coastwatch.pfeg.noaa.gov/erddap/index.html), for the tuna spawning areas near the Balearic Islands, as in Reglero et al. (2018b). We have specified zooplankton prey densities, and their seasonal cycle, mainly based on long-term monitoring of zooplankton on the shelf near Mallorca (Fernández De Puelles and Alemany 2007). Cladocera densities at the spawning areas are also available from annual surveys (Appendix S1: Table S1), and we have used these sources to specify average concentrations of Cladocera prey over the season (Appendix S1: Fig. S1). From the model, the minimum viable prey concentration is c. 300 nauplii/m^3 near the surface throughout the year and we test the sensitivity to values in the range 300–600 nauplii/m^3 (Appendix S1), which is realistic in these very oligotrophic waters (de Puelles and Gras 2003, see Appendix S1).

RESULTS

Larval growth over the season

The larger larvae depend on Cladocera or similar prey larger than nauplii to grow at temperature-limited rates (Fig. 2a). The seasonal warming in summer increases
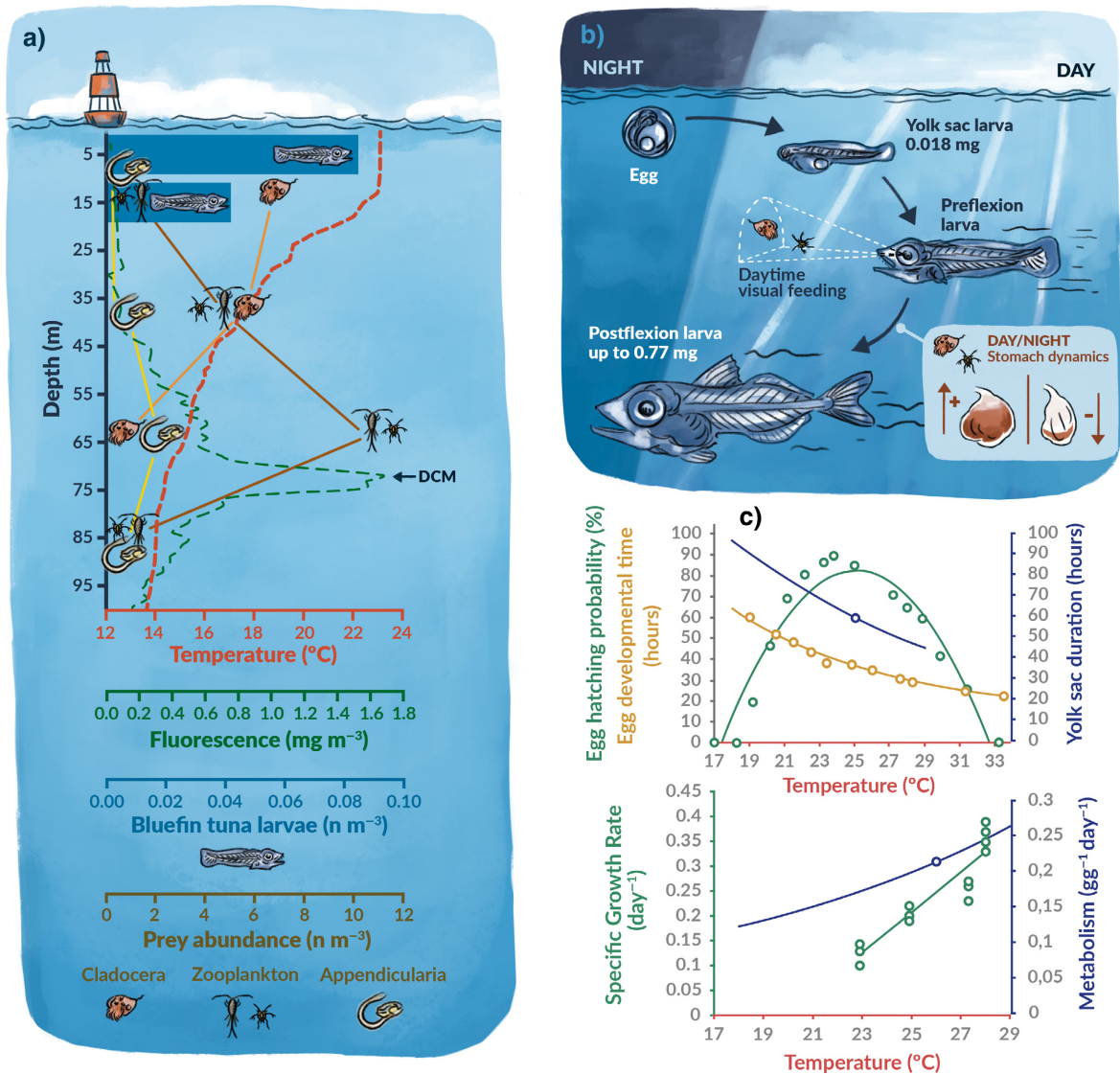
FIG. 1. (a) Vertical habitats of oligotrophic open oceans are characterized by a deep chlorophyll *a*, maximum where zooplankton and nauplii abundances are highest, and a shallow warm surface mixed layer where Cladocera, some copepods, and fish larvae can live. This figure shows a typical station in the spawning area, with Copepods, Cladocera and Appendicularia (Olivar et al. 2014), Atlantic bluefin tuna (ABFT) larvae (Reglero et al. 2018*a*) and also the temperature and fluorescence (Mena et al. 2019). (b) Conceptual illustration of the model and key ontogenetic stages. (c) Key temperature dependencies of hatching success, egg developmental time and larval growth (Reglero et al. 2018*b*), yolk sac duration (Yúfera et al. 2014), and metabolism (Blanco et al. 2020).

both growth potential and metabolic energy needs of larvae, and the daily net growth (ingestion-metabolism) therefore peak around midsummer (Fig. 2b). As summer proceeds (after day 190), the declining Cladocera abundance and increased metabolic costs restrict growth rate.

A 'metabolic meltdown' – in which energy needs to fuel metabolism exceed ingestion as temperature increase (sensu Huey and Kingsolver 2019) – occurs for larvae born later in the season (Fig. 2c). An egg spawned at day 160 encounters a good food supply as a larva relative to its energetic needs, but also low temperatures and growth rates while they are small and vulnerable to predation.

An egg spawned at day 180 grows faster through the egg and first feeding phase, but slower as it approaches the post-flexion stage. The warmer water in summer increases metabolic costs and their need for food. At birthday 200, the temperature is high while Cladocera abundance plunges, and food intake does not support growth of larger larvae, leading to a metabolic meltdown where ingestion rates support metabolic needs, but not growth (Fig. 2c). In summary, these mechanisms create a peak in egg fitness in June/July (at about day 190) for this seasonal pattern in prey supply and temperature, and matches the actual spawning dates quite well.

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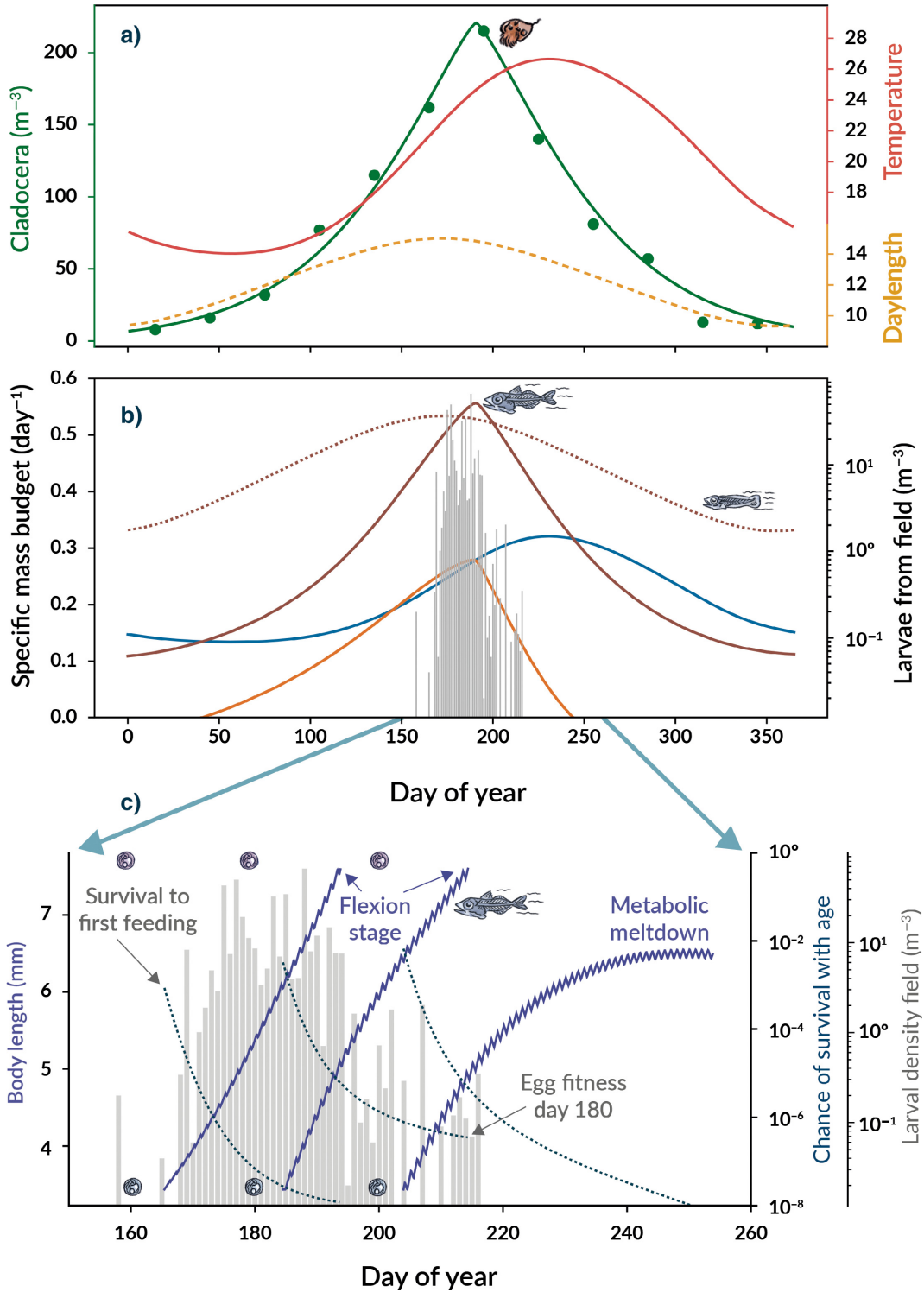
Egg fitness over the season

Next, we tested how prey size-spectra and concentrations shape the seasonal pattern of egg fitness (Fig. 3a). If eggs and larvae grow according to their temperature potential, with no limits from darkness, digestion, or food, then relative egg fitness follows the temperature cycle. This prediction does not match the observed

Fig. 2. The seasonal cycle of the environment, feeding, metabolic budgets, growth, and survival of bluefin tuna larvae. (a) Abundance of the important Cladocera prey *Pseudoevadne* sp. peaks in the summer (green dots, average monthly mean values from a coastal monitoring time series described in Fernández De Puelles et al. (2007); see Appendix S1). Temperature (red line) is the long-term sea surface temperature (SST) daily average in the spawning area, and daylength the number of hours available for feeding. (b) For larger larvae (brown line, in units of ingestion body mass^{-1} d^{-1}) the Cladocera are important prey, while smaller larvae (dotted line) feed and grow mainly on nauplii, which are constantly abundant over the season. The specific routine metabolic rate (blue line) is a function of temperature, only. Realized growth (orange line) is the difference between ingestion (assimilation) and routine metabolic rate (shown for a 7.5 mm larvae). (c) Growth (blue lines) and survival (grey broken lines) of individual tuna born at three different dates (blue dots) in the season, with our baseline assumption about food availability (Cladocera density is 10% of nearshore long-term average, 400 nauplii/m^3) and predation. After spawning, individuals must survive the egg and yolk stage before first feeding. Eggs born later (after day 200) do not find enough food to grow through preflexion, and their growth stalls with severe consequences for survival. The saw-tooth pattern in size reflects the day–night cycle in feeding success, at night the gut runs empty and growth is negative, particularly at high temperatures late in season.

breeding time (Fig. 3a; no food limitation). The more food limited is the larval growth, the earlier is the egg fitness peak, as ingestion needed for growth increases with high temperatures later in season (Fig. 3a).

The predicted egg fitness is quite sensitive to supply of nauplii, with the peak appearing *c.* 20 d later for every 100 nauplii/m^3 added (Fig. 3a). Both the seasonal curve and the absolute value of fitness depend more on the concentration of first feeding prey (nauplii) than on Cladocera, as slow growth for small larvae is more costly for survival than for larger larvae, but survival still increases by an order of magnitude if the density is 30 rather than 20 Cladocera/m^3. Also, the presence of Cladocera increases viability later in the season, when temperatures are high (Appendix S1: Fig. S3). The seasonal peak in egg fitness does not depend on the peak in Cladocera and is present even if both prey types are kept constant over time (see Appendix S1: Fig. S3 for sensitivity analyses of different combinations of nauplii and Cladocera; Appendix S1: Fig. S4 for validation of modeled growth rates with field observations; and Appendix S1: Fig. S5 for combinations of temperature and prey ingestion leading to metabolic meltdown).

Egg fitness during a heatwave

In 2003 a heatwave hit the Mediterranean Sea. For eggs in the main spawning period (days 170–190), the 2003 heatwave increased fitness by one order of magnitude compared with the cold 2004, while metabolic meltdown occurs earlier (Fig. 3b). By comparison, fitness is three orders of magnitude higher when nauplii concentrations increase from 300 to 500/m^3 (at 30 Cladocera/m^3) (Appendix S1: Fig. S3).

Growth of larvae in the field and in the model

Malca et al. (2017) measured the growth rate of surviving bluefin tuna larvae, based on otolith readings from a survey in the spawning area (Appendix S1: Fig. S4). These larvae appear to grow near the temperature maximum estimated by Reglero et al. (2018*b*), indicating these survivors were not limited by their food supply. The model matches this growth rate at *c.* 500 nauplii/m^3 (Appendix S1: Fig. S4), while the predicted peak in egg fitness remains within the observed

spawning period (Appendix S1: Fig. S3). Metabolic meltdown occurs at 22, 25 and 28°C if ingestion is 30%, 60% and 90% of body mass per day, respectively (Appendix S1: Fig. S5).

Discussion

Many organisms breed at specific times of the year, normally as an adaptation to the seasonal cycle in some important resource, most notably food and temperature, and often in response to needs of early life stages. Here, we have modeled the development, growth and survival of individual fish eggs in a seasonal cycle of environmental variables and show that phenology can be predicted from fundamental physiological and ecological processes. The optimal growth rate occurs before peak temperatures, at a time when food intake supports both the potential growth rate and the metabolic rate. Later in the season, temperatures increase and food intake cannot cover larval metabolic needs, and late offspring face a metabolic meltdown (*sensu* Huey and Kingsolver 2019) in which no energy is available for growth. This may explain why ABFT spawn earlier than predicted with temperature as the only driver of growth (Reglero et al. 2018*b*). The temperature–food ration dependence is a logical and well known response in fishes (Brett 1979), and recently also seen in a tropical larval tuna (Gleiber et al. 2020), but often ignored in predictions of thermal performance, phenology and spatial distributions.

The surface mixed layer of the Mediterranean Sea is an oligotrophic ecosystem, and not an obvious place for offspring with high growth potential and food requirements. The first feeding tuna larvae depend on production of copepod nauplii and Cladocera, which are tightly linked to the microbial food web (Landry et al. 2019). At the right temperature, the presence of these prey creates an opportunity in time and space where first feeding tuna larvae can grow. Similar conditions occur in the Gulf of Mexico, another main spawning area for ABFT (Landry et al. 2019). Based on measured metabolic needs, growth potential and a mechanistic model of prey encounter rates, we show that there is enough food for the larvae during the short time window in June–July. The cooler temperatures earlier in the year allow ABFT
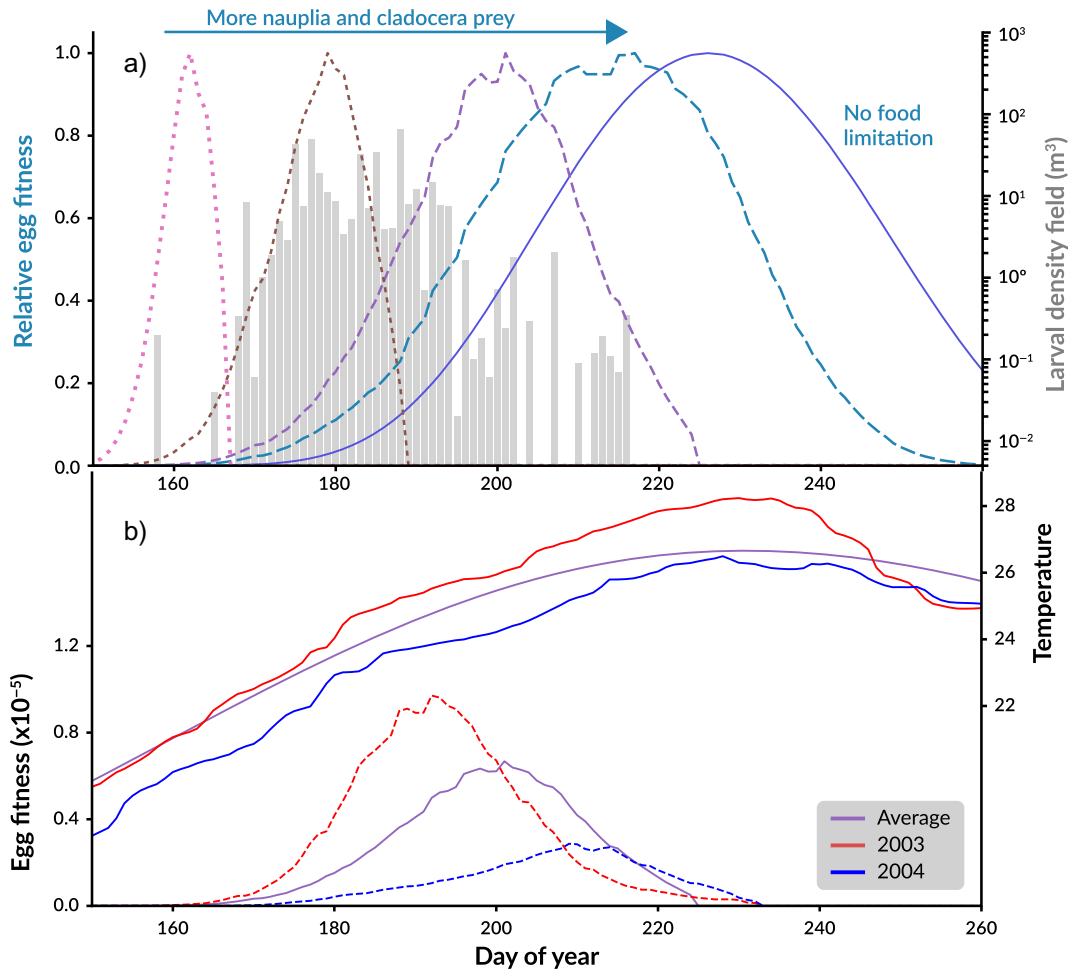
FIG. 3. Food and temperature determine the fitness of BFT eggs in the Mediterranean Sea. (a) Eggs born on each day have an accrued chance of survival to the flexion metamorphosis based on their growth trajectory through the seasonal temperature and prey availability. The light blue line shows egg fitness scaled to the maximum value if growth is driven only by temperature (see Reglero et al. 2018*b*). Dotted line (pink) indicates the lowest viable prey density of 300 nauplii/m^3: 10% of the coastal Cladocera concentration in Fig. 2a, then 400 + 10% (brown), 500 + 15% (turquoise), and 600 nauplii/m^3 + 20% (blue dashed line). Bars show data from larval surveys around the Balearic Sea during 2003–2017. (b) Egg fitness under a heat wave (2003) and a cooler year (2004) compared with baseline average temperature and prey (turquoise line, average at prey density of 500 nauplii/m^3 and 15% of the coastal Cladocera concentration), with numeral fitness values.

to spawn in these offshore waters with few prey and predators for their offspring.

The seasonal peak in Cladocera suggests a classical match–mismatch driven phenology in ABFT, but the seasonally stable abundance of nauplii was more decisive for predicted phenology and growth of first feeding larvae in the model. As food supply increases, the optimal breeding time is progressively later in the season as potential for larval growth is higher under warmer temperatures.

In our model, the first feeding larva is the most temperature-sensitive stage. Development of eggs and yolk-sac larvae are faster if temperature increases, but the first feeding larva needs abundant food supplies to grow fast. Eggs and spawners may be the most sensitive

stages for climate vulnerability in fish (Dahlke et al. 2020), as embryos often have a narrower thermal tolerance range than larvae and later stages (Pörtner and Peck 2010). In contrast, thermal tolerance in terms of hatching success is quite wide in ABFT embryos, and our model shows how food limitation can narrow the viable thermal range of feeding stages. The mechanistic reasoning in Dahlke et al. (2020) is that aerobic capacity improves in larvae due to a more developed cardiorespiratory system that improves oxygen supply to cells and therefore tolerance to extreme temperatures. However, the tolerance measured for larvae fed *ad libitum* may not reflect ecologically relevant temperature tolerance under food limitation and can be an overestimate for natural conditions. At a global scale, growth in fishes is not a

direct function of temperature (van Denderen et al. 2020), because growth is a complex phenomenon in which ecology, physiology and life-history strategies play central roles (Holt and Jørgensen 2015, Lefevre et al. 2021).

Some elements relevant to phenology are more difficult to quantify and model than other. The growth potential under excess food supply is well known, but the prey abundance where food becomes limiting is dependent on the ability of larvae to build intermittent stores to continue growing during periods without food, such as during the night or if prey is patchily distributed. The energetic costs of activity and swimming are not explicitly represented in the model, and metabolism and ingestion have been assumed to be independent, although ingestion, specific dynamic action and assimilation efficiency may interact. Despite these limitations, the model does predict *in situ* larval growth with realistic prey abundances, and the predictions of spawning time compare well with observations.

Marine heatwaves may increase in frequency with climate change (Oliver et al. 2018). Such interannual temperature variation affects egg fitness differently, depending on the level of food limitation: more food increases the threshold for metabolic meltdown, and then warmer water is beneficial to ABFT larvae. During the heatwave in 2003, the predicted metabolic meltdown for tuna larvae occurred early, lowering the optimal temperature, and shifted optimal time of birth 2–4 weeks earlier in the season compared with cooler years. The predicted fitness benefit of the 2003 heatwave assumes that prey populations do not decline, but this depends on how productivity in the lower trophic layers responds. The Cladocera species in ABFT spawning areas are heat tolerant, and increased in abundance during the 2003 heatwave (Atienza et al. 2016). ABFT abundance increased after 2003, and the heatwave may have contributed to this. The recovery of the Eastern stock of ABFT in the last decade is an example of management success, but this recovery was made possible by some good years of recruitment at the main breeding grounds.

Phenologies may shift quickly in response to climate change, and the scientific understanding of phenology shifts needs to move from correlative studies to mechanistic, causal and testable hypotheses (Chmura et al. 2019). A model that integrates physiology and ecological foraging mechanics to predict the fitness of an egg is a powerful tool to understand how environmental drivers shape phenologies and selection pressures for shifting breeding schedules.

Many tuna species spawn in the warm oligotrophic open ocean, where metabolic meltdown is a constant risk for the early life stages. The mechanistic model allows us to identify windows in spatial and temporal cycles of temperature and resources between which animals can migrate to ease physiological stress, reproduce or increase growth rates. This research opens up a deep integration of laboratory studies covering physiology, ecological processes, environmental drivers from field observations or modeled future scenarios to predict both shifting phenology, recruitment success and biogeography.

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