

# Spawning site distribution of a bluefin tuna reduces jellyfish predation on early life stages

Daniel Ottmann<sup>1\*</sup>, Øyvind Fiksen,<sup>2</sup> Melissa Martín,<sup>1</sup> Francisco Alemany,<sup>1</sup> Laura Prieto,<sup>3</sup>  
Diego Álvarez-Berastegui,<sup>1</sup> Patricia Reglero<sup>1</sup>

<sup>1</sup>Centro Oceanográfico de Baleares (IEO, CSIC), Palma de Mallorca, Spain

<sup>2</sup>Department of Biological Sciences, University of Bergen, Bergen, Norway

<sup>3</sup>Instituto de Ciencias Marinas de Andalucía, Consejo Superior de Investigaciones Científicas (ICMAN-CSIC), Puerto Real, Spain

## Abstract

Bluefin tunas across the world migrate long distances to spawn in particularly warm and oligotrophic areas constrained by oceanographic fronts. The low abundance of predators in these areas increases survival chances of their early life stages, but its importance for choice of spawning habitat is unknown. Here, we use estimated clearance rates and data on spatial distributions of Atlantic bluefin tuna larvae *Thunnus thynnus* and metaephyrae of the jellyfish *Pelagia noctiluca* to quantify predation at a major spawning ground in the Mediterranean Sea. We found that high densities of *P. noctiluca* can rapidly deplete tuna eggs and preflexion larvae, but their patchy distribution and low spatial and temporal overlap results in overall low predation. The specific distribution of the spawning sites suggests that bluefin tunas may use local oceanography as cues to spawn outside areas with high predator densities.

All species have strategies to maximize offspring survival, including selection of breeding places with increased food provisioning or safeguarding offspring from predators by seeking refuge within physical barriers (e.g., bird nests in trees or burrows) or nursery habitats (e.g., mangroves, kelp forests). In the marine realm, only a small proportion of the offspring will survive the first days of life, and minor variations of survival chance can generate order-of-magnitude differences in the supply of new recruits (Houde 2008). Sea birds, planktivorous fishes, and invertebrates prey on eggs and larvae of marine organisms, but their uneven distribution create spatial loopholes of survival opportunities (Irigoin et al. 2007). Therefore, migrating and reproduce in areas with low predator abundance may be the best option to invest in offspring survival (McKinnon et al. 2010; Ims et al. 2019).

Across the world, temperate tunas migrate long distances to spawn in areas where temperature favors growth of the offspring (Block et al. 2005, 2011; Muhling et al. 2017). The Atlantic bluefin tuna *Thunnus thynnus* swims from its vast feeding grounds to reproduce in areas of the Gulf of Mexico,

Slope Sea, and the Mediterranean Sea (Muhling et al. 2013; Richardson et al. 2016), where primary productivity tends to be low. Spawning events usually occur near oceanographic structures of barren waters (García et al. 2005; Teo et al. 2007; Alemany et al. 2010; Álvarez-Berastegui et al. 2014) posing a paradox about why they spawn in sites where offspring may risk starvation. To make this strategy effective, something else must outweigh the risk of starved offspring. The answer to this paradox may be reduced predation on eggs and larvae, as these oligotrophic regions sustain few planktivore fishes and other carnivorous invertebrates (Bailey and Houde 1989; Bakun and Broad 2003; Bakun 2013). However, this hypothesis remains unverified.

Gelatinous organisms can be major predators of plankton in the oceans and cause regime shifts of entire marine systems (Purcell and Arai 2001; Daskalov et al. 2007). *Pelagia noctiluca* is a dominant holopelagic jellyfish in the Mediterranean Sea whose early life stages remain near the surface along with tuna eggs and larvae (Ottmann et al. 2021). In the western Mediterranean Sea, these early stages are most abundant in late-spring (Milisenda et al. 2018a), shortly before bluefin tuna arrive for their spawning rendezvous (Aranda et al. 2013). Early life stages of *P. noctiluca* are opportunistic and voracious predators on a wide range of micro- and mesozooplankton (Tilves et al. 2018; Milisenda et al. 2018b), and are therefore more abundant in more productive waters (Ottmann et al. 2021). Their capacity to capture prey develops rapidly in their early life, and tuna eggs (Gordoa et al. 2013) and larvae (Purcell

\*Correspondence: daniel.ottmann.riera@gmail.com

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et al. 2014) have been observed in the diet of metaephyrae (4–8 mm in diameter; Fig. S1).

Combining empirical observations with mechanistic models of capture efficiency is a powerful way to predict the interaction strength between predator and prey at meaningful scales (Estes 1998). Here, we use estimated clearance rates to test the hypothesis that predation by early life stages of *P. noctiluca* on bluefin tuna offspring is low. We focus on *P. noctiluca* metaephyrae because they are voracious predators and regionally abundant organisms that overlap in depth with tuna early life stages. Thus, we model the predatory potential of metaephyrae considering tuna's temperature-dependent development time from egg through the end of the preflexion stage and combine it with observed field distributions. Larvae at this stage are particularly vulnerable to metaephyrae, as they lack sufficient visual and swimming capacities to effectively escape from predators. Our 6-yr sampling took place during the bluefin tuna reproduction peak in the Balearic archipelago, one of the main spawning areas in the Mediterranean Sea (Fig. S1). At this time of the year, newly arrived water from the Atlantic collides with more haline resident water forming a front with a characteristic salinity signature (Balbín et al. 2014), whose position ranged from more than 40 n miles south of the archipelago in 2012 to about 10 n miles off northern Mallorca in 2016. We model how the metaephyra's predator potential depends on the spatial distribution of both *P. noctiluca* metaephyrae and tuna preflexion larvae in relation to local oceanography.

## Methods

### Field sampling and laboratory processing

To map the distribution and overlap of early life stages of bluefin tuna and *P. noctiluca*, we analyzed samples from a series of six annual cruises in the western Mediterranean (Table S1). Briefly, plankton samples were collected on a 10 × 10 nautical mile grid during the peak of the tuna spawning season (June 17–July 11; Fig. S1). Because more than 95% of the larval tuna and *P. noctiluca* early life stages permanently remain in the top 30 m of the water column (Fig. S2; Reglero et al. 2018a; Ottmann et al. 2021), we selected samples of 540 oblique bongo tows (90 cm diameter and 500 µm mesh size) deployed down to 30 m depth in 2012–2017 and consider them representative of both populations. Immediately after each tow, samples were preserved in 4% formalin buffered with borax for quantitative analysis. Temperature and salinity profiles were recorded immediately after each plankton tow deploying a CTD to >350 m depth. With these profiles, we could identify the mixed layer depth and calculate its mean water temperature and salinity.

In the laboratory, tuna larvae and early life stages of *P. noctiluca* were counted for all stations. When a sample appeared to contain more than 500 *P. noctiluca*, we took an aliquot with a Folsom divider and the number of counted individuals was multiplied by the corresponding factor to calculate the

total number of jellyfish in each sample. To calculate population densities, we divided the total number of individuals in each tow by the filtered volume in cubic meters. We then calculated overlap by multiplying the densities of each species. Jellyfish smaller than 4 mm in total body diameter do not consume fish eggs and larvae (Gordoa et al. 2013; Purcell et al. 2014), so we multiplied the *P. noctiluca* count of each sample by the overall proportion of metaephyrae stages (>4 mm after correcting for 25% shrinkage in formalin [personal observation]) to exclude the nonpredatory fraction of the *P. noctiluca* population. Likewise, we truncated the tuna population to include only preflexion larvae (≤4.5 mm in formalin) that have weak swimming capacity at most and limited visual capacity.

Measurements were taken for all tuna larvae (standard length) and for 2576 *P. noctiluca* (total body diameters) of 23 randomly selected field stations of 2014–2016 with ImageJ v1 (Schneider et al. 2012) on images taken with a camera-attached stereoscope.

### Data analysis

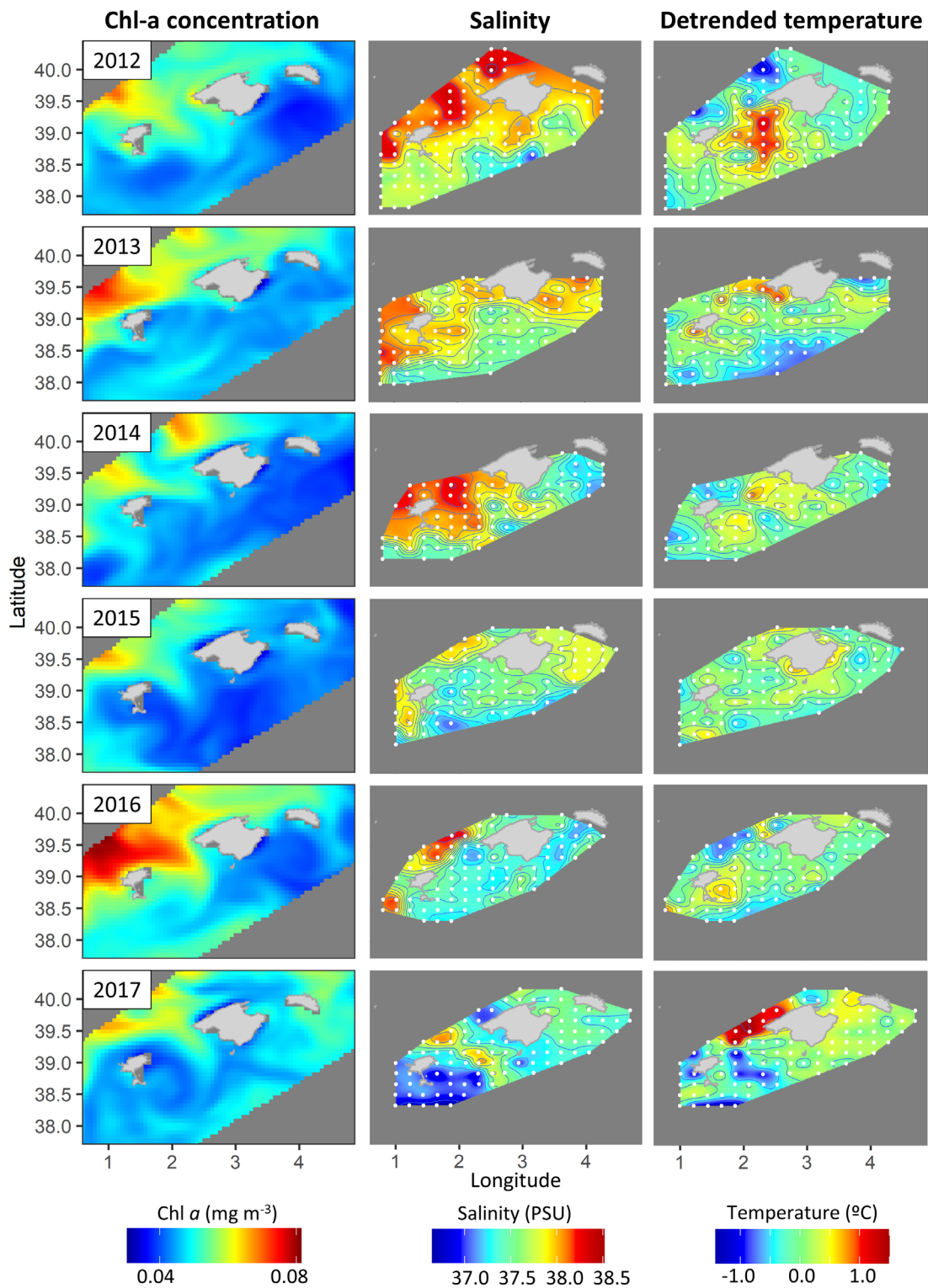
What is the risk that a tuna egg or larva is eaten by *P. noctiluca* metaephyrae? We use encounter theory to find an answer to this question and assume that each predator–prey encounter is fatal for the prey. This is reasonable given the limited ability of eggs and preflexion larvae to escape. For an individual egg or larva, the expected predator encounter rate  $E$  (d<sup>-1</sup>) follows a Holling type I functional response (Sørnes and Aksnes 2004):

$$E = Nc \quad (1)$$

where  $N$  is the predator density (metaephyrae m<sup>-3</sup>), and  $c$  is the predator clearance rate (m<sup>3</sup> metaephyrae<sup>-1</sup> d<sup>-1</sup>). We apply a clearance rate of 0.099 m<sup>3</sup> metaephyrae<sup>-1</sup> d<sup>-1</sup>, which is the mean clearance rate estimated for 5 mm metaephyrae of *P. noctiluca* preying on tuna eggs in a set of experiments at 23°C where each individual could clear 0.018–0.181 m<sup>3</sup> d<sup>-1</sup> (Gordoa et al. 2013). Their digestion time on fish larvae (Purcell et al. 2014) enables them to eat about eight larvae per day before getting satiated. Larval densities would need to be four times the maximum observed in the field for satiation to affect our model. Feeding rate of invertebrate organisms increase with temperature  $T$  (°C), thus we applied a  $Q_{10} = 2.8$  to include temperature-dependence effects on clearance rate (Hansen et al. 1997).

$$c = 0.099 \times Q_{10}^{(23-T)/10} \quad (2)$$

Shorter stage durations at higher temperatures can increase survival in eggs and larvae (Bailey and Houde 1989). Since tuna eggs and larvae develop faster at higher temperatures (Reglero et al. 2018b), we can predict survival chance from metaephyrae predation for an egg and through the vulnerable preflexion larval stage as a function of predator encounter rate  $E$  and temperature-dependent development time  $d$ . Egg development time  $d_E$  of tuna vary with water temperature between 1 and 2.5 d at 19°C and 32°C, respectively (Reglero et al. 2018b):



**Fig 1.** Surface chlorophyll concentration and salinity and detrended temperature of the mixed layer. Chlorophyll concentration was calculated from model reanalysis and salinity and detrended temperature were calculated from CTD data as in Ottmann et al. (2021).

$$d_E = 8787.5T^{-1.701} \quad (3)$$

Once the egg has hatched, the yolk-sack larvae will remain some time without growing while developing feeding structures. The time (days) it takes from the egg hatch to first feeding  $d_{YS}$  is temperature  $T$  dependent and can be calculated using the recorded 2.5 d duration at a temperature of 25°C (Yúfera et al. 2014) and a  $Q_{10_{YS}} = 2$  coefficient (Blank et al. 2007; Peck and Moyano 2016):

$$d_{YS} = 2.5 \times Q_{10_{YS}}^{(25-T)/10} \quad (4)$$

Similarly, the time (days) it takes from a first feeding larva to begin the notochordal flexion  $d_{PF}$  can be estimated using its specific growth rate  $SGR$  (mg mg d<sup>-1</sup>) and the yolk-sac and preflexion dry weights ( $w_{ys} = 0.018$  mg and  $w_{pf} = 0.10$  mg, respectively) (Reglero et al. 2018b; Blanco et al. 2019):

$$SGR = 0.0418T - 0.8355 \quad (5)$$

$$d_{PF} = \frac{\ln(w_{pf}/w_{ys})}{SGR} \quad (6)$$

Then, we can calculate the total larval development time  $d_L$  from egg hatch to the beginning of flexion by simply adding  $d_{YS}$  and  $d_{PF}$ .

To illustrate how water temperature and predator abundance affect the probability of survival, we conducted a sensitivity analysis under different scenarios of temperatures and predator densities. We then used water temperature as measured from the upper mixed layer with a CTD for every year

between 2012 and 2017 to calculate the development time from egg to hatch and begin the flexion transformation ( $d_E + d_{YS} + d_{PF}$ ). Combining this with the observed abundance of metaephyrae from each sampling station and year, we can find a theoretical chance to survive predation from ephyrae for a single newborn tuna egg at each station, to hatching  $S_E$  or to flexion  $S_L$ :

$$S_E = e^{-Ed_E} \quad (7)$$

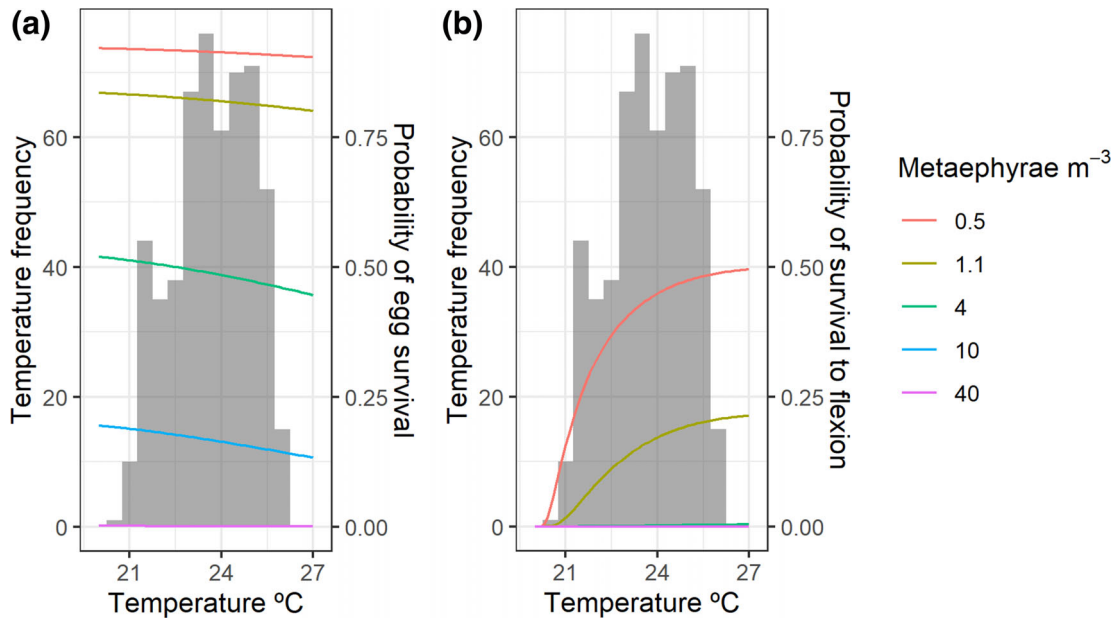
$$S_L = e^{-E(d_E+d_L)} \quad (8)$$

Then, we use the metaephyra's clearance rate (m<sup>3</sup> metaephyra<sup>-1</sup> d<sup>-1</sup>) and densities of metaephyrae  $N$  and preflexion larvae  $n$  (individuals m<sup>-3</sup>) from each station sampled in the different cruises to find consumption rate of larvae  $P$  (larvae m<sup>-3</sup> d<sup>-1</sup>):

$$P = Nnc \quad (9)$$

To illustrate how patchiness of tuna larvae and metaephyrae affects the predator-prey interaction strength, we compare the number of larvae consumed in each sampling station with the equivalent metric assuming all larvae and metaephyrae are homogeneously distributed across stations within each year.

To evaluate spatial segregation of spawning sites and stations with high predatory pressure, we apply a  $t$ -test to evaluate if metaephyrae densities  $\ln(N + 1)$  were lower in spawning sites with at least one larvae, compared to stations with absence of larvae (no recent spawning). Similarly, we evaluate



**Fig 2.** Survival probability of a *T. thynnus* (a) through egg (Eq. 7) and (b) accumulated egg and preflexion larva (Eq. 8) as a function of temperature-dependent development time at four densities of *P. noctiluca*. Shaded histogram indicates the frequency of observed field temperatures at a 0.5°C binwidth.



differences in the featured oceanography of tuna larvae and metaephyrae applying *t*-tests on their abundances as a function of water temperature and salinity of the mixed layer, and surface chlorophyll concentration (Fig. 1) as calculated from model reanalysis in Ottmann et al. (2021).

All analyses and figures were conducted in R v3.6.1 (R Core Team 2020) using packages “tidyverse” v1.3.0 (Wikham 2019), “maps” v3.3.0 (Becker et al. 2018), “raster” v3.1.5 (Hijmans 2020), and “MBA” v0.0.9 (Finley et al. 2017). The data and R code are available at [https://github.com/dottmann/tuna\\_jellyfish\\_predation](https://github.com/dottmann/tuna_jellyfish_predation).

## Results

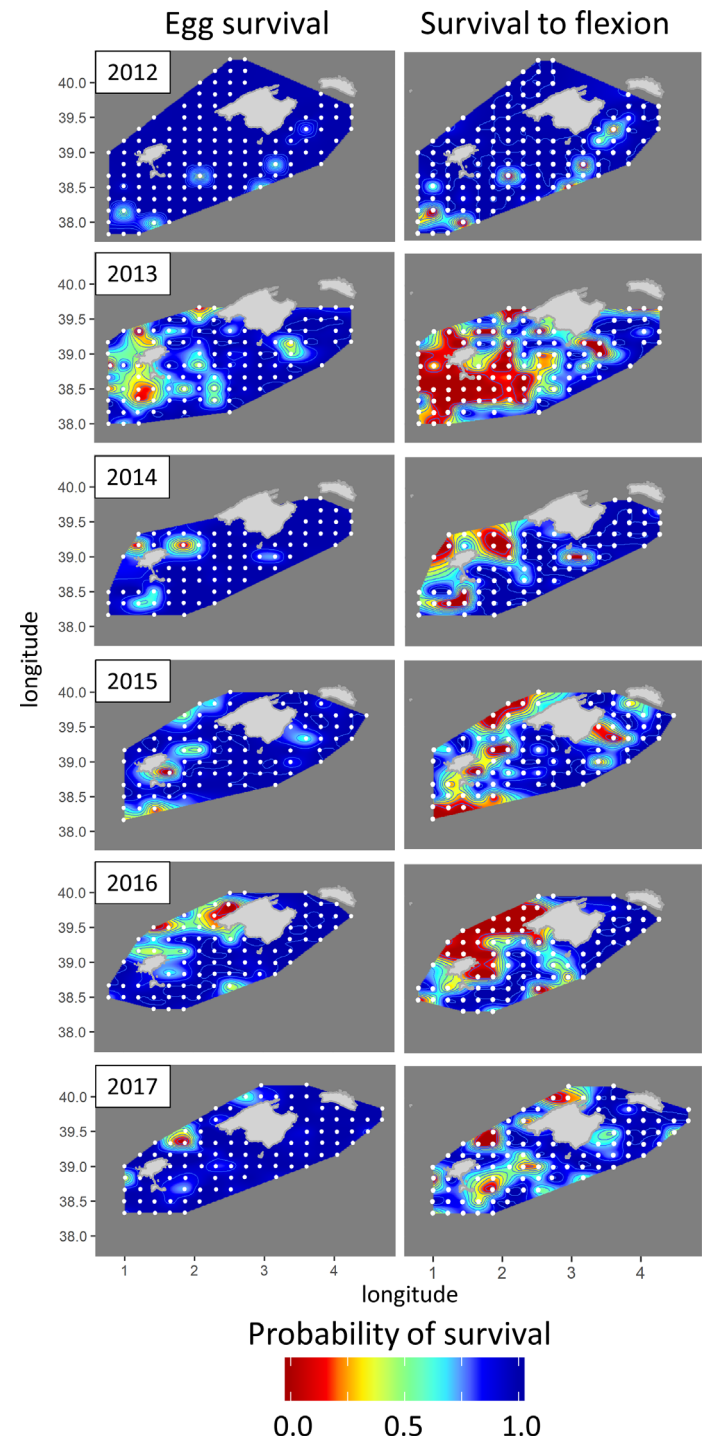
Temperature has mixed effect on survival of tuna early life stages (Fig. 2). Warmer temperature accelerates hatching time and larval growth, favoring shorter stage duration. However, warmer temperature also increases the clearance rate of metaephyrae. Egg duration does not shorten enough to compensate for the increased clearance rate. However, faster larval growth with temperature does compensate for the increase in metaephyrae clearance rate, and survival of the entire egg and preflexion is finally favored with warmer temperature.

Tuna survival is reduced at higher metaephyrae densities (Fig. 2). At 1.1 metaephyrae  $\text{m}^{-3}$  (the overall average density of metaephyrae), eggs have an 80–84% probability of survival, and chances to survive the egg and preflexion stage increases rapidly with temperature, up to 21% at 27°C. However, the survival chance is less than 0.1% at 10 metaephyrae  $\text{m}^{-3}$ , and 0 at 40 metaephyrae  $\text{m}^{-3}$  regardless of water temperature.

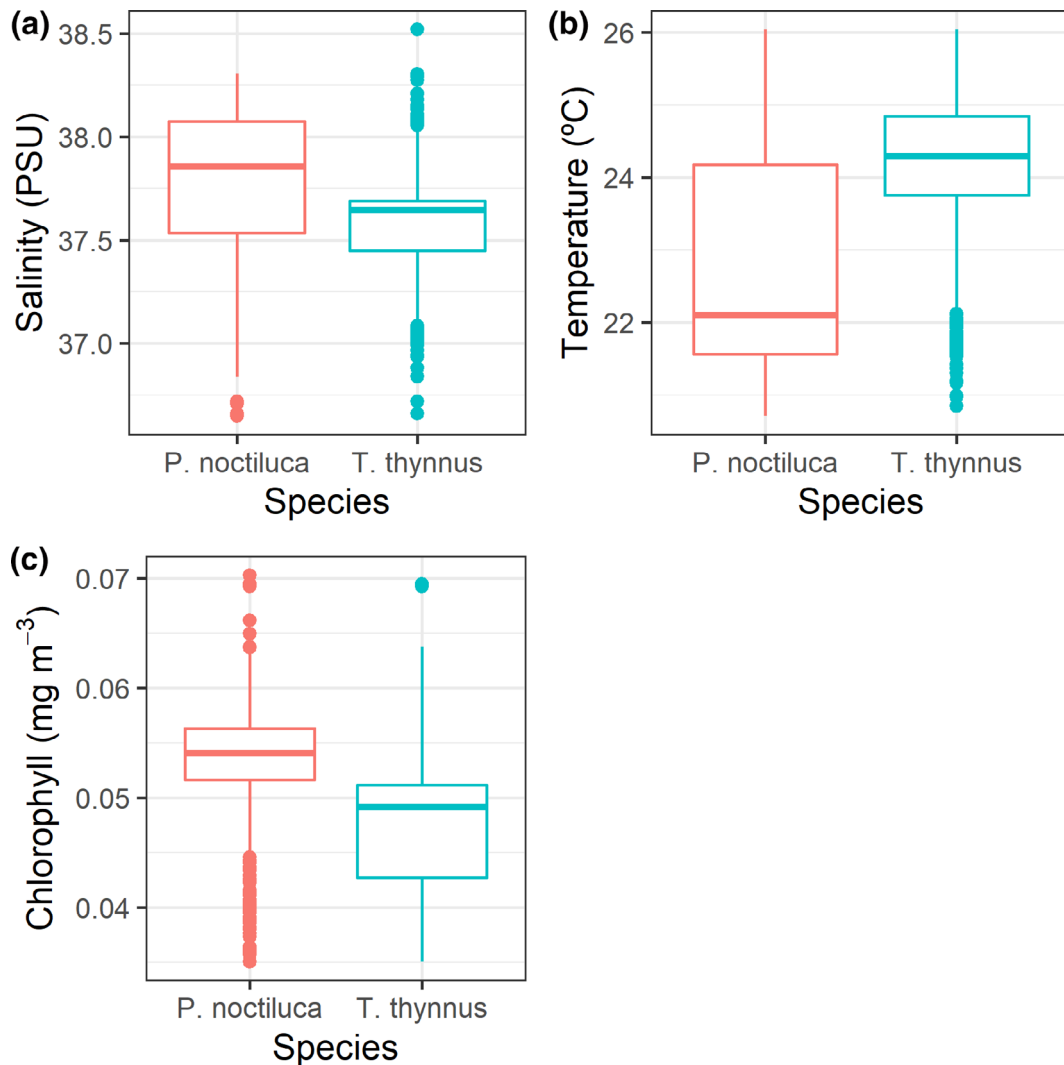
When we apply this model with temperatures and metaephyrae abundances observed in the field, it predicts that 90% of homogeneously distributed eggs can survive to hatching across all years, and 70% survive long enough to begin the flexion transition (Fig. 3). The probability of survival varies across years due to differences in metaephyrae abundances, with 2012 having the greatest survival chances, as opposed to 2013, when metaephyrae exerted major predatory pressure. Across all years, the probability of survival tended to be greater in the south-east side of the study area, while the probability of being preyed by metaephyrae before becoming a flexion-stage larva was greater than 99% in some parts of the western and northwestern sides of the study area. Metaephyra could clear an average of 0.11  $\text{m}^3 \text{d}^{-1}$  (SD = 0.38; median = 0.004) based on the average abundance across all years and stations, with an extreme case as high as 4.71  $\text{m}^3 \text{d}^{-1}$ . However, combining the spatial pattern of both predators and prey reveals that only three stations had an instantaneous predation rate greater than 0.1 larvae  $\text{m}^{-3} \text{d}^{-1}$ . In fact, the annual mean predation rate was 3.3–27.9 times lower across years compared to the hypothetical situation that all metaephyrae and larvae were homogeneously distributed.

The lack of spatial overlap between predator and prey prevents *P. noctiluca* to unleash its full predatory potential on

tuna larvae. Metaephyrae were more prevalent (75.6% positive stations) than tuna larvae (68.3% positive stations), and about



**Fig 3.** Probability of surviving predation from metaephyrae at the spawning ground. Predicted probability that an egg survives to hatch (left panels) and to notochordal flexion transition (right panels) given the water temperature and abundance of *P. noctiluca* metaephyrae observed at each station. The surveys took place during the *T. thynnus* spawning period every year from 2012 to 2017 around the Balearic Islands.



**Fig 4.** Predator and prey habitat difference in oceanographic variables. Frequency distribution, shown as boxplots, of *P. noctiluca* metaephyrae (red) and *T. thynnus* larvae (green) in relation to (a) mean salinity and (b) temperature of the mixed layer, and (c) surface chlorophyll concentration derived from a model reanalysis following Ottmann et al. (2021). All differences are significant (*t*-test;  $p < 0.001$ ).

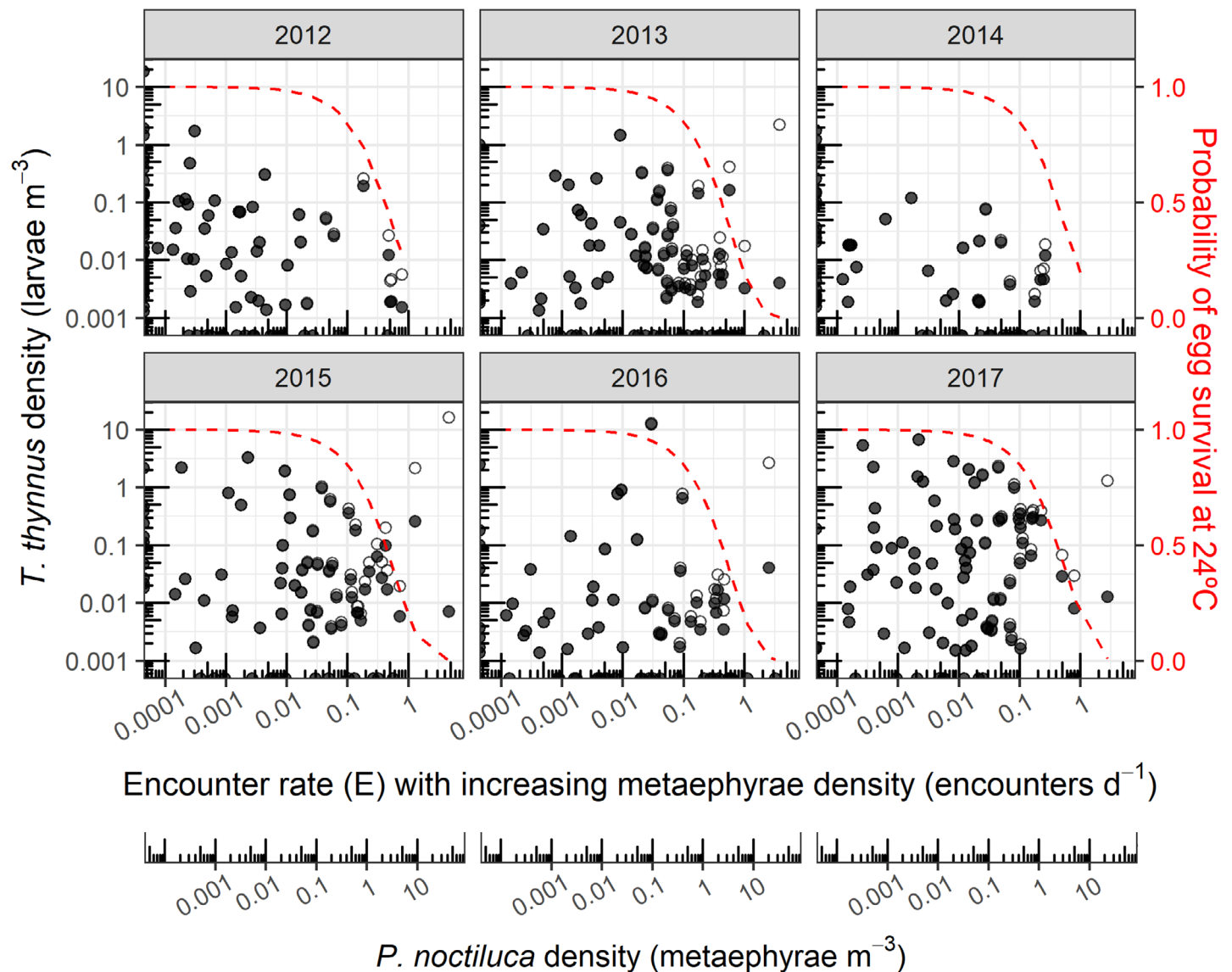
five times more abundant. The densities were on average 1.1 metaephyrae  $\text{m}^{-3}$  and 0.2 preflexion larvae  $\text{m}^{-3}$ , but they were not homogeneously distributed. Densities were low in most sampling sites, but some patches had up to 46.0 metaephyrae  $\text{m}^{-3}$  and 18.5 preflexion larvae  $\text{m}^{-3}$  (Fig. S3). Compared to metaephyrae, tuna larvae tended to be more abundant in sites with higher water temperature, lower salinity, and lower chlorophyll concentration (*t*-test;  $p < 0.001$ ; Fig. 4), which are oceanographic tracers of newly arrived Atlantic water to the Mediterranean Sea.

Moderate-to-high abundances of tuna generally occurred in stations with low encounter rate with metaephyrae (Fig. 5). Such distribution resulted in low spatial overlap with some exceptional hotspots where both species were abundant (Fig. 6). Back-calculated egg densities show that, in years when metaephyrae were most abundant and widespread (2013,

2015, and 2016), the high predator sites ( $>1$  encounter  $\text{d}^{-1}$ ) decimated larval densities (Fig. 5). However, top-down effects were weaker in years when metaephyrae abundances were low to medium (2012, 2014, and 2017). Stations that had at least one tuna larva (a spawning site) had fewer metaephyrae than stations where larvae were absent (no recent spawning; *t*-test,  $p = 0.012$ ).

## Discussion

*P. noctiluca* metaephyrae can be devastating predators of tuna early life stages when they occur at large densities ( $>10$  metaephyrae  $\text{m}^{-3}$ ). At more typical densities (e.g., 1.1 metaephyrae  $\text{m}^{-3}$ ), the probability of survival is substantially greater. Therefore, predation from metaephyrae can be a driver of natural selection towards spawning sites of the Atlantic

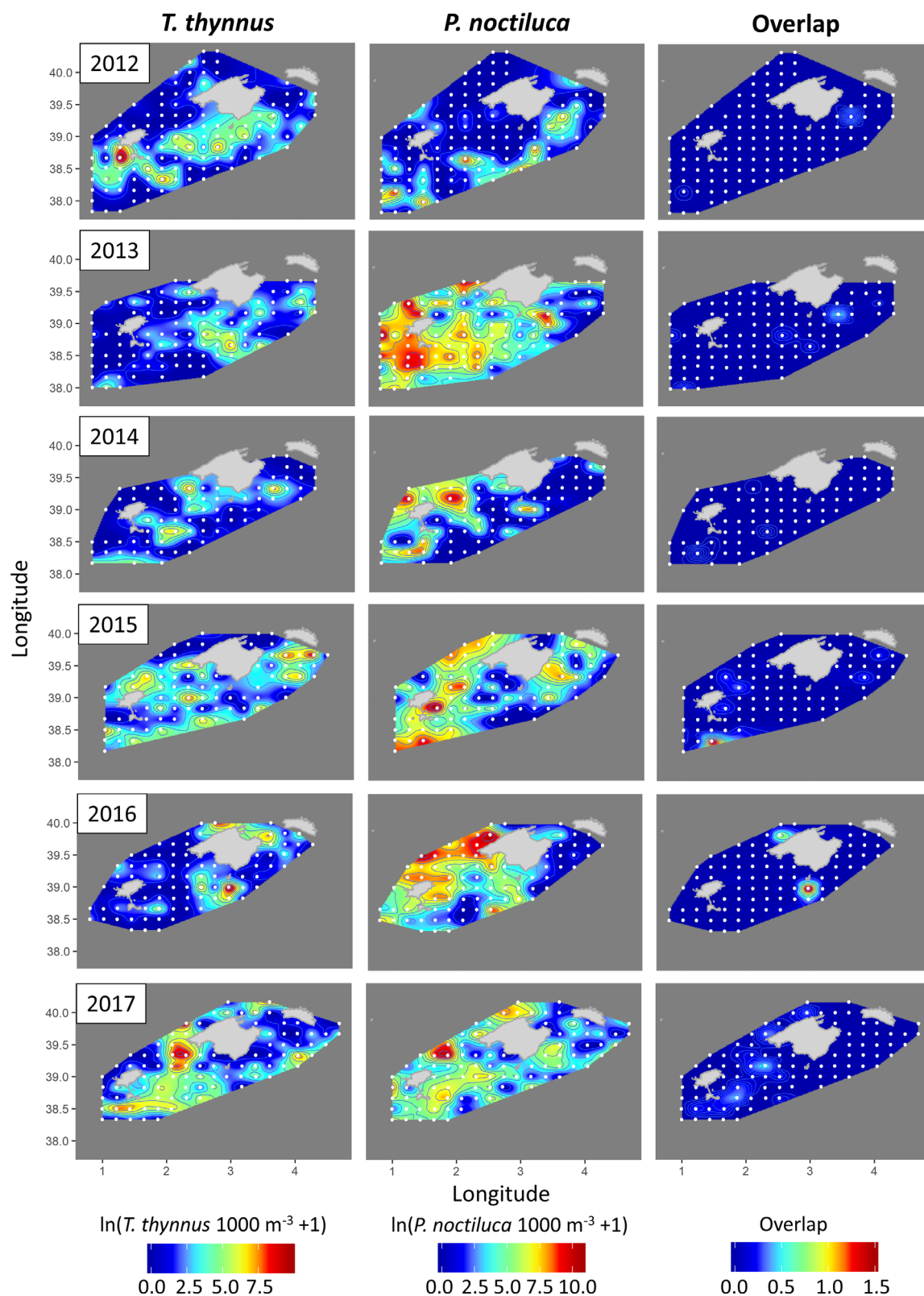


**Fig 5.** Density distribution of *T. thynnus* preflexion larvae relative to predatory pressure. *T. thynnus* preflexion larvae (filled dots) are scarcer at greater predatory pressure by *P. noctiluca* (shown as encounter rate and metaephyrae density). To visualize the predation effect, initial egg densities are back-calculated (empty dots) applying the model-predicted probability of survival during 40 h. The predicted probability that a tuna egg survives 40 h (egg development time at 24°C) as a function of metaephyrae concentration is shown with dashed red line. The low larval densities in sites with high predator encounter rates ( $>1$  encounter  $d^{-1}$ ) can reflect spawning site selection or a top-down effect from abundant metaephyrae.

bluefin tuna. In the spawning grounds around the Balearic Islands, fewer than 8% of the surveyed stations had more than 4 metaephyrae  $m^{-3}$  and only 17% had more than 1.1 metaephyrae  $m^{-3}$ . Therefore, the total predatory potential of metaephyrae was rather low across the spawning ground. Nevertheless, the average predicted survival over the whole study area was notably different across years, with 2012 having high chances of survival almost everywhere, while in years like 2013, the probability of survival was low in about half the spawning area. Including the actual distribution of both preflexion larvae and metaephyrae at each station showed that

predator-prey overlap occurred only in about half the sampling stations and annual mean captures were about 3–28 times lower than if larvae and metaephyrae were homogeneously distributed.

*P. noctiluca* can tolerate a wide range of temperatures and food regimes, but they thrive particularly well when the water temperature is warm, and food is abundant (Milisenda et al. 2018a). After the winter bloom, micro and mesozooplankton remain relatively abundant in spring, and water temperature warms up, starting to form a thermocline. Therefore, early life stages of *P. noctiluca* are relatively abundant at



**Fig 6.** Predator and prey distribution and overlap. Samples of *T. thynnus* preflexion larvae and *P. noctiluca* metaephyrae were collected around the Balearic archipelago during the *T. thynnus* spawning peak of 2012–2017. Abundances are log-transformed to facilitate visualization and overlap is calculated as the product of *T. thynnus* and *P. noctiluca* densities (individuals  $\text{m}^{-3}$ ).



this time of the year and located in the warmer waters near the surface (Ottmann et al. 2021; Pastor-Prieto et al. 2021). Mesoscale oceanographic processes feature local areas with enhanced productivity, favoring a patchy distribution of *P. noctiluca* early life stages.

Bluefin tuna appear to use oceanographic signatures to spawn within or near the front zone, mostly in fresher recently arrived Atlantic waters (García et al. 2005; Teo et al. 2007; Alemany et al. 2010; Alvarez-Berastegui et al. 2014), where metaephyrae are fewer than in the saltier side of the front (Fig. 4). This, combined with the patchy distribution of both species reduces the probability of predator-prey overlap (Ioannou et al. 2011). *P. noctiluca* metaephyra tend to be most abundant in the northwest side of the study area (Ottmann et al. 2021), where oceanographic characteristics feature typical resident Atlantic water and greater productivity fosters micro- and mesozooplankton sources of food. On the other hand, adult tuna spawn near the front area, with an increased tendency for the side with newly arrived and plankton impoverished Atlantic water (Alemany et al. 2010; Alvarez-Berastegui et al. 2014). Although this pattern rises from a correlative analysis, we speculate that tuna spawn in or near the front to improve egg fitness and that this can favor the selection of such spawning sites over evolutionary time scales. However, such benefits are reduced in years when metaephyrae are abundant and widespread in the spawning areas. Mixing of water masses further challenges the chances of spawning in low-predator sites (Pinot et al. 2002). The front usually traverses the study area during the tuna spawning season and occasionally loops around the islands. Why they target this oceanographic structure is still a mystery. Bluefin tunas across the world spawn in low-productivity areas where predatory pressure on their offspring is minimal. The oligotrophic condition of the Balearic archipelago provides such a place for them to spawn, and the front zone oceanography displays cues for an area where invertebrate predators like *P. noctiluca* are less abundant.

Similarly, productivity in the Gulf of Mexico is relatively low, and the eddies of the Loop Current generate a patchy distribution of the diluted invertebrate predators. Spawning bluefin tuna target the edge of anticyclonic eddies, where divergent forces reduce the density of carnivorous invertebrates and enable growing larvae to drift towards patches of enhanced food availability (Bakun 2013; Domingues et al. 2016).

Other bluefin tunas have similar strategies to reduce planktonic predation on their offspring. For instance, the Pacific bluefin tuna *T. orientalis* breed at specific spawning grounds in the western Pacific Ocean, particularly in an area between the Philippines and Japan that is separated from the East China Sea by the Kuroshio Current (Fujioka et al. 2016). While the productivity in the East China Sea fuel a community of piscivorous plankton, including bloom-forming jellyfish like *Nemopilema nomurai* (Zhang et al. 2012; Sun et al. 2015), the

relatively low productivity within and east of the Kuroshio Current supports few predators. Thus, oceanographic signatures from the Kuroshio Current may be identified by the Pacific bluefin tuna as the limit of an offshore, oligotrophic, and low-predator spawning ground (Tawa et al. 2020). A second spawning ground is found in the more productive Sea of Japan. Here too, tuna larvae appear in low chlorophyll concentrations (Ohshimo et al. 2017), and in an area of low seasonal productivity and zooplankton biomass cycles (Hirota and Hasegawa 1999; Ishizaka and Yamada 2019). The spawning ground is delimited from more productive waters by the Tsushima Current, a branch of the Kuroshio Current, that introduces warm and plankton-poor water into the south-east Sea of Japan. However, increasing blooms of *N. nomurai* in the Yellow Sea and East China Sea are frequently swept by the Kuroshio Current and carried to the Sea of Japan (Kawahara et al. 2006), limiting the viability of this spawning ground.

Less is known about the reproductive ecology of the southern bluefin tuna *T. maccoyii*, but they also appear to spawn in a well-defined low productivity area between Indonesia and Australia where weak fronts may serve as indicators delimiting zones with greater productivity and predatory pressure to the north and south of the spawning area (Nieblas et al. 2014).

Albacore tuna *T. alalunga* is another temperate species that migrate to spawn in warm and low productivity waters, largely overlapping with bluefin tuna (Nikolic et al. 2017). As such, they too benefit from reduced predation of carnivorous invertebrates on larval stages. However, their spawning period and area extend beyond that of bluefin tunas, suggesting a more generalized reproductive strategy that simultaneously reduces intraguild piscivory of larval stages. At the opposite end of the spectrum, tropical tunas like skipjack tuna *Katsuwonus pelamis* and yellowfin tuna *T. albacares* can spawn throughout the year in vast, warm regions that largely overlap with their feeding grounds (Itano 2000; Ashida 2020). Such broad spawning areas and period makes studying predator-prey processes at population level more complicated than in tunas with more restricted spawning characteristics, but their pattern suggests that predator avoidance may have a lighter leverage on their spawning strategy than optimal water temperature for growth.

Temporal avoidance of invertebrate predators also plays a role reducing mortality of bluefin tuna offspring in the Mediterranean, as the adults arrive to the Balearic spawning ground when the reproductive activity of *P. noctiluca* has already dropped and metaephyrae are much scarcer than in late spring (Milisenda et al. 2018a). Thus, the timing of tuna spawning mismatches the peak of predator abundance and increases chances of offspring survival. Furthermore, tuna's peak spawning activity occurs at the time when water temperature starts rising above 20°C, and small changes in water temperature at this point can rapidly improve the probability of survival to flexion transition due to shorter stage duration.

High abundances of *P. noctiluca* metaephyrae can potentially inflict severe predation on tuna eggs and preflexion larvae, but their patchy distributions and low spatial overlap limit the population level predation effect across most the Balearic spawning grounds. Apparently, *P. noctiluca* metaephyrae do not remove enough tuna as to explain their high early-life mortality, and further suspects include other gelatinous plankton, chaetognaths, piscivorous crustaceans, and mollusks (Bailey and Houde 1989; Albaina et al. 2015). Among them, adult *P. noctiluca* are likely to be major candidate predators of tuna eggs and larvae, despite they only overlap during night hours (they perform diel vertical migrations) and are less abundant and patchier than the younger metaephyrae (personal observation). In any case, other invertebrate predators have similar spatial distribution patterns as metaephyrae, all being more abundant in more productive areas. Alternatively, larval piscivory plays a role in early life mortality, including cannibalism among siblings of the same spawning batch (Bakun 2013; Uriarte et al. 2019). This may lead to a game between adults for the optimal breeding time, driving spawning forward in time and out of the best environmental conditions (Reglero et al. 2018b; Takashina and Fiksen 2020).

Targeting the most barren waters of warm oligotrophic systems comes at the cost of risking starvation. Larvae of most tunas are fast-growing fishes that require frequent ingestion of food to sustain growth and survival. This trait makes them particularly vulnerable to food shortage, as it increases stage duration and facilitates starvation (Ishihara et al. 2019). Small bluefin tuna larvae adapt their diet to local available food sources, including appendicularians, cladocerans, nauplii, copepods, and fish larvae (Llopiz and Hobday 2015; Kodama 2020), but even this local adaptation may not be enough to meet the energy requirements. Some mechanisms may minimize this tradeoff. Bakun (2006, 2013) proposed that small-scale hydrodynamic activity can create pockets of enhanced food availability which fish larvae may feed on, and that cannibalism among larval tuna is key for larval success. Adult individuals may also shift the spawning peak as early as it is metabolically possible to reduce starvation due to temperature-dependent metabolic demands (Reglero et al. 2018b). Alternatively, younger adults that reproduce later in the season may target more productive waters for spawning (Richardson et al. 2016; Ohshimo et al. 2017), but this strategy has not been confirmed yet (Walter et al. 2016).

Not all interactions of tuna with *P. noctiluca* are necessarily negative. Stomach content and stable isotope analyses indicate that young and adult bluefin tuna prey on gelatinous plankton in the Mediterranean Sea (Sinopoli et al. 2004; Cardona 2012). Other studies found that leptocephalus larvae of the European eel *A. anguilla*, another migratory fish that targets frontal zones for spawning in the Atlantic (Munk et al. 2010), preys extensively on hydrozoan jellyfish and do not face food shortage (Ayala et al. 2018). Although leptocephalus are very different to tuna larvae, they show that

some fish consume gelatinous plankton early in their life. It is currently unknown at what age tuna start feeding on gelatinous plankton, but this could provide an additional food source in such oligotrophic system. New molecular techniques applied to analyze stomach contents of larval and juvenile tunas can answer this question (Hays et al. 2018). Identifying the interaction-strength of tuna early life stages with other marine organisms will further clarify benefits and trade-offs of spawning in warm, oligotrophic regions.

### Author Contributions

D.O., Ø.F. and P.R. designed the research; P.R. and F.A. provided research funding; D.O. M.M. F.A. and D.A.-B. collected field samples; D.O., F.A. M.M. and D.A.-B analyzed the samples and data; All authors discussed the results; D.O. and Ø.F. wrote the paper and all other authors edited the text and provided insights and comments.

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## Conflict of Interest

None declared.

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