



**Universitat**  
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**WHO EATS WHO IN THE WORLD OF BLUEFIN TUNA**  
***THUNNUS THYNNUS***

**DANIEL OTTMANN RIERA**





**Universitat**  
de les Illes Balears



Instituto Español  
de Oceanografía



University  
of Bergen

**DOCTORAL THESIS**  
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**Doctoral Programme in Marine Ecology**

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WHO EATS WHO IN THE WORLD OF BLUEFIN TUNA *THUNNUS THYNNUS*

Doctoral thesis completed by Daniel Ottmann fulfilling the requirements for the doctoral degree of the Marine Ecology Doctoral Programme of the *Universitat de les Illes Balears*

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## Thesis format

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*"Our planet is a blue planet"*

David Attenborough

*To my Dad, my Mum, and my Brother.  
To Eva.*



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## Abstract

Predator-prey interactions are important drivers of animal evolution and can shape their life history. Some species conduct large migrations to reproduce in areas with low density of predators where offspring have a greater chance to survive, but quantifying predator-prey interactions of marine migratory animals at meaningful population level is almost impossible using traditional observational methods.

In this thesis my collaborators and I combine field observations with biological modeling to evaluate predator-prey interactions of two tuna fishes and a jellyfish. We then speculate how their interaction strength may shape their life history. As study species we use the Atlantic bluefin tuna *Thunnus thynnus*, the Mediterranean albacore *Thunnus alalunga*, and the jellyfish *Pelagia noctiluca*. These species are relatively well studied, have ecological traits that turn them in good case studies, and are economically important.

Our study focusses on the early life stages of all three species, as they overlap in space and time and represent the life stage where most individuals die, mainly preyed by other animals. We start evaluating the distribution of *P. noctiluca* ephyrae and metaephyrae (early life stages) and the environmental factors favoring their presence and abundance in a major tuna spawning ground in the Western Mediterranean. We then classify them in developmental stages based on their size and feeding structures and model their predatory potential on egg and larval bluefin tuna in relation to their distribution. Similarly, we model the predatory potential of larval bluefin tuna on albacore based on their relative size and distribution in the spawning ground.

Our findings indicate that the abundance and distribution of early life stages of *P. noctiluca* are heavily influenced by temperature of the water column and primary productivity at the end of spring, which is greater in the northwest part of the study area, where surface water often depicts typical resident water, as opposed to the newly arrived Atlantic water streaming from the southwest. Those that have achieved the metaephyrae stage can prey on pre-flexion fish larvae (those that have not yet flexed the caudal tip of the notochord). Although metaephyrae are generally found in low abundances, occasionally high-density sites can remove most fish larvae before they reach the flexion stage (those that have started to flex the caudal tip of the notochord). However, bluefin tuna tend to spawn near or within the front of both water masses, where predators tend to be few. This suggests that by selecting spawning sites based on oceanographic signatures of the front, bluefin tuna could be preventing metaephyrae to unleash their full predatory potential.

When looking at the predator-prey interaction between bluefin tuna and albacore, we see that post-flexion larvae (those that have finished flexing the caudal tip of the notochord) can rapidly deplete smaller albacore, particularly first feeding ones that are too small to escape predator encounters. The probability that piscivorous bluefin tuna encounter albacore depends largely on the spawning distribution and timing of each species, which is characteristic for each species. Nonetheless, increasing abundances of bluefin tuna has risen their overall piscivorous pressure on larval albacore since 2001, and this pattern correlates with opposite trends in the population stock biomass of each species.

This thesis covers knowledge gaps in the understanding of ecology and population dynamics of *P. noctiluca* and pioneers our understanding of how the strength of predator-prey interactions in tuna early life stages can influence their reproductive strategy.



## Resumen

Las interacciones depredador-presa son motores de la evolución animal que pueden determinar su ciclo de vida. Algunas especies realizan grandes migraciones para reproducirse en áreas con pocos depredadores, donde la descendencia tiene mayores probabilidades de sobrevivir. Sin embargo, cuantificar las interacciones depredador-presa de los animales marinos a nivel de población es casi imposible utilizando métodos tradicionales de observación.

En esta tesis, mis colaboradores y yo combinamos observaciones de campo con modelos biológicos para evaluar las interacciones depredador-presa de dos especies de atún y una de medusa. Basándonos en estos resultados, especulamos sobre cómo esta interacción puede moldear su ciclo de vida. Como especies de estudio usamos el atún rojo Atlántico *Thunnus thynnus*, la albacora del Mediterráneo *Thunnus alalunga* y la medusa *Pelagia noctiluca*. Estas especies están relativamente bien estudiadas, tienen características ecológicas que las convierte en buenos ejemplos y son de interés económico.

Nuestro estudio se centra en las primeras etapas de vida de las tres especies, ya que se superponen en el espacio y tiempo y representan la etapa donde mueren la mayoría de los individuos, principalmente como presa de otros animales. Comenzamos evaluando la distribución de éfiras y metaéfiras (estadios tempranos de vida) de *P. noctiluca* y los factores ambientales que favorecen su presencia y abundancia en una zona clave para el desove de atún rojo y albacora en el Mediterráneo Occidental. Luego los clasificamos en etapas de desarrollo según su tamaño y estructuras de alimentación y modelamos su potencial como depredador de huevos y larvas de atún en función de su distribución. De manera similar, modelamos el potencial depredador de las larvas de atún rojo sobre las de albacora en función de su distribución y tamaño relativo.

Nuestros hallazgos indican que la abundancia y distribución de las etapas de vida tempranas de *P. noctiluca* están fuertemente influidas por la temperatura en la columna de agua y la productividad primaria al final de la primavera, que es mayor en la parte noroeste del área de estudio, donde el agua superficial suele ser residente (a diferencia del agua recién llegada desde el Atlántico). Concluimos que las medusas en estado de metaéfira o superior ya pueden alimentarse de larvas de peces en estado pre-flexión (aquellas que no han flexionado el extremo caudal de la notocorda). Por lo general las metaéfiras suelen ser escasas, pero ocasionalmente pueden ser suficientemente abundantes como para eliminar la mayoría de las larvas de peces antes de que estas alcancen la etapa de flexión (aquellas que han empezado a flexionar el extremo caudal de la notocorda). Sin embargo, el atún rojo tiende a desovar cerca o dentro del frente entre las masas de agua, donde los depredadores suelen ser más escasos. Esto sugiere que el atún rojo podría estar seleccionando sitios de desove basándose en señales oceanográficas del frente y así evitar que las metaéfiras ejerzan todo su potencial depredador sobre las larvas.

Al observar la interacción depredador-presa entre el atún rojo y la albacora, vemos que las larvas post-flexión (aquellas que ya han terminado de flexionar el extremo caudal de la notocorda) pueden depredar rápidamente larvas de albacora, en

particular las que son demasiado pequeñas como para escapar de los encuentros con los depredadores. La probabilidad de que larvas de atún rojo piscívoras se encuentre con la albacora depende en gran medida de la distribución de cada especie, así como de su momento de desove, el cual es característico para cada una. No obstante, la creciente abundancia de atún rojo ha incrementado su presión piscívora sobre las larvas de albacora desde 2001, y este patrón se correlaciona con tendencias opuestas en la biomasa de la población de cada especie.

Esta tesis cubre nociones clave para entender mejor la ecología y la dinámica poblacional de *P. noctiluca* y contribuye mejorar nuestro conocimiento sobre cómo las interacciones tróficas en etapas tempranas del atún influyen en su estrategia reproductiva.

## Resúm

Les interaccions depredador-presa són motors importants de l'evolució animal que poden determinar el seu cicle de vida. Algunes espècies realitzen grans migracions per reproduir-se en àrees amb pocs depredadors, on la descendència té majors probabilitats de sobreviure. No obstant això, quantificar les interaccions depredador-presa dels animals marins a nivell de població és pràcticament impossible utilitzant mètodes tradicionals d'observació.

En aquesta tesi, els meus col·laboradors i jo combinem observacions de camp amb models biològics per avaluar les interaccions depredador-presa de dues espècies de tonyina i una de grumer. Basant-nos en aquests resultats, especulem sobre com aquesta interacció pot moldejar el seu cicle de vida. Com a espècies d'estudi feim servir la tonyina vermella de s'Atlàntic *Thunnus thynnus*, s'albacora Mediterrània *Thunnus alalunga* i es grumer *Pelagia noctiluca*. Aquestes espècies estan relativament ben estudiades, tenen característiques ecològiques que els converteix en bons exemples i son d'interès econòmic.

El nostre estudi se centra en les primeres etapes de vida de les tres espècies, ja que se superposen en espai i temps i representen l'etapa on mor la majoria d'individus, principalment com a presa d'altres animals. Comencem avaluant la distribució d'èfirs i metaèfirs (estadis primerencs de vida) de *P. noctiluca* i els factors ambientals que afavoreixen la seva presència i abundància en una zona clau per la posta de tonyina vermella i albacora a sa Mediterrània Occidental. Després els classifiquem en etapes de desenvolupament segons la seva grandària i estructures d'alimentació i modelem el seu potencial com a depredador d'ous i larves de tonyina en funció de la seva distribució. De manera similar, modelem el potencial depredador de les larves de tonyina vermella sobre les d'albacora en funció de la seva distribució i grandària relativa.

Els nostres descobriments indiquen que l'abundància i distribució de les etapes de vida primerenques de *P. noctiluca* estan fortament influïdes per la temperatura a la columna d'aigua i la productivitat primària finals de primavera, que és més gran a la part nord-oest de l'àrea d'estudi, on l'aigua superficial sol ser resident (a diferència de l'aigua recent arribada des de l'Atlàntic). Concloem que els grumer en estat de metaèfira o superior ja poden alimentar-se de larves de peixos en estat pre-flexió (aquelles que no han flexionat l'extrem caudal de la notocorda). En general les metaèfirs solen ser escasses, però ocasionalment poden ser prou abundants com per eliminar la majoria de larves de peixos abans de que aquestes arribin a l'etapa de flexió (aquelles que han començat a flexionar l'extrem caudal de la notocorda). No obstant això, la tonyina vermella tendeix a posar ous a prop o dins des front de les dues masses d'aigua, on els depredadors solen ser més escassos. Això suggereix que la tonyina vermella podria estar seleccionant llocs de posta basant-se en senyals oceanogràfiques del front i així evitar que les metaèfirs exerceixin tot el seu potencial depredador sobre les larves.

Al observar la interacció depredador-presa entre la tonyina vermella i l'albacora, veim que les larves post-flexió (aquelles que han flexionat l'extrem caudal de la notocorda) poden depredar ràpidament larves d'albacora, en particular les que

són massa petites com per escapar de les trobades amb els depredadors. La probabilitat que larves de tonyina vermella piscívores es trobin amb les d'albacora depèn en gran mesura de la distribució de cada espècie, així com des seu moment de posta, que és característic per cada un. No obstant això, la creixent abundància de tonyina vermella ha incrementat la seva pressió piscívora sobre les larves d'albacora des de 2001, i aquest patró se correlaciona amb tendències oposades en la biomassa de la població de cada espècie.

Aquesta tesi cobreix nocions clau per entendre millor l'ecologia i la dinàmica poblacional de *P. noctiluca* i contribueix a millorar el nostre coneixement sobre com les interaccions tròfiques en etapes primàries de la tonyina influeixen en la seva estratègia reproductiva.

## Acronyms

ALB	Albacore
ANOVA	Analysis of variance
BFT	Bluefin tuna
CDD	Central disc diameter
CTD	Conductivity-temperature-depth instrument
EU	European Union
EMFF	European Maritime and Fisheries Fund
GMT	Greenwich mean time
IBM	Individual Based Model
ICCAT	International commission for the conservation of Atlantic tuna
MLD	Mixed layer depth
NEMO	Nucleus for European Modelling of the Ocean
MOCNESS	Multiple Opening/Closing Net and Environmental Sensing System
Q10	Metabolic temperature coefficient
SGR	Specific growth rate
SL	Standard length
SST	Sea surface temperature
SOCIB	Balearic Islands Coastal Observing and Forecasting System
TBD	Total Body diameter
VIF	Variance inflation factor
WMD	Weighted mean depth



# 1. Introduction

*"Nothing in biology makes sense except in the light of evolution."*

Theodosius Dobzhansky





To eat and not get eaten are two of the most powerful forces of animal evolution. Indeed, failing in any of these efforts often has fatal consequences and genes will no longer be transferred to new generations. Therefore, animals have developed all sorts of adaptations to increase acquisition of food and reduce predation. For instance, developing large body sizes, rapid mobility or defense structures like sharp teeth, horns, spines, shells, crypsis, or venom can prevent getting eaten by other animals. Similarly, many of these adaptations can also be used to increase capture success of a prey, often leading to an evolutionary arms race between predators and prey. Not all mechanisms require anatomical adaptations. Behavioral, phenological, or a combination of multiple adaptations are, often the best strategy to increase fitness both, as predator and as prey.

The relation between a predator and its prey is called trophic interaction, and trophic ecology reflects all aspects related to trophic interactions at any ecological scale from individual to ecosystem levels (Garvey & Whiles 2016). The most common trophic interaction among animals is predation, which is here referred to as when one animal kills and consumes another animal (Stevens 2010).

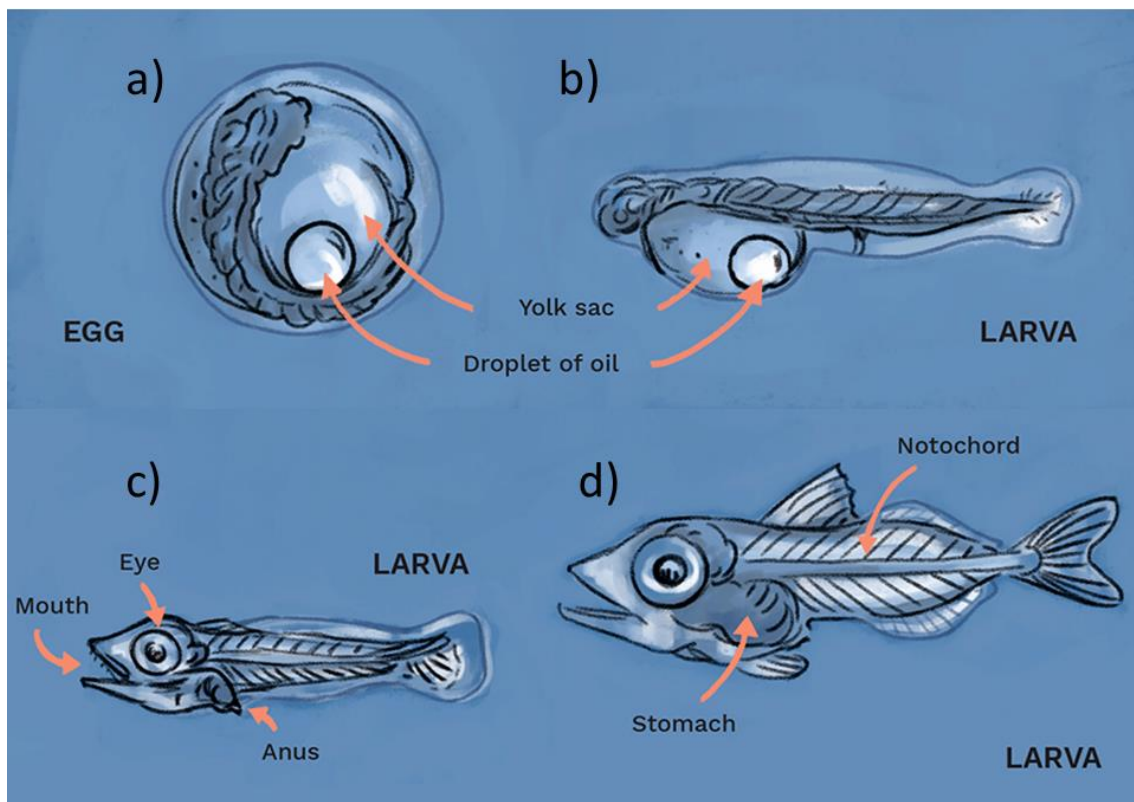
For most people, what first comes to mind when thinking of predation is a carnivorous mammal hunting a grazer, or perhaps a big fish eating a little fish. However, predator-prey interactions are more complex and can sometimes reverse depending on the life stage of each player. This is quite common in the marine realm, where the fact that most fishes and invertebrates are small (i.e. <5 mm) when they hatch means that many other predators can feed on them, including those who are prey in later stages.

Tuna is a good fish example to illustrate the ontogenetic change in its role as prey or predator. Adult tunas are considered marine top predators feeding on foraging fishes, cephalopods, and crustaceans (Estrada et al. 2005). However, tuna larvae are barely 3 mm long when they hatch, and most plankton feeders can prey on them during their first days of life. This includes filter-feeding and small pelagic fishes like clupeids and myctophids, invertebrate predators like jellyfish or ctenophores, and even other fish larvae like piscivorous scombrids (Bailey & Houde 1989). Unsurprisingly, although some large tunas like the Atlantic bluefin tuna *Thunnus thynnus* can spawn over 100 million eggs per year (Medina 2020), less than 1 may survive long enough to reach maturity. Such brutal early mortality rate sets two questions: Why do they invest their resources in so many small offspring that will mostly die? And who is eating all this tuna?

The answer to the first question is related to how food resources are distributed in the ocean. Winemiller & Rose (1993) found that large-scale patchiness of resources favor the reproductive fitness of large broods of small-size larvae compared to small broods of large-size larvae. Therefore, tuna's strategy of releasing many small eggs is to ensure that at least some offspring will make it to a suitable habitat, despite most of them dying early. Answering the second question is more challenging, as quantifying the interaction strength, (i.e. predicted effect that one species has on another species; Wootton & Emmerson 2005) of predators in natural habitats is almost impossible using direct, visual methods.

Understanding predator-prey processes of tuna eggs and larvae is key to understand drivers of natural mortality. It is estimated that predation is the primary cause of direct mortality of fishes in the ocean (Bailey & Houde 1989), and small changes in mortality rate of early life stages can lead to order-of-magnitude variation in the number of individuals recruiting to the adult population. However, predicting early mortality of fishes in natural systems is virtually impossible. Who are the main predators? What is their contribution to total mortality? How does it vary over time and space? How do bluefin tuna adapt its life strategy to minimize early predation? We are currently far of being able to answer these questions with confidence, but research on trophic interactions in the early life stages can put us in the right path.

The ecological patterns and trophic interactions my collaborators and I evaluate here focus on the early life stages of bluefin tuna, which comprise the period of life from egg to the juvenile stage (Fuiman & Werner 2002). This is the most vulnerable life period to predators, and larvae grow and develop fast to leave this vulnerable period as quickly as possible. After hatching, larval tuna progressively morph to juvenile stage by developing functional body structures like eyes, mouth, digestive system, gills, swim-bladder, and fins (Fig. 1.1)(Yúfera et al. 2014). By the time they finish this metamorphosis, what started as a highly vulnerable fish larvae turns into a voracious “killing machine” of other fish larvae.



**Figure 1.1.** Early life stages of bluefin tuna. a) Egg; b) yolk-sack-larva; c) pre-flexion larva; d) post-flexion larva. Source Planet tuna.

We are now in a good position to advance knowledge in larval tuna ecology, as research in this field is building momentum with leading ecological studies at different parts of the World, including the Mediterranean Sea. In the last decade, larval surveys in the Mediterranean Sea, the Gulf of Mexico and the Slope Sea have identified key habitat features, like frontal zones and temperature thresholds, that favor reproductive activity of bluefin tuna (Reglero et al. 2012, Richardson et al. 2016, Muhling et al. 2017). Similar studies have been conducted in the Sea of Japan and the Kuroshio current with the Pacific bluefin tuna *T. orientalis* (Ohshimo et al. 2017, Tawa et al. 2020) and between Indonesia and Australia with the Indian bluefin tuna *T. maccoii* (Nieblas et al. 2014). Diet analyses are linking feeding behavior with larval growth and survival in the field (Gleiber et al. 2020, Kodama 2020), and recent studies on visual acuity (Hilder et al. 2019) and temperature- and food-dependent growth (Reglero et al. 2014a, 2018b, Blanco et al. 2018) enable to link larval metabolism with habitat conditions to predict larval fitness in the field (Fiksen & Reglero 2021).

While a good body of research has been developed over the past decades on feeding behavior and metabolism of larval bluefin tuna, less is known about the trophic interactions they have with other species or about what consequences such interactions have in their life-history. Among the few studies in this topic, larval cannibalism (Reglero et al. 2011, Uriarte et al. 2019, Takashina & Fiksen 2020) and predation by early life stages of the jellyfish *Pelagia noctiluca* on tuna eggs (Gordoa et al. 2013) are the most relevant ones. These studies have set the precedent on which I build my thesis. Using bluefin tuna as the central character of my thesis, I explore the predator-prey interaction strength they have with *P. noctiluca* and larval albacore.



## 2. Research goals

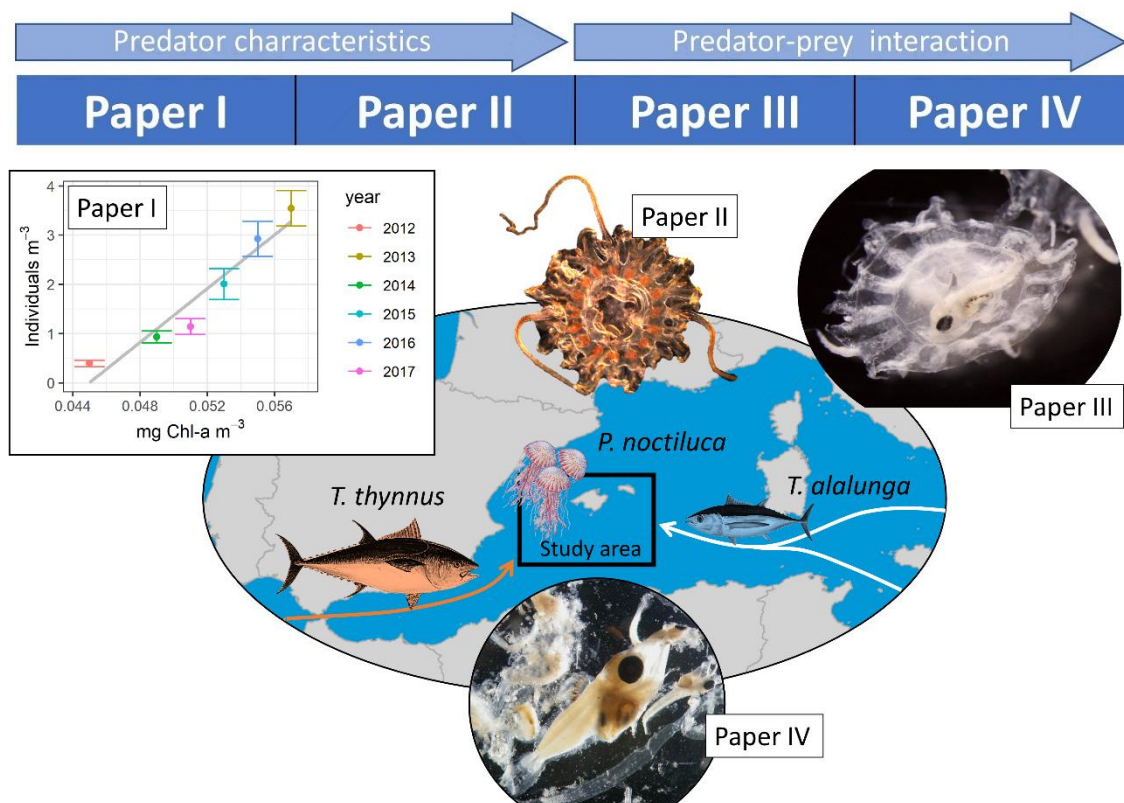
*“Setting goals is the first step in turning the invisible into the visible.”*

Tony Robbins



The overarching goal of my thesis is to shed some light on trophic interactions of bluefin tuna *Thunnus thynnus* with the jellyfish *Pelagia noctiluca* and the Mediterranean albacore *Thunnus alalunga*. This general goal is broken into four specific goals that constitute each Paper (Fig. 2.1). The first two papers focus on ecological and biological aspects of *P. noctiluca* early life stages. In the latter two, my collaborators and I test the interaction strength of *P. noctiluca* early life stages preying on bluefin tuna eggs and larvae, and of bluefin tuna larvae preying on albacore larvae.

The research approach is as following: we formulate a question that can bring relevant understanding regarding predator-prey interactions of larval tuna. This question underlies a hypothesis that needs to be tested with state-of-the-art knowledge and available tools. If the knowledge is not available, we take a step back and formulate a question that can generate it. This is the reason why the first two papers focus on ecological aspects of *P. noctiluca* – to model its interaction with bluefin tuna we first had to generate basic knowledge of the distribution and feeding capacity *P. noctiluca*. I expect the findings from this work extend beyond simple predator-prey relationships and provide new ecological insights that will act as ground-knowledge to explore evolutionary and life-history speculations of all three species.



**Figure 2.1. Contributions of this thesis.** Each paper chapter corresponds to an ecological question and follow a logical order indicated by the arrows in the top: In Papers I and II we generate basic information of *P. noctiluca* a key predator of tuna early life stages. Paper I focus on habitat conditions like chlorophyll concentration favoring early life stages of *P. noctiluca* and Paper II classifies these stages based on morphological structures associated to their feeding capacity. In Papers III and IV we use information from the literature and from Papers I and II to investigate predator-prey interactions of bluefin tuna early life stages. Paper III focuses on the interaction

strength of *P. noctiluca* metaephyrae preying on bluefin tuna eggs and larvae, and Paper IV focuses on the interaction strength of larval bluefin tuna preying on smaller larvae of albacore. Arrows on the map indicate migratory paths of Atlantic bluefin tuna (orange) and Mediterranean albacore (white).

The specific goals of each Paper are listed below.

**Goal 1.** Describing favorable habitat conditions of *P. noctiluca* early life stages in the western Mediterranean Sea.

Question: What are the conditions favoring the presence and abundance of *P. noctiluca* early life stages?

Hypothesis: The distribution of *P. noctiluca* early life stages is not random, instead, it is determined by conditions of the habitat.

Paper I.

**Goal 2.** Defining morphological and morphometric stages of *P. noctiluca* during its early development in relation to its feeding capacity.

Question: Can we differentiate ephyrae and metaephyrae stages of *P. noctiluca*?

Hypothesis: Larger ephyrae and metaephyrae progressively develop feeding structures to be more effective predators. Development stages can be classified based on these traits.

Paper II.

**Goal 3.** Evaluating the interaction strength of *P. noctiluca* early life stages preying on egg and larval bluefin tuna.

Question: Are metaephyrae of *P. noctiluca* important invertebrate predators of egg and larval bluefin tuna in the western Mediterranean Sea?

Hypothesis: Metaephyrae of *P. noctiluca* can potentially inflict severe mortality on egg and larval bluefin tuna, and bluefin tuna has adapted its reproductive strategy to reduce invertebrate predation accordingly.

Paper III.

**Goal 4.** Evaluating the interaction strength of larval bluefin tuna preying on larval albacore.

Question: Are larval bluefin tuna important predators of larval albacore in the western Mediterranean Sea?

Hypothesis: Predation of larval bluefin tuna can significantly remove larval albacore and potentially affect its stock recruitment.

Paper IV.



### 3. General methods

*"For every complex problem there is an answer that is clear, simple, and wrong."*

Henry Mencken



### 3.1. Analytical approach

To quantify predation in the field, the best proxy we currently have is to combine mechanistical models based on information of laboratory experiments with field observations of predator and prey distributions (Kiørboe 2008, Baum & Worm 2009). On the one hand, laboratory experiments enable to estimate parameters involved in predator-prey mechanics like clearance rate, predator visual range, digestions time, growth rate, etc. It also enables to estimate how these variables evolve at different water temperatures and body lengths. On the other hand, appropriate sampling in the field enables to estimate instantaneous predator-prey overlap in their natural habitat. Putting both things together can be used to estimate predation at large scale.

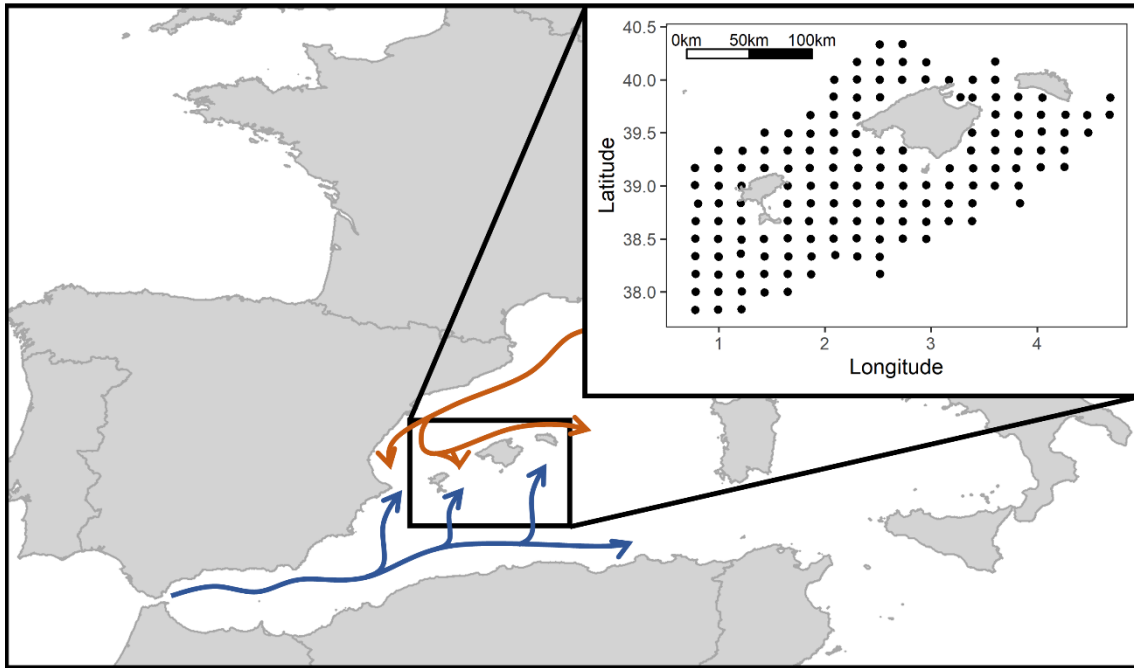
For my thesis I combined systematic sampling in the field with laboratory processing of samples, statistical modeling, and mechanistical models. The experimental design resides in the comparison of response variables under the different scenarios of each year. Additionally, a field experiment was conducted in 2019 to determine the vertical distribution and migration of *Pelagia noctiluca* early life stages.

### 3.2. Study area

All the field samples used in this thesis were collected around the Balearic Islands in the western Mediterranean Sea, in an area compressed between 37-41° N and 1-5° E (Fig. 3.1). The Mediterranean Sea is a semi-enclosed water mass of 2.5 million km<sup>2</sup> adjacent to the Atlantic Ocean. Human civilizations have benefited from its resources for thousands of years, and it is currently home to over half a billion people (Lemaitre-Curri & Tode 2020). The strait of Sicilia in southern Italy separates the western and eastern Mediterranean basins, which feature different biological and oceanographic traits (Krom et al. 1991).

The Mediterranean Sea is an oligotrophic system with limited productivity (Siokou-Frangou et al. 2010). The area around the Balearic Islands is a particularly unproductive region of the western Mediterranean, as nutrient discharges from land are very limited and upwelling systems are weak and ephemeral (Bakun & Agostini 2001). In fact, much of the surface productivity during summer relies heavily on the limited photosynthesis of bacteria and picoeukaryotes (Mena et al. 2016, 2019). Such low productivity sustains a rather small community of zooplankton that in turn sustains an also small community of nekton. Nevertheless, this area is targeted as spawning ground by several migratory species, posing interesting questions about the tradeoffs of reproducing in such oligotrophic area.

Hydrographic and biological traits of the study area are patchy. Moderate mesoscale oceanographic activity can create small pockets of enhanced productivity supporting greater food availability (Bakun 2006), and the seasonal arrival of surface water from the Atlantic creates a salinity front with the resident Atlantic water that fosters further complexity in the system (Balbín et al. 2014). Differences in the hydrography at each side of the front propel differences in the plankton community, and migratory species that come here to spawn may trace these hydrographic signatures to spawn in sites that feature better conditions for their offspring (Teo et al. 2007, Alemany et al. 2010).



**Figure 1.1. Study area.** All samples used in this thesis were collected around the Balearic Islands (square) in the western Mediterranean Sea. Sampling stations (black dots) were distributed at a 10x10 nautical mile grid. During the period of sampling, resident Atlantic waters (orange arrows) collides with newly arrived Atlantic (blue arrows) water creating a salinity front whose shape and position varies across the season and among years.

Vertical stratification adds further structural complexity to the system during the summer months. Although many organisms follow diel vertical migrations, the shallow (15-30 m) summer thermocline splits two different communities of plankton, including primary producers (Olivar et al. 2014), invertebrate zooplankton (Puelles et al. 2003), and ichthyoplankton (Olivar et al. 2014, Alvarez et al. 2021).

### 3.3. Field sampling

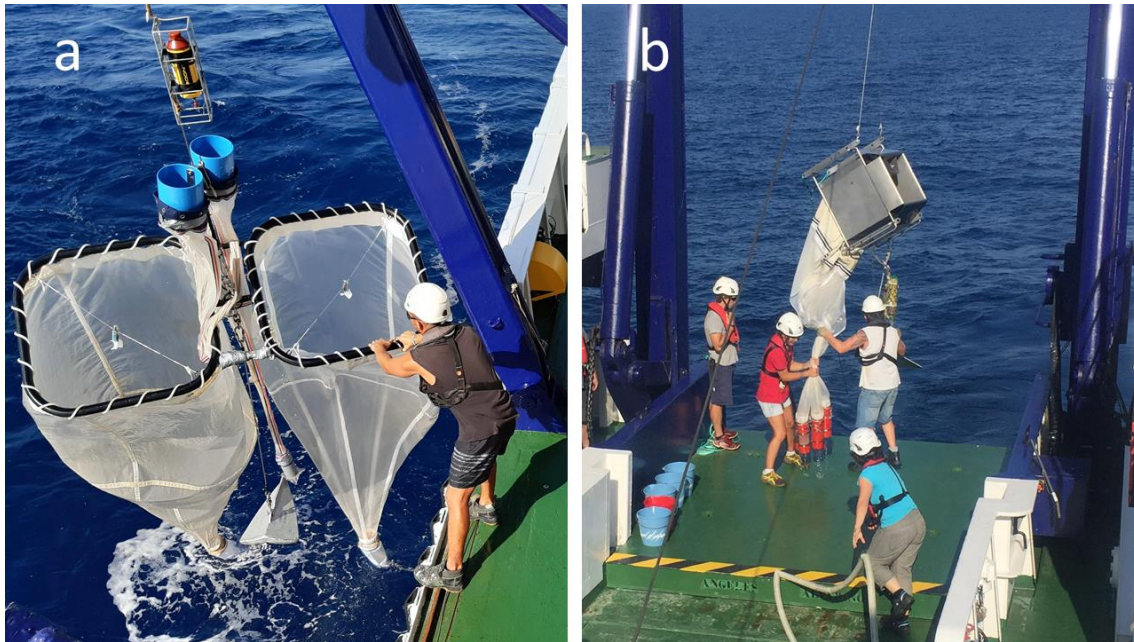
For the field observations, my collaborators and I collected plankton samples and vertical CTD profiles of oceanographic variables between June 21 and July 12 onboard research vessels of the Spanish Institute of Oceanography (IEO) and the Balearic Islands Coastal Observing and Forecasting System (SOCIB). The vessel name, sampling period, and number of net tows are listed in Table 1.

Plankton samples were collected with either a 1-m<sup>2</sup> frame bongo net or with a 0.25-m<sup>2</sup> frame multinet (Hydrobios), for horizontal and vertical sampling, respectively (Fig. 3.1), and stored in 4% formaldehyde solution for further processing in the lab. Exceptionally, some samples were sorted and photographed onboard using a camera-attached dissecting microscope (Fig. 3.2a).

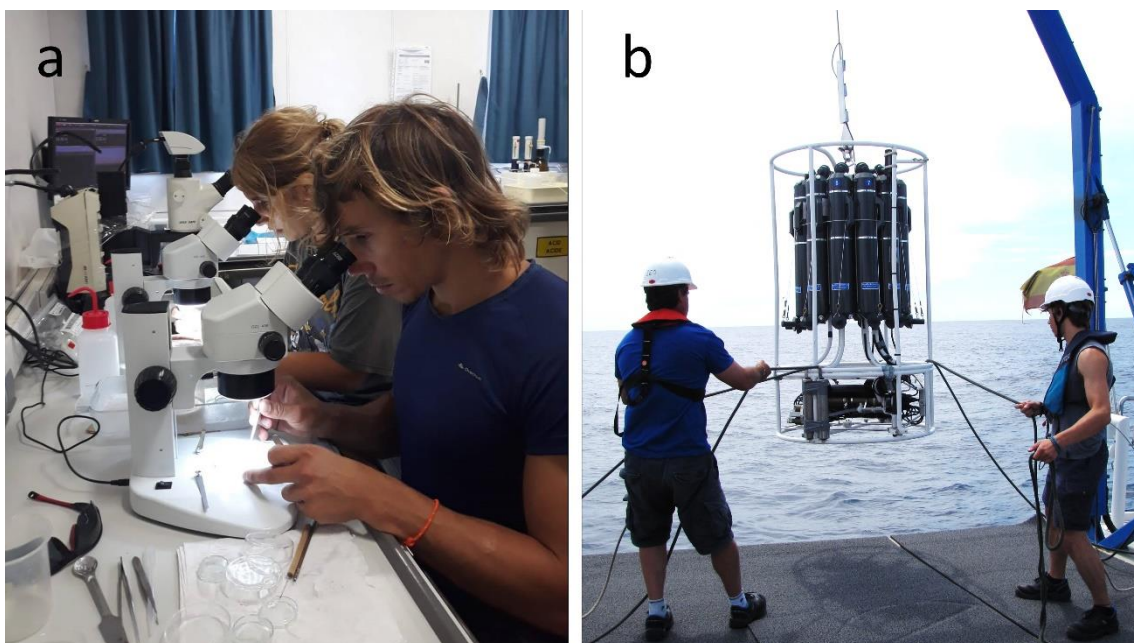
**Table 1. Field sampling.** Summary of annual cruises to collect observations for this study. Bongo tows correspond to the number of sampling stations of each year. All 8 multinet tows were conducted at the same sampling station.

Year	Research vessel	Sampling period	Bongo tows	Multinet tows	Papers
2001		June 21 – July 7	156	0	IV
2002		June 18 – June 28	85	0	IV
2003		July 3 – July 29	198	0	IV
2004		June 18 – July 8	166	0	IV
2005		June 27 – July 27	185	0	IV
2012	Ramón Margalef	June 21 – July 4	118	0	I, III & IV
2013	SOCIB	June 20 – July 9	99	0	I, III & IV
2014	SOCIB	June 18 – June 30	74	0	I, II, III & IV
2015	SOCIB	June 23 – July 9	81	0	I, II, III & IV
2016	SOCIB	June 21 – July 7	79	0	I, II, III & IV
2017	SOCIB	June 26 – July 12	89	0	I, III & IV
2019	Ángeles Alvariño	July 2 – July 4	0	8	I, III

The CTD rosettes (Fig. 3.2b) had at least 14 Niskin bottles and sensors to measure temperature, salinity, fluorescence, and dissolved oxygen. In addition to the field data, we also downloaded temperature and chlorophyll data from the Mediterranean Sea (Med Sea) physical (v1.4) and biogeochemistry (v2.2) model re-analyses of the EU Copernicus Marine Environment Monitoring Service (Simoncelli et al. 2014, Teruzzi et al. 2014).



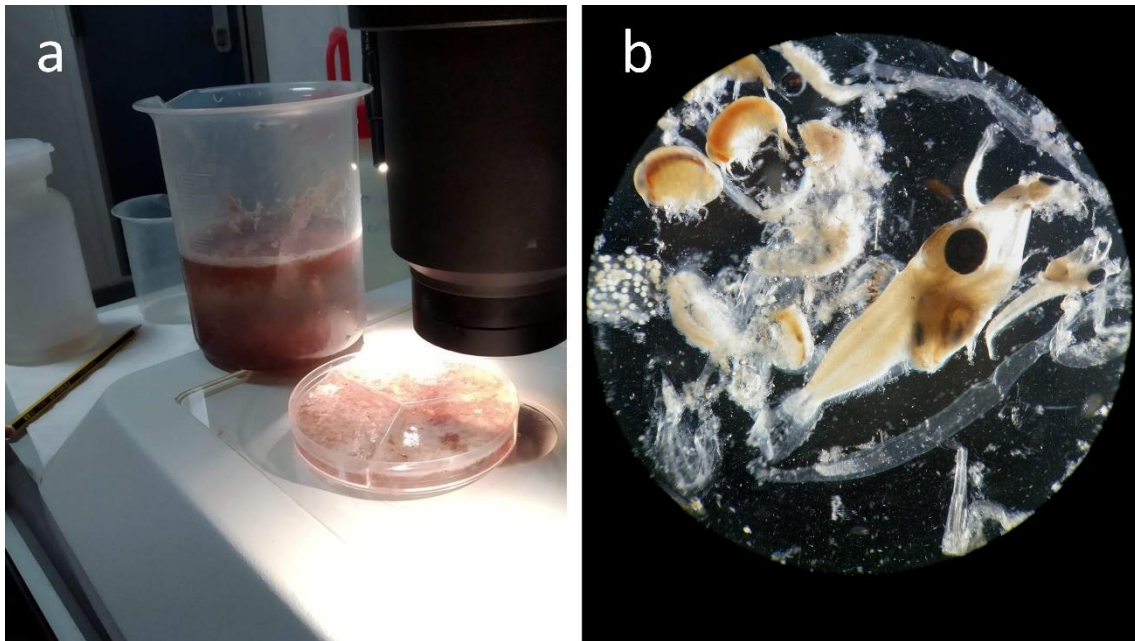
**Figure 3.1. Plankton nets.** a) 1-m<sup>2</sup> frame bongo net (with a smaller bongo net attached). b) 0.25-m<sup>2</sup> frame multinet. Photos by D. Ottmann and R. Santiago.



**Figure 3.2. Onboard plankton sorting and CTD rosette.** a) Samples were sorted and photographed with a camera-attached dissecting microscope. b) A CTD rosette was deployed in each sampling site to record vertical profiles of environmental conditions. Photos by P. Reglero and S. Mele.

### 3.4. Laboratory processing

My collaborators and I sorted all fish larvae and *P. noctiluca* early life stages in the lab with a dissecting microscope (Fig. 3.3). To take size measurements, we photographed them with a camera-attached dissecting microscope coupled to a computer with an image analysis software. Measurements were taken with ImagePro or ImageJ image-analysis software.



**Figure 3.3. Plankton sorting in the lab.** a) Plankton sample (in beaker) and dissecting Petry dish under a dissecting microscope. b) Microscope view of a plankton sample containing crustaceans, chaetognaths and tuna larvae of different sizes. Photos by D. Ottmann.



### 3.5. Statistical modeling

It is broadly accepted that statistical testing is required to evaluate significant differences between two sample populations, or to determine significant relationships between one or more explanatory variables and a response variable. A statistical model is essentially a mathematical relationship between the explanatory and response variables. The simplest one is a linear regression where the explanatory variable has a direct, linear effect on the response variable:

$$y_i = \beta_0 + \beta_1 x_i + \varepsilon_i \quad \text{M.1}$$

where  $y$  is the response variable,  $x$  is the explanatory variable,  $\beta_0$  is the intercept,  $\beta_1$  is the slope and  $\varepsilon$  is the error. The subscript  $i$  refers to each of the observations. An example of this linear regression is Model 2 in Paper II, where metaephyrae shrinkage is estimated as a function of the central disc diameter (see Paper II). The model can include as many explanatory variables as we want to test, and the effect of each variable is tested comparing the performance of models with and without the tested variable. An example of a linear model with more variables is Model 1 in Paper I, where temperature is estimated as a function of year and day of the year (see paper I).

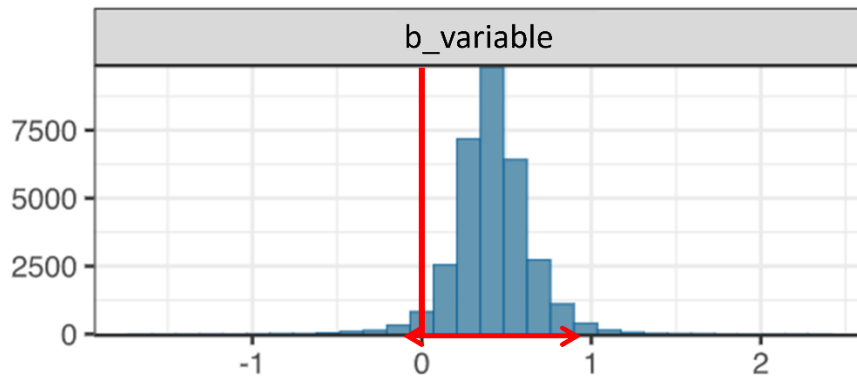
For statistical models to be trustworthy, they must comply to a certain degree with basic assumptions of normal distribution, linearity, equality of variance, and independence of explanatory variables (Zuur et al. 2010). Unfortunately, most datasets in ecology violate some, if not all these assumptions. Thus, statistical models need to become more complex to overcome such violations. This includes non-linear relations between the explanatory and the response variables (i.e. generalized additive model), changing the sample distribution (i.e. generalized linear model), combining two different distributions in a model (i.e. hurdle model), include random effects (i.e. mixed models), or include zero-inflation, among other variations (Zuur et al. 2009). Given the complexity of our data, I applied all these variations in the statistical models presented in this thesis.

There are two ways to approach statistical modeling: the frequentist approach and the Bayesian approach. Classic modeling applies the frequentist approach, where the data analyst designs the model architecture and runs the model to get the best possible parameter values that explain the observations. In our M.1 model above, this would be like obtaining  $\beta$  values that minimizes the differences between the fitted values  $y_i$  and the observations. The model performance is then evaluated by checking how similar the observations are to the fitted values.

On the other hand, a Bayesian data analyst can set a range of  $\beta$  values *a priori* based on previous information. It will run the model multiple times, usually 10.000 times, to create 10.000 models with slight variations of the  $\beta$  values. To test the model performance, the fitted  $y_i$  values of each model is compared to the observations. At the end, a range of values is obtained for each  $\beta$  following a probabilistic shape called posterior distribution (Fig. 3.4). In the posterior distribution, the most frequently obtained  $\beta$  values are the most probable ones. If well performed, both statistical approaches should yield similar results, but current statistical software cannot cope with



some of the most complex models applying the frequentist approach. Therefore, I combined frequentist and Bayesian approaches in the statistical models of this thesis.



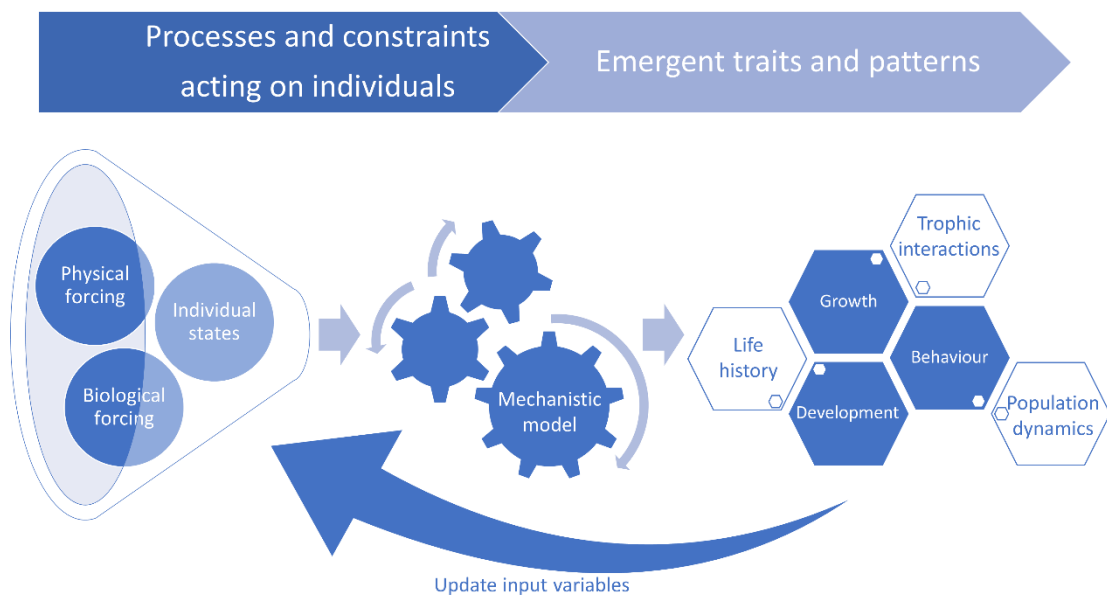
**Figure 3.4. Example of the posterior distribution of  $\beta$  values of a variable in a Bayesian model.** After 40.000 runs, the frequency of each  $\beta$  value depends on how well the fitted  $y_i$  of each model matches the observed data. The most frequent values are the most probable ones. The horizontal red arrow indicates the range where 95% of the posterior  $\beta$  values are found (95% credible interval). The vertical red line indicates where  $\beta = 0$ . If the 95% credible interval includes 0 (like in this example), this explanatory variable is not an important predictor of the response variable and would be excluded from the final model.

### 3.6. Mechanical modeling

My collaborators and I developed individual based models (IBM) of tuna larvae, which are a type of mechanical model that allow for a high degree of complexity of individuals and of interactions among individuals (DeAngelis & Grimm 2014).

Contrary to statistical modeling, where significant relationships between variables can be determined even if the linking mechanism is missing, mechanical modeling is all about understanding the mechanism. They draw input variables from the environment and the individual state and follow simple biological rules to produce emergent traits of the system (Fig. 3.5). Some of these traits may then alter the input variable. Ideally, all biological rules and parameters have been tested empirically to reduce uncertainty of each process. However, such information is often lacking, and basic assumptions based on relative species must be used instead.

An advantage of these models is that it enables to understand processes from a mechanical perspective, as well as to test emergent traits under different hypothetical scenarios or to variations of structural parameters. A drawback is that the model alone fails to provide empirical evidence of such processes, and similarities between the patterns emerging from the model or from the field observations are merely correlative.



**Figure 3.5. Schematic of a mechanical model.** Input variables drawn from the environment and the individual feed the mechanistic model. This model simulates natural processes in response to the input variables and generates emergent traits and patterns of the individual. Some of the emergent traits can alter the input variables. For example, warmer temperature of the water will accelerate growth and development resulting in a larger fish larva. This larger larva will then have a greater feeding capacity and can therefore grow even faster.

#### 4. Paper I - Abundance of *Pelagia noctiluca* early life stages in the western Mediterranean Sea scales with surface chlorophyll

*"To understand what happens in nature, you first need to know what is out there."*

Francisco Alemany



Publication information:

Ottmann, D., Álvarez-Berastegui, D., Prieto, L., Balbín, R., Alemany, F., Fiksen, Ø., Gordo, A., Reglero, P. (2021). Abundance of *Pelagia noctiluca* early life stages in the western Mediterranean Sea scales with surface chlorophyll. *Marine Ecology Progress Series*, 658, 75-88. DOI: <https://doi.org/10.3354/meps13423>

- Journal: *Marine Ecology Progress Series*
- JCR impact factor in 2021: 2.824
- Ranking in oceanography: 21/61 – Q2
- Ranking in ecology: 76/166 – Q2
- Ranking in marine & freshwater biology: 24/110 – Q1



## 5. Paper II - Ephyrae and metaephyrae of *Pelagia noctiluca*: stage determination, morphometry, and shrinkage

*"You can't draw a fine painting with a thick brush."*

Raul Laiz





Publication information:

Ottmann D, Leyva L, Reglero P, Prieto L, Álvarez I. (2021). Ephyrae and metaephyrae of *Pelagia noctiluca*: stage determination, morphometry, and shrinkage. *Journal of Plankton Research*. DOI: <https://doi.org/10.1093/plankt/fbab060>

- Journal: *Journal of Plankton Research*
- JCR impact factor in 2021: 2.455
- Ranking in oceanography: 30/65 – Q2
- Ranking in marine & freshwater biology: 36/110 – Q2



## 6. Paper III - Spawning site distribution of a bluefin tuna reduces jellyfish predation on early life stages

*"Life is too short to live it stressed out."*

Patricia Reglero



Publication information:

Ottmann D, Fiksen Ø, Martín M, Alemany F, Prieto L, Álvarez-Berastegui D, Reglero P. Spawning site distribution of a bluefin tuna reduces jellyfish predation on early life stages. *Limnology and Oceanography*. <https://doi.org/10.1002/lno.11908>

- Journal: *Limnology and Oceanography*
- JCR impact factor in 2021: 4.745
- Ranking in oceanography: 4/64 – Q1
- Ranking in limnology: 3/21 – Q1



## 7. Paper IV - Small fish eat smaller fish: a model of interaction strength in early life stages of two tuna species

*"Sometimes you have to re-think your conceptions."*

Øyvind Fiksen





Publication information:

Ottmann D, Reglero P, Alemany F, Alvarez-Berastegui D, Martín M, Fiksen Ø (*in review*)  
Small fish eat smaller fish: a model of interaction strength in early life stages of  
two tuna species. *Limn and Ocean Lett.*

- Journal: *Limnology and Oceanography Letters*
- JCR impact factor in 2021: 7.875
- Ranking in oceanography: 3/65 – Q1
- Ranking in limnology: 1/21 – Q1



**ARTICLE TYPE:**

Letter

**TITLE**

Small fish eat smaller fish: a model of interaction strength in early life stages of two tuna species

**RUNNING HEAD:**

Predation among larval tuna

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**DATA AVAILABILITY STATEMENT**

Data and R code are available in Github repository

[https://github.com/dottmann/bluefin\\_tuna\\_albacore\\_piscivory](https://github.com/dottmann/bluefin_tuna_albacore_piscivory)

## **SCIENTIFIC SIGNIFICANCE STATEMENT**

Most marine fishes die during their first days of life falling prey for other animals, and even minor changes in early predation rates can lead to order-of-magnitude variation in the number of individuals recruiting to the adult population. However, quantifying predation in fish early life stages and linking species-specific interactions to recruitment and population dynamics is challenging. Here we test the hypothesis that recovery of the commercially exploited Atlantic bluefin tuna can affect early survival of the Mediterranean albacore through predator-prey interactions of their early life stages. We find that when the predator species is present, they have a large predatory capacity on the prey species, but their patchy distribution may limit their total effect. Along with other processes affecting early survival, this interaction can contribute to a loss of recruitment potential to later stages.

## **ABSTRACT**

Fish larvae are rarely a major driver of fish mortality, but tunas can produce large batches of larvae that rapidly develop the capacity to kill other fish. We combine a model for the killing potential from Atlantic bluefin tuna (BFT) larvae on larval albacore (ALB) with field observations at a major spawning ground. Both species spawn from June to August, but BFT has a narrow spawning peak at the beginning of the season that results in priority effects. Our model shows that, following a recent stock recovery, BFT larvae have increased their killing pressure, leaving areas of up to 1000km<sup>2</sup> with <1% chance of ALB daily survival. Such increase in killing pressure suggests larval ALB has reduced chances to survive, yet in large areas with few BFT other drivers of early survival prevail over BFT predation. This shows that strong predatory interactions can occur during larval stages in some fishes.

## INTRODUCTION

Can predation by days-old fish larvae change reproductive success in other fish species? Although most fishes get killed by predators early in their life, piscivorous fish larvae are usually considered a minor cause of mortality because they are a small fraction of the total predator guild (Bailey & Houde 1989, Folkvord 1997, Houde 2008). This paradigm is likely true for most fishes, but tunas may be an exception, as they rapidly develop morphological traits (fast swimming speed, large eyes, large mouth-gap, voracious behavior, and rapid development of digestive system) that turn them into effective piscivores (Kaji et al. 2002, Llopiz & Hobday 2015). Further, adults are highly fecund fishes that target spawning grounds shared with other tunas, facilitating encounters among larvae (Reglero et al. 2014b). The Mediterranean albacore *Thunnus alalunga* (hereafter ALB) and Atlantic bluefin tuna *Thunnus thynnus* (BFT) are large, migratory species that share a major spawning ground in the western Mediterranean Sea (Alemany et al. 2010). Here, they spawn from June to August, but BFT has a narrower spawning peak than ALB, shifted towards the beginning of the breeding season (Saber et al. 2015, Reglero et al. 2018b).

During the tuna spawning season in the Mediterranean Sea, invertebrate predators are few and patchy (Ottmann et al. 2021b), but piscivorous fish larvae may be important predators of smaller larvae. The fact that BFT and ALB can produce large batches of larvae that are restricted to the warm water above the shallow (~20 m depth) thermocline (Torres et al. 2011, Reglero et al. 2018a) increase encounter rates and strengthen interactions. However, the strength of predatory interactions among tuna larvae has never been quantified.

Can predation from BFT larvae limit the early survival of ALB? The current rise of the eastern stock of Atlantic BFT (ICCAT 2020) and the concurrent decline of ALB makes this question relevant and provides an opportunity to explore this interaction. After decision makers implemented strict fishing quotas on BFT, the eastern stock has boosted from 348 thousand MT in 2007 to over one million MT in 2018 (Porch et al. 2019, ICCAT 2020). In contrast, the unmanaged population of Mediterranean ALB has recently declined in different parts of the Sea (Alvarez-Berastegui et al. 2018, ICCAT 2021). This decline cannot be attributed to fisheries because fishing pressure has remained relatively constant over the past decades (ICCAT 2020). Larval and fishery surveys indicate that, although larval abundances of ALB in western Mediterranean have dropped in recent years, adults target the same spawning sites and spawn during the same period (Saber et al. 2015, Alvarez-Berastegui et al. 2018). Thus, it is unlikely that a change in their spawning grounds or in the spawning window is causing the drop in larval abundance. One intriguing possibility is that the increasing BFT population affects ALB abundance through predation on the larval stages.

Here we model the predatory potential of larval BFT and assess its effect on early survival of ALB in the western Mediterranean Sea. Quantifying predator-prey encounters is difficult in any natural system, and for plankton we need to combine observations and mechanistic models (Kjørboe 2008). We develop a size-dependent model of predation for BFT larvae to assess how their increasing density affect survival of ALB, including observed size distributions from surveys in a major spawning ground. Then, we compare ALB's predicted probability of survival and observed densities before (2001-2005) and after (2012-2017) the eastern stock recovery of BFT.

## MATERIAL AND METHODS

### Field sampling and laboratory processing

We collected larval tuna with bongo nets in a major spawning ground around the Balearic Islands, western Mediterranean, in 11 surveys grouped in two discrete intervals from 2001-2005 and 2012-2017, representing periods before and after the BFT stock recovery, respectively (Supporting information). Sampling was timed to coincide with the peak spawning of BFT, and all 1429 samples were preserved in 4% formalin buffered with borax.

In the laboratory, we counted and identified all fishes to the lowest possible taxon and measured standard length for ALB and BFT with a camera-attached stereoscope and Image-Pro analysis software. Larval lengths were then corrected for the effect of shrinkage in formalin so we can use functional parameters obtained from live experiments (Supporting information).

### Defining predators and prey

BFT (and ALB) larvae complete the notochordal flexion (bending of the notochord in the caudal fin) and switch to a dominantly piscivorous diet at about 7.5 mm standard length (Uriarte et al. 2019, SL; Blanco et al. 2019). Therefore, we assume all BFT larvae  $\geq 7.5$  mm to be piscivorous predators on ALB that have not yet completed the notochordal flexion (Fig. 1). Yolk-sac is the smallest and least developed of the larval stages, with a negligible ability to detect and escape attacks from piscivorous larvae. We used the lower standard deviation of pre-flexion larval size (4.2 mm; Figure S1) as the threshold of first feeding and, since larvae  $\leq 4.1$  mm are yolk-sack larvae, their probability of capture success  $P = 1$ . Larvae between 4.2-7.4 mm standard length gradually flex their notochord and improve their swimming and evasive abilities (Reglero et al. 2015, Blanco et al. 2019, Downie et al. 2020). For these, we assume that the probability of capture success  $P_{ij}$  for a BFT of size  $i$  hunting an ALB of size  $j$  decreases with relative predator-prey length (Eq. 1):

$$(1) P_{ij} = \begin{cases} 1 & \text{for } L_j \leq 4.1 \\ \left(1 - \frac{L_j - 4.1}{L_i - 4.1}\right)^k & \text{for } L_j > 4.1 \end{cases}$$

Here,  $k$  is set to a basic value of 10 (see Supporting information for justification and sensitivity analysis of  $k$ ) and  $L_i$  and  $L_j$  are the BFT and ALB standard length (m), respectively.

### The predator-prey encounter model

BFT larvae are visual predators that detect prey at increasing distance through ontogeny (Hilder et al. 2019). Here, we quantify how often a BFT larva encounters and captures an ALB larva based on a mechanistic model for volume scanned for prey and survey-data on densities and size-distributions of both larval species. From this, we integrate the potential predation mortality suffered by ALB larvae.

First, we need to know how far away a BFT larva can detect an ALB, and how this depends on the body size or ontogeny of both predator and prey. The ability to resolve and detect objects depend, among other things, on the eye size, focal length and density of rods and cones on the retina – the visual acuity (Caves et al. 2018, Hilder et al. 2019). Visual acuity can be measured as minimum separable angle  $M$ ,

which determines the smallest visual angle at which two separate objects can be distinguished. Here we use an empirical estimate of  $M$  from the southern BFT *T. macoyii*:  $M = 4.699L^{-1.129}$  where  $L$  is the prey length (Hilder et al. 2019). Southern BFT is a close relative of Atlantic BFT with a similar ontogenetic development of eye and retina (Yúfera et al. 2014). The maximum visual prey detection distance  $R_{ij}$  (m) of a BFT of length  $i$  on an ALB of length  $j$  then becomes

$$(2) R_{ij} = \frac{0.5L_j z q}{\tan(0.5M_i)},$$

where  $z = 0.5$  is the behavioral/anatomical correction ratio (Job & Bellwood 1996). This equation applies to a spherical object; therefore, we reduce  $R_{ij}$  by  $q = 0.5$  since the projected image area of a fish larva is about half that of a circle.

Southern BFT larvae develop higher cone density in the ventral retinal region, which suggest they detect most prey looking upward with the surface as a contrasting background (Hilder et al. 2019). We therefore reduce their potential sectional search area from a full circle to a half circle (Fig. 1) (Fiksen & Folkvord 1999). We further assume random directional swimming of prey and predators in three dimensions, and apply the encounter model of Gerritsen & Strickler (1977) to calculate the clearance rate  $C_{ij}$  ( $\text{m}^3 \text{h}^{-1}$ ), or volume of water scanned by a BFT of size  $i$  for ALB of size  $j$  per hour:

$$(3) C_{ij} = 0.5\pi R_{ij}^2 \frac{V_j^2 + 3V_i^2}{3V_i}$$

where  $V_i$  and  $V_j$  are the BFT and ALB swimming velocities ( $\text{m h}^{-1}$ ), respectively. Larval BFT swimming velocity  $V_i$  is about 3 body-lengths  $\text{s}^{-1}$  (Reglero et al. 2015), and we assume  $V_j$  is the same. The rate  $E_{ij}$  at which an ALB of size  $j$  may encounter BFT of size  $i$  per hour is obtained by simply multiplying  $C_{ij}$  by the predator density  $D_i$  (BFT larvae  $\text{m}^{-3}$ ),  $E_{ij} = C_{ij} \times D_i$ . We assessed the sensitivity of visual radius (m) and clearance rate ( $\text{m}^3 \text{h}^{-1}$ ) to all model parameters and predictions (Supporting information).

For each  $ij$  predator-prey size combination (Fig. 1), a BFT larva's immediate consumption rate is  $E_{ij} \times P_{ij}$ . BFT larvae do not feed in darkness (Blanco et al. 2017), and we assume no satiation or handling limitations, which is reasonable given the low observed densities of ALB (Fig. S6). Therefore, the daily consumption rate becomes  $E_{ij} \times P_{ij} \times h$  and daily survival chance is  $S_{ij} = \exp^{-E_{ij} \times P_{ij} \times h}$ , where  $h$  is the number of daylight hours (15 h). Following the multiplication rule of probability, for each station, all  $S_{ij}$  of a given  $j$ -size ALB can be multiplied to calculate daily chance  $S_j$  to survive to all size-predators  $i$  combined. Then, we multiply  $S_j \times D_j$  to find the density of surviving ALB after one day of exposure to predation.

### Size-structure and vulnerability to increasing BFT abundance

For ALB, survival depends on BFT's total density  $\Sigma D_i$  and relative size. Field densities of piscivorous BFT range from 0 to 0.168 larvae  $\text{m}^{-3}$ , and the size-structure of ALB and BFT is unique in each station. Because we want to test the vulnerability of each ALB cohort based on its size structure, regardless of the predator size-structure, we standardize BFT to an idealized continuous size structure (Supporting information) and estimate ALB survival of each station to increasing densities of BFT. To further illustrate how piscivory differs among ALB size-classes, we simulate another idealized

size-structured cohort, this time of larval ALB, and focus on size-class effects at  $\Sigma D_i = 0.002, 0.020, 0.080$  and  $0.168$  BFT larvae  $m^{-3}$ .

### **BFT and survival of ALB larvae**

We test the effect of BFT on ALB survival along spatial and temporal dimensions. Spatially, we use annual survey data to map piscivorous BFT distribution over the spawning ground, including their size-structure, and estimate daily probability of dying ( $1 - \text{probability of survival}$ ) for a vulnerable (4.1 mm SL) ALB yolk-sack larva at each station. Mortality will be greater in stations with denser and larger BFT than in stations with fewer and smaller BFT and will have no effect where BFT are absent (89.8% of surveyed stations).

For the temporal analysis, we apply a Welch's 2-sample t-test to compare densities and daily probability of survival for a 4.1 mm ALB yolk-sack larva in each sampling station before and after the BFT recovery. Then, we correlate the temporal trends in ALB larval densities in relation with presence and abundance of piscivorous BFT and in relation to their predatory potential (survival for a 4.1 mm yolk-sack larva).

## **RESULTS**

### **Size-structure and vulnerability to increasing BFT abundance**

Piscivorous BFT ( $\geq 7.5$  mm SL) accounted for less than 1% of the total BFT larvae observed in the field, but they were relatively widespread (in 10.2% of all stations) and found in densities up to  $0.167$  larvae  $m^{-3}$ . Almost half the stations with piscivorous BFT had  $< 0.005$  larvae  $m^{-3}$ , and only 3 stations (0.2%) had more than  $0.10$  larvae  $m^{-3}$  (Fig. 2a).

The average proportion of observed ALB that would survive daily predation at the highest density of BFT is 17.2% ( $0.168$  larvae  $m^{-3}$ , assuming idealized BFT size structure [Fig. S5]) (Fig. 2a). However, observed ALB size structures differ among stations, resulting in large variance in survival. Among the 33.3% stations with presence of ALB (Fig. S6), 81% of them had only small ( $< 4.5$  mm) ALB. Thus, ALB larvae at most stations are vulnerable to high BFT abundance (Fig. 2a).

BFTs' killing potential increase proportionally with density, but mostly small ALB larvae are vulnerable to predation. In the simulated size-structured cohort of larval ALB (Fig. 2b-e), their probability to survive one day increase with size after the yolk-sack larvae threshold, regardless of predator abundance. Small individuals ( $< 4.5$  mm SL) are removed much faster than larger individuals (4.5-7.4 mm), which is illustrated with a greater drop of surviving ALB. Thus, although BFT's killing potential increase proportionally with density, the size-distribution of the surviving ALB cohort will differ upon BFT density.

### **BFT and survival of ALB larvae**

Overall, the probability that an ALB is predated by a piscivorous BFT larva is low and patchy due to absence of piscivorous BFT in most stations. However, patches of high daily mortality were up to 5 times larger and over 10 times more abundant in the 2012-2017 interval compared to the 2001-2005 interval (Fig. S7). Estimated daily mortality was lowest in 2001 when no piscivorous BFT was observed and greatest off



southeast Ibiza in 2017, where vulnerable ALB (i.e. 4.1 mm SL yolk-sack larva) had <1% estimated daily chance to survive predation from BFT in an area of 1000 km<sup>2</sup>.

Across the 17-year period of this study, BFTs' presence and abundance increased after the stock recovery (Fig. 3). Thus, ALB's estimated daily probability of survival dropped in 2012-2017 compared to 2001-2005 (*F*-test,  $p < 0.001$ ). Conversely, ALB was less abundant in 2012-2017 than in 2001-2005 despite interannual fluctuations within each period (*F*-test,  $p < 0.001$ ).

## DISCUSSION

Trophic interactions among fish larvae have been largely neglected, but we show that some voracious and piscivorous larvae can be an important driver of mortality in other fish species. Piscivorous BFT larvae can cause severe mortality in small ALB larvae and truncate their size distribution. Even at low densities (0.02 larvae m<sup>-3</sup>) BFT can kill more than half the yolk-sack and small pre-flexion ALB larvae in a single day (Fig. 2c), and real predation may exceed the values reported here because piscivorous BFT are likely underestimated due to net avoidance (Habtes et al. 2014). This predator-prey interaction is strong because larval BFT are unusually abundant in the western Mediterranean spawning grounds compared to tunas elsewhere (Ohshimo et al. 2017, Tawa et al. 2020). However, larvae of other billfishes and scombrids may have an even greater piscivorous potential than BFT, as some are more voracious (Llopiz & Hobday 2015) and can be more abundant. Thus, strong piscivorous interactions among fish larvae are likely more widespread than previously thought. This conclusion may extend to freshwater systems too, as fishes like pike *Esox* spp. or pikeperch *Sander* spp. also become piscivorous during their larval stage (Colchen et al. 2020).

Our model shows that the increase in piscivorous BFT larvae has resulted in an increased risk of mortality for ALB, but does this mean that BFT can reduce the recruitment potential of ALB? Predation only takes place when both predator and prey cooccur in the same place, and because only a fraction of newly hatched individuals survive to the post-flexion stage, BFT are relatively few and patchy by the time they become piscivorous. Thus, most areas of the ALB spawning ground are relatively safe from piscivorous BFT (Fig. S7). However, the number and size of these patches has increased after the BFT stock recovery, reducing the ALB piscivore-safe zones. Piscivorous BFT rose from an average 0.0003 to 0.0016 larvae m<sup>-3</sup> after the stock recovery and estimated mean daily survival of ALB dropped from 99% to 95% (Fig. 3). This suggests that predator-prey interactions may have contributed to the reduction of observed ALB density with the recovery BFT (Fig. 3). Nonetheless, the increase in BFT piscivorous pressure is just one of several contributing processes driving the ALB decay, as the larval abundances of both species are not always negatively correlated. In 2017, for instance, larval abundances of both species increased, suggesting that factors like warm water temperature, food availability, or low abundance of invertebrate predators (Fiksen & Reglero 2021, Ottmann et al. 2021b) could favor both species.

Other processes, like a decrease of ALB biomass due to fishing activities (ICCAT 2021), changes in food availability (Gleiber et al. 2020), or increase of tropical species with piscivorous behavior (Báez et al. 2018) may also contribute to the observed

decline of ALB larval densities, especially in the stations where piscivorous BFT is absent. It is difficult to say which processes have a greater contribution to ALB mortality, as they may vary over time and space. The effect of piscivorous BFT, for instance, is strongest at the beginning of ALB's spawning season, as this is when BFT is most actively reproducing (Reglero et al. 2018b). Mesocosm experiments under different temperature and food regimes can help determine the vulnerability of ALB larvae to other habitat conditions.

A meta-analysis study (Mittelbach & Persson 1998) reveals that freshwater fishes that develop piscivorous behavior early in life tend to be larger at hatch, grow faster and spawn earlier than their prey. In our case, both tuna species have similar size-at-hatch and growth rate, thus, it is the early spawning of BFT (Reglero et al. 2018b) that results in a priority effect. The fact that their larvae are large enough to be piscivorous when ALB yolk-sack and pre-flexion larvae are most abundant may be an adaptive life-history strategy in a long-distance migrator to provide fish prey to their offspring and simultaneously reduce food competition with other larvae of the same guild (Siepielski et al. 2020), yet this hypothesis remains untested. Either way, it suggests that timing of spawning is an important modulator of the interaction strength among piscivorous fishes of the same guild.

Predation and predator-related processes are the major drivers of fish mortality, especially during the early stages of life (Bailey & Houde 1989, Houde 2008, Fouzai et al. 2019). However, mortality processes in larval stages may differ from those in juvenile stage. Current studies show that juvenile ALB have not been observed in stomach content of other juvenile or adult scombrids (Fletcher et al. 2013, Sorell et al. 2017, Varela et al. 2019), and they are thought to be too few to cause density-dependent regulation (Arregui et al. 2006, Bakun 2013). Thus, although predation and density-dependence may occur in juvenile stages, it appears that processes driving mortality of larval stages have a heavier leverage on recruitment success (Watai et al. 2017, Ishihara et al. 2019).

The eastern stock of Atlantic BFT has recovered from overfishing thanks to effective fisheries management (Porch et al. 2019), but the rise of BFT may have unintended consequences on the Mediterranean ALB stock due to predation in larval stages. Predator-prey interactions can cause alternative stable states in both marine and freshwater systems (e.g. Barkai & McQuaid 1988, Persson et al. 2007, Eklöf et al. 2020), where changes in the prey or predator populations, often triggered by human activities, can reverse the predator-prey role. Although the degree to which larval piscivory can affect recruitment of ALB remains uncertain, this study is the first to consider population-level effects of a fish by a larval predator of the same guild. Clarifying the effect that the recovery of BFT may have on ALB is important. While the stock appears to be declining and has entered in overfishing status, current management of the Mediterranean ALB fishery aims to "avoid increases in catch and effort" (Alvarez-Berastegui et al. 2018, ICCAT 2021). Now that some stocks of top predator fishes are recovering world-wide (Hilborn et al. 2020), further understanding of trophic interactions between commercially important species can help decision makers move beyond single-stock management.

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## **AUTHOR CONTRIBUTIONS**

D.O., P.R. and Ø.F. designed the research; P.R. and F.A. provided research funding; D.O., P.R., F.A., M.M. and D.A.-B. collected field samples; D.O., F.A. and D.A.-B. and M.M. 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.

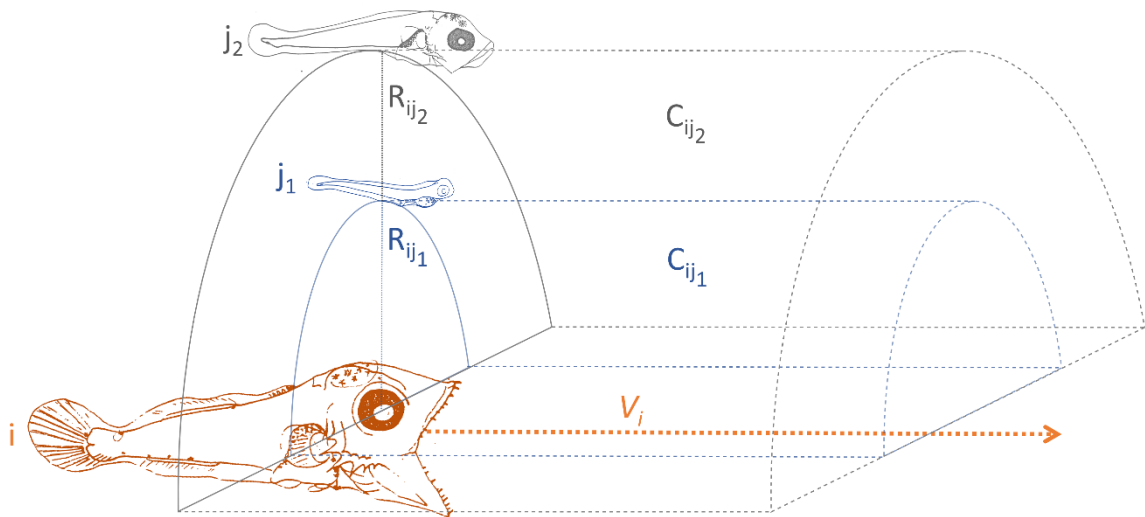
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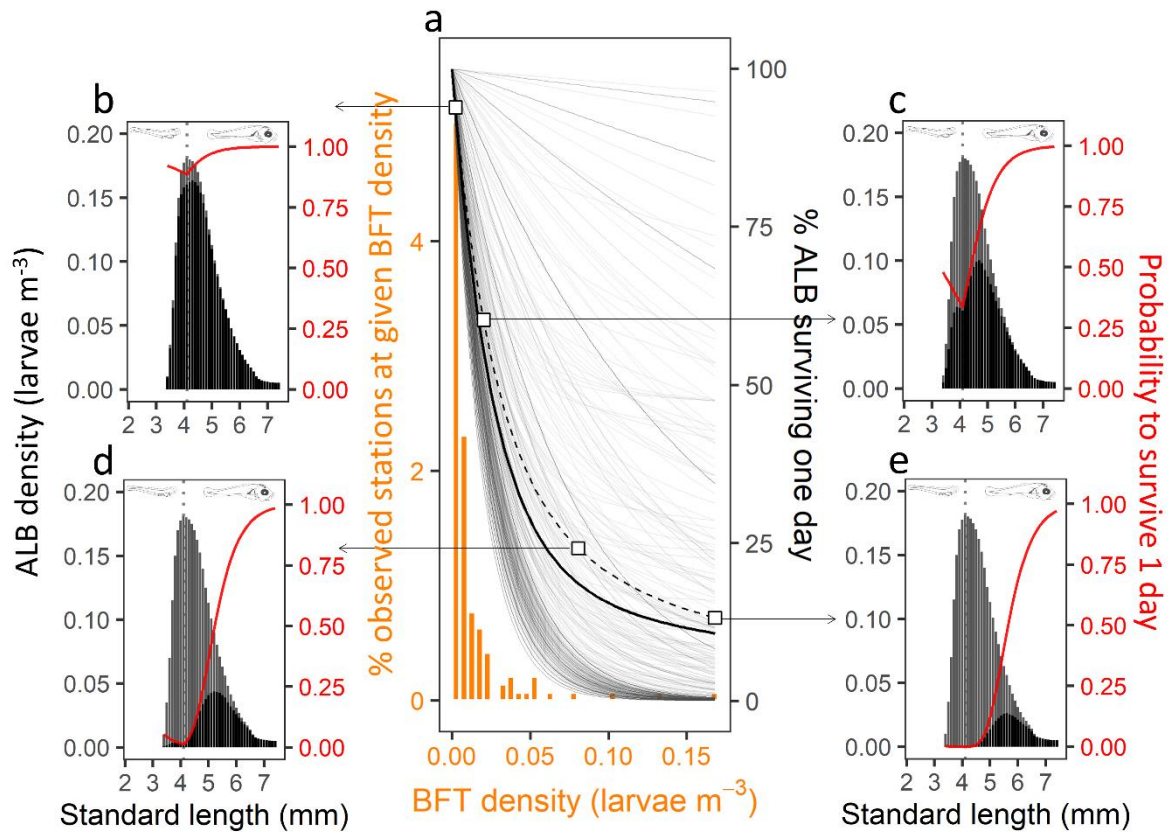
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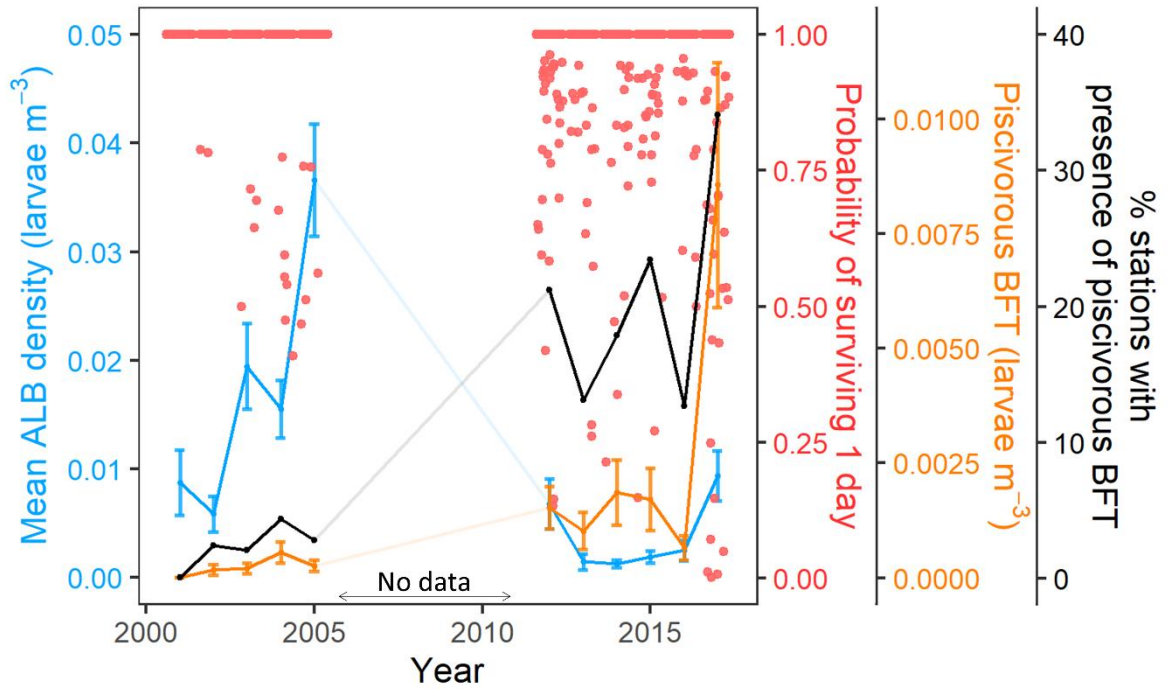


**Figure 1. Schematic representation of the modelled visual radius  $R_{ij}$  (m) and clearance rate  $C_{ij}$  ( $\text{m}^3 \text{s}^{-1}$ ) for each predator-prey interaction between piscivorous bluefin tuna larvae ( $i = 7.5\text{-}13 \text{ mm}$ ) cruising at a speed  $V_i$  of 3 body lengths ( $L_i$ )  $\text{s}^{-1}$  and albacore larvae ( $j = \leq 7.4 \text{ mm}$ ).**





**Figure 2. Daily survival probability of albacore (ALB) larvae exposed to increasing densities of piscivorous bluefin tuna (BFT $\geq$ 7.5 mm SL).** a) Orange bars indicate frequency of observed field stations with specific BFT densities (larvae  $m^{-3}$ ) excluding zeros (89.8%); grey lines indicate daily proportion of surviving ALB to increasing BFT density ( $\Sigma D_i$ ) given the ALB size structure of each sampled station ( $n = 1429$  stations), solid black line is the mean of all stations, and the dashed black line represents a simulated idealized size-structure (corresponding to the grey bars in panels b-e); white squares set at density  $\Sigma D_i = 0.002, 0.020, 0.080$  and  $0.168$  BFT larvae  $m^{-3}$ . b-e) Size distributions of a simulated idealized cohort of ALB before (grey bars in the background) and after (black bars) one day of light exposure to four BFT densities  $\Sigma D_i = 0.002$  (b),  $0.020$  (c),  $0.080$  (d) and  $0.168$  (e) larvae  $m^{-3}$ . The proportion of ALB removed in each case is 6 %, 40%, 76%, and 87%, respectively. Red line indicates daily probability of surviving of ALB in each size group. The vertical dotted line is the size-limit of yolk-sack larvae ( $\leq 4.1$  mm).



**Figure 3. Temporal trends on abundances and predatory pressure of bluefin tuna (BFT) and albacore (ALB).** Annual mean observed ALB density (blue; mean larvae m<sup>-3</sup> ±SE), abundance of piscivorous bluefin tuna (orange; mean larvae m<sup>-3</sup> ±SE), percent stations with presence of piscivorous larvae (black); and probability that a vulnerable yolk-sack ALB larva (4.1 mm SL) survive one day in the field considering the density and size-structure of BFT found in each station (red dots).

## 8. Discussion

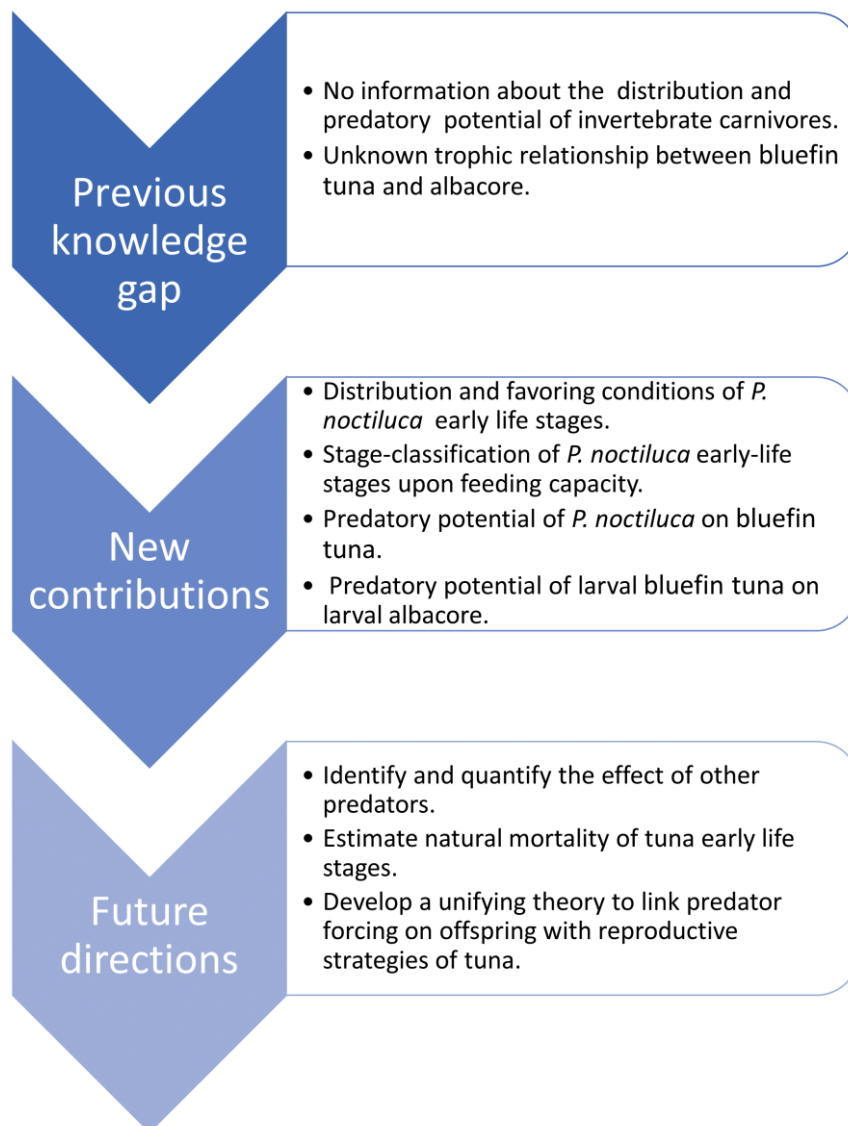
*"The more I know, the more I realize I know nothing."*

Socrates



## 8.1. Advancing knowledge

Why do bluefin tuna target warm and oligotrophic waters as spawning grounds? What are the benefits? What are the drawbacks? Several decades of research have made good progress towards understanding tuna migratory behavior and ecology (Reglero et al. 2014b, Kitagawa, T & Kimura, S 2015, Muhling et al. 2017). However, many questions regarding the tradeoffs of their reproductive strategy remain open. Understanding trophic interactions of their early life stages can help answering some of these questions, and the work presented in this thesis contributes to advance knowledge in this field (Fig. 8.1).



**Figure 9.1. Schematic showing how this thesis has contributed to fill knowledge gaps in tuna larval ecology.**

The first step that my collaborators and I have taken for studying trophic interactions of bluefin tuna early life stages is to identify key species that interact with them. Following Gordoia et al. (2013) and Uriarte et. al. (2019) we know that *Pelagia*

*noctiluca* and albacore are two important ones, which also stand for two groups of organisms in the plankton – invertebrate predators and ichthyoplankton prey, respectively. The second step has been to ensure that we have enough previous knowledge of the biology and ecology of these species to cover basic assumptions of the hypotheses, like knowing their distribution, abundance, and feeding traits. Previous knowledge of bluefin tuna and albacore (Alemany et al. 2010, Alvarez-Berastegui et al. 2018) was enough for the purpose of our analysis, but for *P. noctiluca* some of this information was missing and we developed it in Papers I and II. Only then could we test our hypotheses about trophic interactions.

## 8.2 New contributions

In **Paper I** my collaborators and I have identified a relation between water temperature and chlorophyll concentration (taken as an indicator of food availability), with spring reproduction and early survival of *P. noctiluca* in the western Mediterranean Sea.

*P. noctiluca* is a tolerant and opportunistic jellyfish that can thrive in a wide range of conditions. This, combined with erratic dispersal and patchiness further complicates the identification of patterns in the field (e.g. Hecq et al. 2009, Pastor-Prieto et al. 2021). Our capacity to identify patterns resides in three key elements of our data set. 1) Our field collections sample only the top 30 m of the water column, where more than 95% of the ephyrae and metaephyrae are found. By not sampling deeper strata, where they are mostly absent, our collection reduces biased-low densities, and therefore prevents a loss of statistical power. 2) Our 6-year dataset is systematic and spatially extensive. The temporal continuity of this series enables to compare across multiple years with different oceanographic scenarios, and the broad study area of 60 x 90 nautical miles sampled at a relatively fine grid (10 x 10 nautical miles) enables to identify both, patchy and regional trends. 3) The time of sampling is a critical moment in the early survival of *P. noctiluca* because metabolic demands are increasing with warming temperature and food is becoming scarcer. Sampling later in the season would result in fewer presence and abundance of *P. noctiluca* early life stages (e.g. Pastor-Prieto et al. 2021), reducing the statistical power to identify patterns.

In **Paper II** we have defined 4 stages of development of ephyrae and metaephyrae of *P. noctiluca* that feature increasing capacity to capture prey.

While previous work (Rottini Sandrini & Avian 1983) identified 9 stages of larvae, descriptions of subsequent stages were vague and did not clarify the transition from ephyrae to metaephyrae. For the scope of this work, we were interested in identifying and describing this transition, as it is an important milestone towards being able to effectively capture and eat fish larvae. This information, along with descriptions of stage-morphometry and shrinkage due to formalin preservation, is basic information that can be used in future studies of ecology and biology of *P. noctiluca* early life stages.

In **Paper III** we have found that, despite the high predatory potential of *P. noctiluca* metaephyrae on bluefin tuna eggs and larvae, low overlap between both species prevents metaephyrae to unleash its predatory potential. We have proposed a

mechanism whereby adult bluefin tuna may identify signatures from an oceanographic front and to spawn in sites with reduced invertebrate predation.

The fact that bluefin tuna targets frontal zones for spawning is well documented (García et al. 2005, Teo et al. 2007, Alemany et al. 2010), and the hypothesis that it migrates to warm, oligotrophic systems to favor larval growth and reduce predation was formulated almost two decades ago (Bakun & Broad 2003). However, while the hypothesis that tuna benefits from warm water is well supported, the hypothesis of low predation remains unverified, and no clear reason has been consolidated about the benefits of targeting frontal zones. Based on the results of Paper IV, we observe that the frontal zone delimits a water mass with fewer *P. noctiluca* from another water mass with more of *P. noctiluca* (and by extension other invertebrate predators). Thus, by spawning in or right before the frontal zone, tuna offspring will be less exposed to invertebrate predation. We further speculate that bluefin tuna has developed a sensitivity to the front to prevent high exposure of predators on their offspring and that other bluefin tuna across the world may have developed a similar strategy. Thus, this work lends supports that tuna selects spawning sites that are not just warm, but also have few predators.

In **Paper IV** we have modeled the piscivorous pressure of larval bluefin tuna and compared its temporal trend to the decreasing abundance of larval albacore. Although we could not link a direct cause-effect between the opposing trends in stock abundance, our results show that high densities of piscivorous bluefin tuna have the potential to remove an important number of albacore larvae, reducing its recruitment potential.

The capacity of piscivorous bluefin tuna to remove albacore larvae depends on whether if their spawning sites overlap, which in turn is modulated by the position of the salinity front. While albacore tend to spawn in an area located in the southeast side of the study area, spawning sites of bluefin tuna vary depending on the annual position of the front (Reglero et al. 2012). Thus, years when the position is more advanced (north-eastwards) the degree of overlap is greater than in years when the front is less advanced. One caveat of this analysis is the impossibility to link removals of albacore larvae with its population decline, as there are no current estimates of larval natural mortality rate. Thus, although we have evidence that piscivorous bluefin tuna are increasing removals of larval albacore, we cannot conclude that this is causing a recession on the albacore population. What we can affirm is that this increase in albacore removals reduces its recruitment potential.

### 8.3. Limitations of this study

Evaluating predator-prey relations of animals in natural systems requires to understand a network of complex and variable factors. In open marine systems, acquiring this information is hampered by methodological constraints to obtain the right data at meaningful scales. Therefore, a common approach is to link field observations with biological models to see if they match expectations (Kiørboe 2008). This approach enables to test biological mechanisms in natural systems. However, because it is not an empirical approach, hypotheses cannot be explicitly confirmed.

There is an important difference between demonstrating a process with unequivocal findings and identifying correlations, even when these come from biological models built with empirical data. For marine plankton in natural systems, it is virtually impossible to empirically demonstrate the strength of predator-prey interactions and its effects at population and evolutionary scales. However, combining field observations with biological models based on experiments (Baum & Worm 2009) is a good approach to advance our understanding of natural processes and discard alternative hypotheses.

This approach has several caveats that are inherent to sampling constraints (failing to estimate fine-scale patchiness or top-down effects, net avoidance of larger individuals, etc.), and to the IBM architecture (accuracy of experimentally derived parameters, missing biological variables, etc.). Nonetheless, if the sampling and model design are robust to variation of basic assumptions, it is possible to make inferences about predation in the field and speculate on the predator-prey interaction strength and its ecological implications.

### 8.4. Future directions

The last frontier of fishery science is to be able to predict annual recruitment of fishes, but despite centuries of research, our capacity to predict changes in fish populations remains limited. Most fishes die during the first days of life, and linking abundances of larvae with the number of surviving recruits is challenging, as processes determining natural mortality are utterly complex. Predation is the major source of fish natural mortality (Bailey & Houde 1989), and poor fish conditions may increase its vulnerability to predators. Thus, paths to better estimate natural mortality can either focus on the mechanisms that make larvae more vulnerable (i.e. feeding condition, slower growth, longer stage-duration, etc) or focus on specific predator-prey interactions.

In this thesis my collaborators and I have combined field observations with biological models to investigate specific predator-prey interactions in the larval stages of a top-predator fish. Because predator-prey experiments with vertebrates are now considered unethical, combining field observations with current experimental knowledge sets a precedent for upcoming research to quantify predator-prey interactions of larval bluefin tuna in the field. Further research will include studying and comparing the interaction strength of bluefin tuna with other predators, refining the vulnerability of larvae to predators as a function of their size and feeding condition, evaluating different behavior upon lunar cycles and light intensity, analyzing



the tradeoffs of the spawning phenology, and generating a unifying theory to estimate mortality under different conditions. Because the focus of this thesis is centered in three relatively well studied species, it makes for a good case study of trophic interaction studies between larval fish and invertebrate carnivores and piscivorous larvae. Thus, mechanistic understanding developed in this work about the interaction strength between tuna larvae and an invertebrate predator or another fish prey can be used elsewhere in further studies of predation on fish early life stages.



## 9. Conclusions

*“Just because we cannot see clearly the end of the road, it is no reason for not setting out on the essential journey.”*

John F Kennedy



- 1) While both, water temperature and food availability determine the three-dimensional distribution of *Pelagia noctiluca* early life stages, they are located above and within the shallow thermocline, where warmer temperature favors growth and survival, as opposed to deeper strata, where more food is available, but water is colder.
- 2) Surface chlorophyll concentration of June is a good estimator of *P. noctiluca* early life stage abundance and distribution, despite some mismatch at 10-nautical mile scale. This trend suggests that food availability determines the interannual and spatial pattern of reproductive activity and early survival.
- 3) *P. noctiluca* early life stages are more abundant in the north-west side of the Balearic Islands, where surface chlorophyll concentration of resident Atlantic water depicts greater productivity.
- 4) Four stages of development can be identified on ephyrae and metaephyrae of *P. noctiluca* based on the development of feeding structures. Stage III determines the onset of the metaephyrae stage, when they can effectively feed on larval fish.
- 5) The size of each development stage of *P. noctiluca* early life stages is significantly different from each other, and individuals shrink about 24% after storage in 4% formalin, regardless of their stage of development.
- 6) High densities of *P. noctiluca* metaephyrae can remove a large proportion of Atlantic bluefin tuna (BFT) eggs and larvae before they reach the flexion stage. However, low overlap between both species reduces actual predation.
- 7) The overall low effective predation of metaephyrae on BFT supports the hypothesis that adults migrate to this spawning ground not just to benefit from its warm water, but also to benefit from the low predator pressure on offspring. The spatial mismatch between BFT and *P. noctiluca* metaephyrae, following different oceanographic signatures related to the salinity front, suggests BFT may target the front to reduce predation on their offspring.
- 8) The recovery of the eastern stock of the Atlantic BFT is increasing its potential predator pressure on larval albacore. This interaction is strengthened in years when the position of the salinity front fosters a better match between the spawning sites of both species.
- 9) BFT and albacore have developed different reproductive strategies whereby BFT has a major spawning peak early in season while albacore spawns more extensively over the season. These different strategies provide priority effects to most larval BFT, that can feed on younger albacore.



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## Appendix 4. Supplementary information to Paper IV

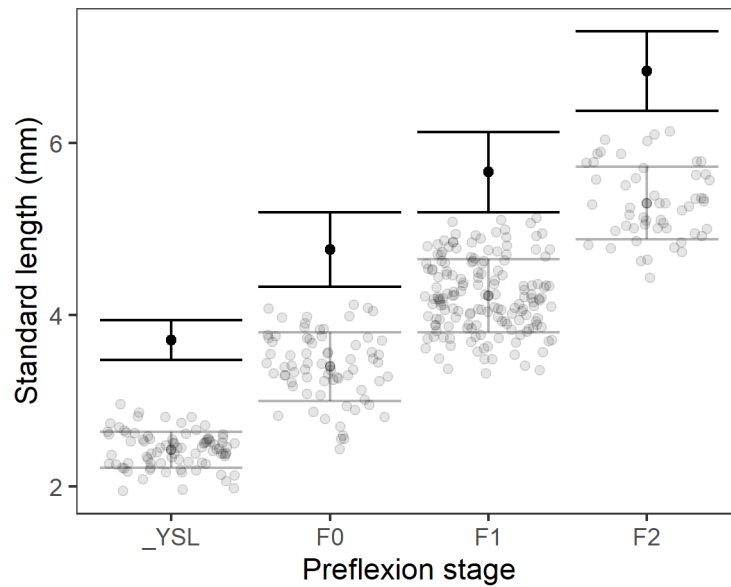
### SUPPLEMENTARY METHODS

#### 1.- Field sampling

Sampling took place between June 18 and July 29, coinciding with peak spawning in bluefin tuna (BFT) and the onset of spawning in albacore (ALB). In each survey, we conducted oblique tows with plankton nets at 2 knots cruising speed on a 10x10 nautical-mile grid and deployed a CTD to alternating depths of 350 and 650 m after each tow. From 2001 to 2005, we towed a bongo net of 60-cm mouth diameter and 333  $\mu\text{m}$  mesh-size down to 70 m, and from 2012 to 2017, we towed a larger bongo (90-cm diameter) with 500  $\mu\text{m}$  mesh-size to only 30 m depth. Bongo frames were always equipped with a depth recorder and flowmeter. The gear and sampling design were changed to optimize captures of larval tunas (both ALB and BFT), which remain close to surface (Reglero et al. 2018a). To compare data collected with both sampling designs, we converted larval densities captured with bongo 60 to its equivalent density with bongo 90 following Álvarez-Berastegui et al (2017), who validated this protocol with sequential tows with both nets in the same station. Post-flexion larvae may have a greater escape rate for bongo 60 than for bongo 90. To evaluate if there is a noticeable difference in the escape rate between these gears, we apply a Welch's t-test to test whether if the ratio of post-flexion:total BFT larvae differs using different nets. The result indicates that there is no significant difference in the ratio of post-flexion:total BFT larvae ( $P = 0.248$ ). Thus, we conclude that the change in sampling gear is unlikely to generate significant bias between the two periods, and our results are robust to this change.

## 2.- Correction for larval shrinkage in formalin

We randomly selected 366 larvae from the field (preserved in formalin) ranging 1.95 – 6.14 mm SL and grouped them into four development stages, yolk sac larvae (YSL), and three different pre-flexion and flexion stages (F0-F2) as described by Blanco et al. (2019). Then, we regressed their mean size-at-stage against measurements from live larvae (Blanco et al. 2019) and used the equation to convert the lengths of field sampled larvae to their size before preservation. The lower standard length from pre-flexion larvae (F0; 4.2 mm) and the upper standard length of larvae finishing their notochordal flexion (F2; 7.5 mm) were used as limits between YSL/pre-flexion (i.e. first feeding) and flexion/post-flexion (piscivory) stages, respectively (Fig. S1).



**Figure S1. Standard lengths (mm) of bluefin tuna larvae preserved in formalin (gray) and back transformed to fresh sizes (black).** Dots indicate individual measurements and error bars indicate standard deviations of yolk-sack larvae (YSL) and larvae with increasing notochordal development (F0-2) (Blanco et al. 2019).  $L_{Fresh} = 1.06 + 1.09 \times L_{Formalin}$

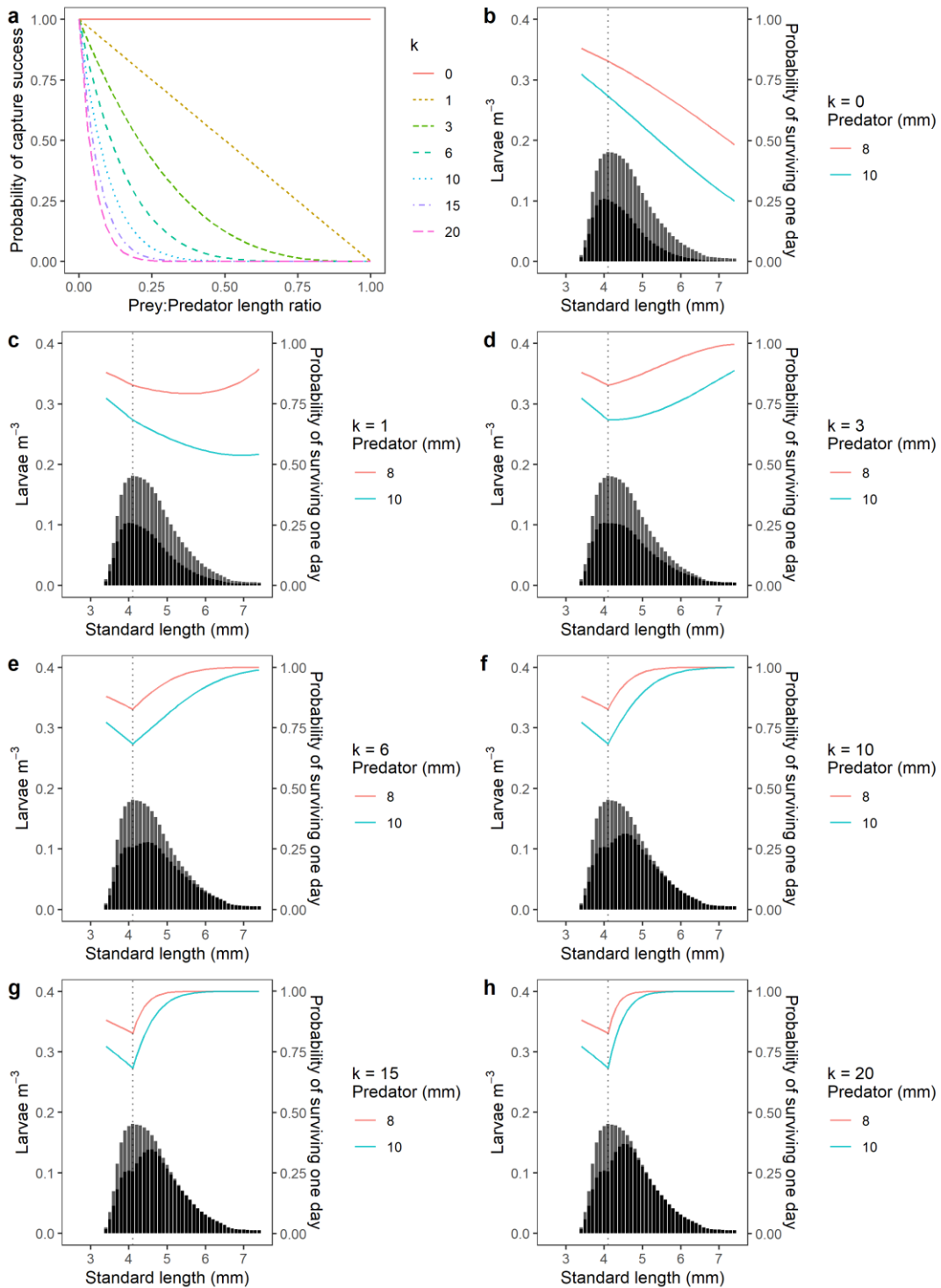
### 3.- Sensitivity of probability of capture success to predator-prey relative size proportion

Yolk-sack larvae ( $\leq 4.1$  mm) have limited swimming and evasive abilities (reviewed in Bailey & Houde 1989). Therefore, we assume piscivorous bluefin tuna (BFT)  $\geq 7.5$  mm will always succeed capturing yolk-sack larvae. On the other hand, larger prey (4.2-7.4 mm) progressively develop their vision and fins (Yúfera et al. 2014), improving their capacity to escape predators. Larger BFT larvae also have better ability to maneuver and capture prey, so we model probability of capture success  $P_{ij}$  from relative predator-prey lengths  $i$  and  $j$ , respectively, where  $P_{ij}$  is close to 1 for ALB first feeders and decreases with greater size (Folkvord & Hunter 1986).

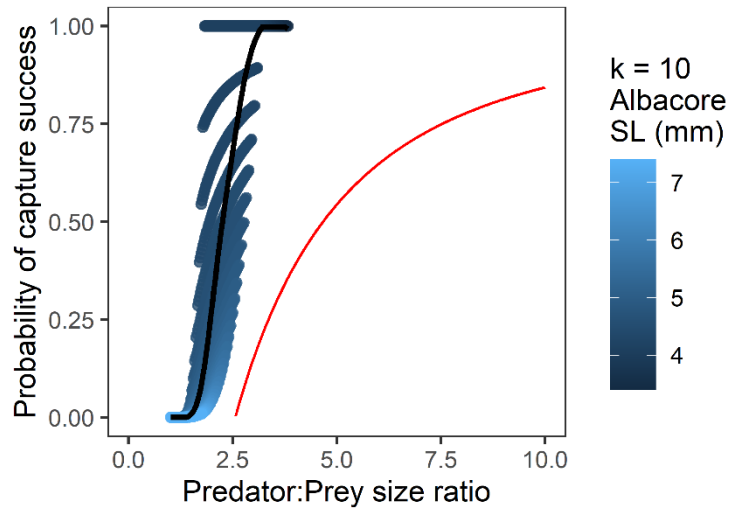
As prey, we simulate a size-structured larval ALB cohort that follows a right-skewed gaussian density distribution emulating an idealized cohort of ALB samples from the surveys. As predators, we introduce 8 and 10 mm long BFT larvae at densities  $D_i = 0.005$  larvae  $m^{-3}$  each (Fig. S2). To calculate the probability  $S_{ij}$  that prey within each size bin will survive one day of exposure to each of these predators we apply the model  $S_{ij} = \exp^{-E_{ij} \times P_{ij} \times h}$ , as defined in the main text.

We conduct a sensitivity analysis of how the shape coefficient  $k$  of Equation 1 affects the probability of capture success and one day survival. If ALB is unable to escape BFT at encounter ( $k = 0$ ), the probability of capture success  $P_{ij}$  is always 1 and survival declines with ALB body length simply because larger larvae can be detected at a greater distance (Fig. S2a-b) and encounter rate is higher (Bailey & Houde 1989). If larvae after first feeding are more likely to escape an encounter ( $k > 0$ ), survival tends to increase with size because larger ALB improve their visual, swimming and escaping abilities (Fig S2c-h). Consequently, in our baseline model ALB prey is most vulnerable at 4.1 mm body length (Fig. S2f), the largest yolk-sack stage before first feeding. This agrees with experimental work (Bailey & Houde 1989, Litvak & Leggett 1992).

Larval BFT are formidable piscivorous predators that can kill and eat conspecific larvae that are larger than half their size (Ishibashi et al. 2013). Applying a  $k = 10$  in our equation of capture success enable piscivorous BFT larvae to start preying on ALB at a predator:prey size ratio  $\sim 2$  and rapidly increase capture success as this ratio increase (Fig. S3). This rapid increase is consistent with Miller et al (1988), who after reviewing how predator:prey relative size affected the probability of capture success among different fish larvae (and crustaceans) found that small predators are more sensible to changes in prey size than large predators. On average, they found that predators start to capture prey when they are about 2.5 times larger than their prey, and capture success rapidly increases with small increments of predator:prey size ratio. Some fish species can start capturing prey at predator:prey  $< 2.5$  and none of them had such early piscivorous behavior as BFT. Thus, a  $k = 10$  fits piscivorous expectations for BFT. The model is robust to larger  $k$  values, as probability of capture success and density of surviving ALB are only weakly affected by larger values of  $k$  (Fig. S2).



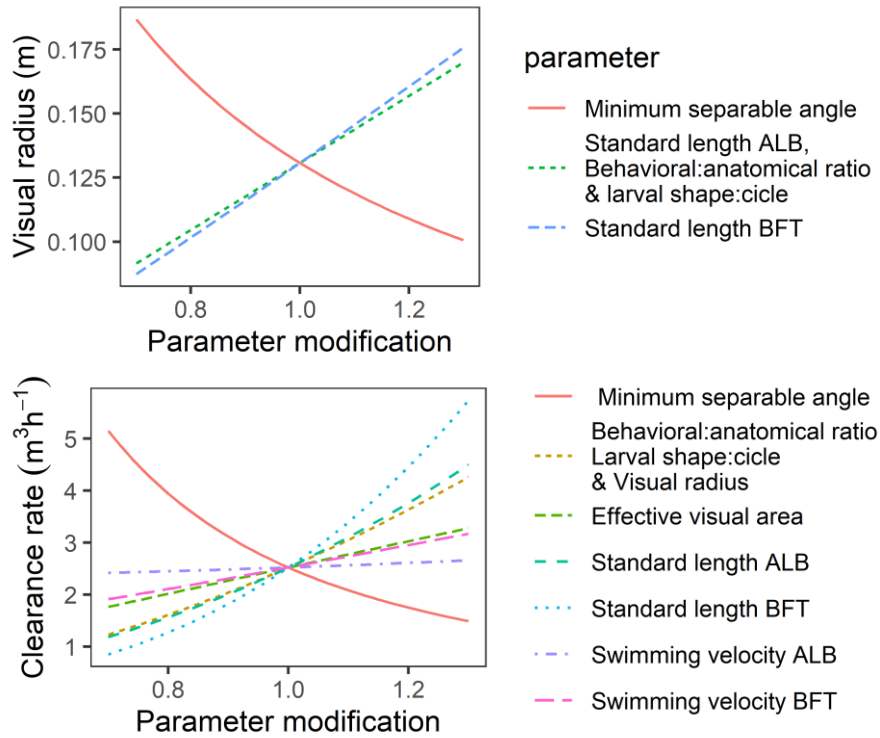
**Fig. S2. Sensitivity of  $k$  on probability of (a) capture success  $P$  and how predation shapes the size distribution of prey over one day (b-h).** Panels b-h show albacore density distributions before (grey bars) and after (black bars) the exposure to two predator size-classes in one day. Red and blue lines indicate the length-dependent probability of survival from 8- and 10-mm larval BFT predators both with density  $D_i = 0.005$  larvae  $m^{-3}$ . Gray dotted lines indicate the limit of yolk-sack larvae ( $\leq 4.1$  mm) and piscivorous larvae (i.e. post-flexion larvae;  $\geq 7.5$  mm).



**Figure S3. Size-dependent capture success of larval bluefin tuna 7.5-13 mm SL with  $k = 10$  (black line) compared to average capture success from other fishes ranging 17-135 mm SL (red line; Miller et al. 1988). Blue lines indicate range of capture success for each albacore larvae 3.4-7.4 mm SL at a 0.1 mm size interval.**

#### 4.- Sensitivity of visual prey detection distance, and clearance rate

Visual prey detection radius  $R_{ij}$  (m) is squared in the model for predator-prey encounters, where  $i$  and  $j$  are predator and prey size-tags, respectively. We find the volume searched for prey per unit time, or a predators' clearance rate ( $\text{m}^3\text{h}^{-1}$ ) as  $C_{ij} = 0.5\pi R_{ij}^2 (V_j^2 + 3V_i^2) / 3V_i^2$  (Fig. S4). Clearance rate depends on factors related to visual acuity, prey size and shape, predator search area (Fig. 2) and light (here limited to day and night).



**Figure S4.** The effect on a) visual radius and b) clearance rate of shifting parameter values 30% up or down from our basic values. The crossing point represents the visual baseline of an 8 mm bluefin tuna (BFT) searching for a 4.1 mm albacore (ALB).



## 5.- Standardized size-structure of an idealized cohort of piscivorous BFT

The idealized size-structure is obtained fitting a function to the maximum densities observed for each size group  $i$  in the field. Size-specific densities  $D_i$  decline from 0.032 to 0.001 larvae  $m^{-3}$  at 7.5 mm and 13 mm SL, respectively (Fig. S5). To describe and approximate this cohort at a given time, we fit an equation to the maximum density of each size-group, so that  $D_i = 0.0005 + 0.0315^{0.926 \times i}$  where  $i$  ranges 0-55 size groups. Then, we multiply  $D_i$  by a sequence of values  $\beta = 0 - 0.375$  so the total density of BFT larvae  $\Sigma D_i$  range from 0 (no predation) to 0.168 larvae  $m^{-3}$  (maximum density observed in the field). The value of  $\beta = 0.375$  is obtained dividing  $0.168/\Sigma D_i$ .

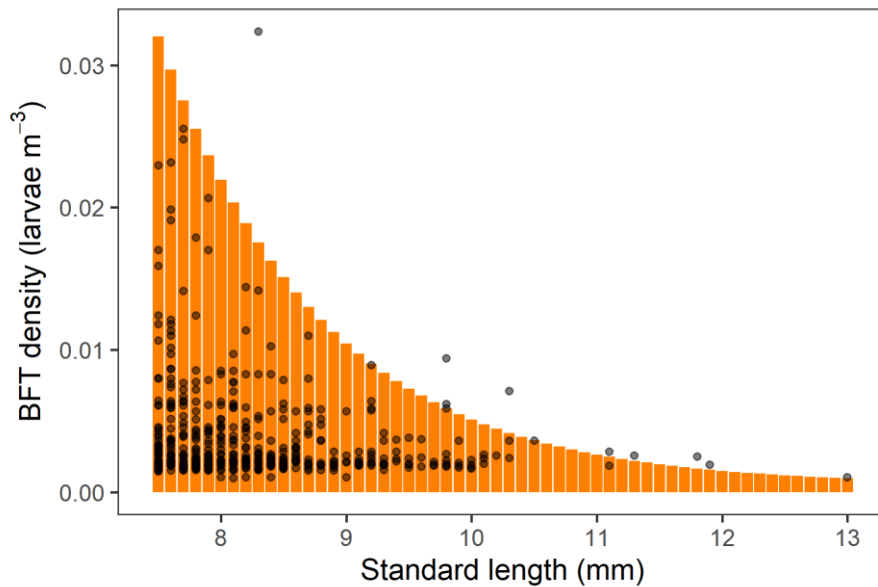
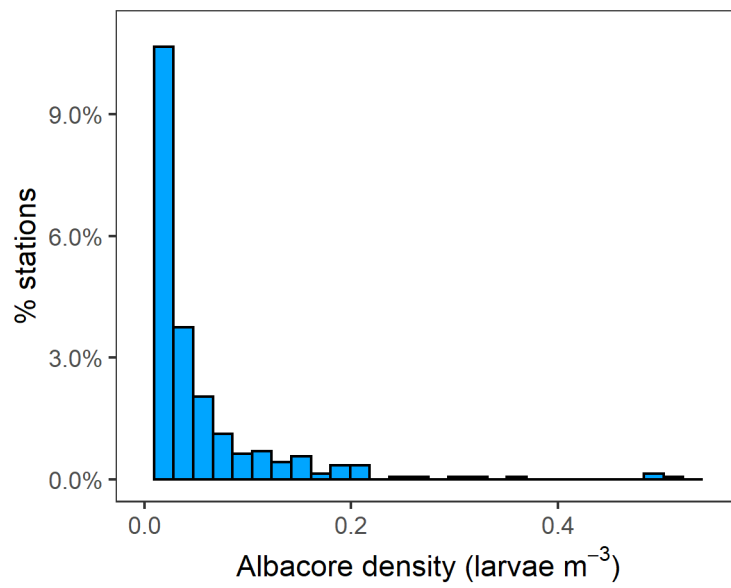


Figure S5. Idealized density distribution of *T. thynnus* (BFT) size-classes 7.5-13 mm SL from the surveys (dots), and the fitted maximum number  $D_i$  calculated for each size class (bars).

## 6.- Density distribution of albacore larvae



**Fig. S6. Frequency distribution of albacore density collected in all stations. Zero values (66.7%) are excluded.**

## 7.- Probability of dying in one day

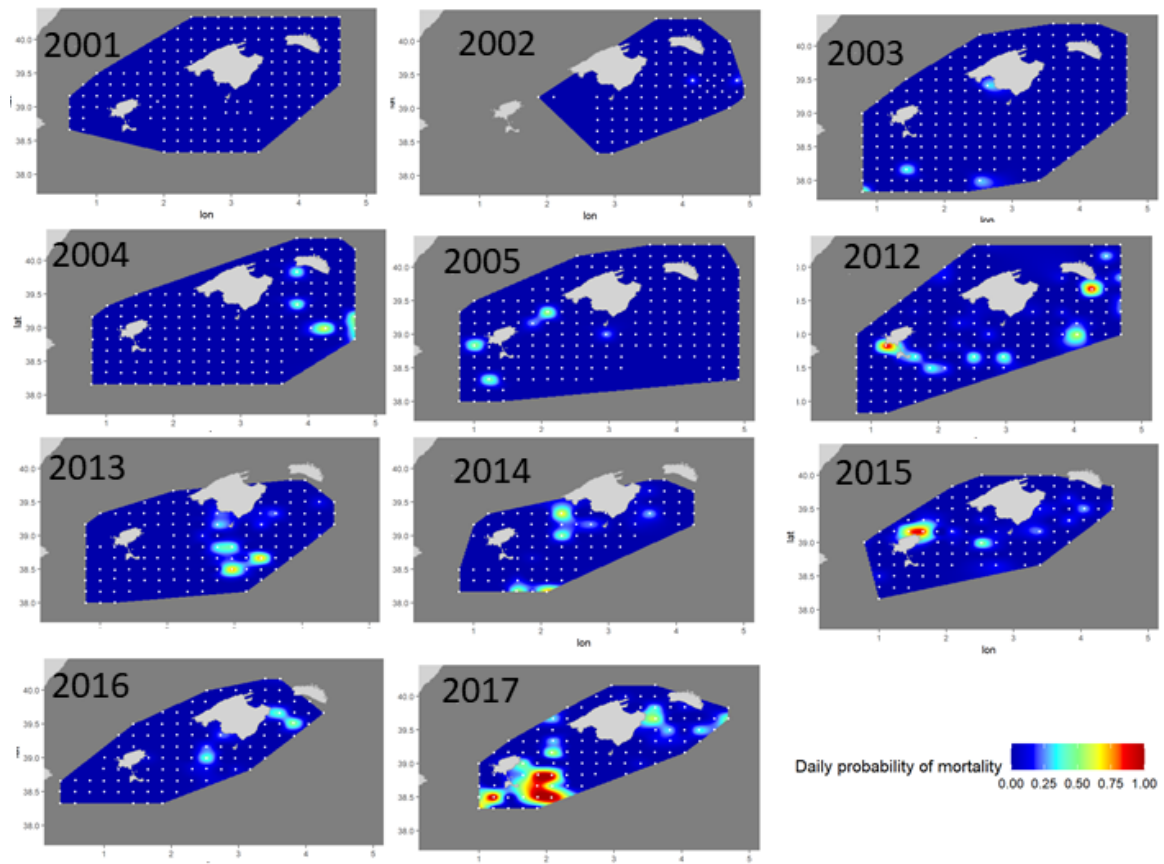


Figure S7. Probability that an albacore larva 4.1 mm SL will die ( $1 -$  probability of survival) in 1 day of exposure to observed piscivorous bluefin tuna.

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