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Environmental and biological characteristics of Atlantic bluefin tuna and albacore spawning habitats based on their egg distributions

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ABSTRACT

Tuna spawning habitats are traditionally characterized using data sets of larvae or gonads from mature adults and concurrent environmental variables. Data on egg distributions have never previously been used since molecular analyses are mandatory to identify tuna eggs to species level. However, in this study we use molecularly derived egg distribution data, in addition to larval data, to characterize hydrographic and biological drivers of the spatial distribution of eggs and larvae of bluefin *Thunnus thynnus* and albacore tuna *Thunnus alalunga* in the Balearic Sea, a main spawning area of these species in the Mediterranean. The effects of the hydrography, characterized by salinity, temperature and geostrophic velocity, on the spatial distributions of the eggs and larvae are investigated. Three biological variables are used to describe the productivity in the area: chlorophyll a in the mixed layer, chlorophyll a in the deep chlorophyll maximum and mesozooplankton biomass in the mixed layer. Our results point to the importance of salinity fronts and temperatures above a minimum threshold in shaping the egg and larval distribution of both species. The spatial distribution of the biotic variables was very scattered, and they did not emerge as significant variables in the presence-absence models. However, they became significant when modeling egg and larval abundances. The lack of correlation between the three biotic variables challenges the use of chlorophyll a to describe trophic scenarios for the larvae and suggests that the spatial distribution of resources is not persistent in time. The different patterns in relation to biotic variables across species and stages found in this and other studies indicate a still elusive understanding of the link between trophic levels involving tuna early larval stages. Our ability to improve short-term forecasting and long-term predictions of climate effects on the egg and larval distributions is discussed based on the consistency of the environmentally driven spatial patterns for the two species.

1. Introduction

Larval habitats have been used to infer a preference of tuna species worldwide to spawn in warm areas with mesoscale structures close to fronts (Alemany et al., 2010; Muhling et al., 2013; Reglero et al., 2014; Alvarez-Berastegui et al., 2014). Similar results are also observed using adult data (Schaefer, 2001; Teo et al., 2007). Such studies have led us to hypothesize that tuna spawn in areas with enhanced productivity that result in better feeding and hence growth conditions for the larvae (Bakun, 2006). Besides, fronts may act as dispersal/retention mechanisms for the eggs and through the larval stage (Mariani et al., 2010), which could favor the spatial overlap of tuna early life stages and their prey. A change of habitat requirements can be expected between fish spawning sites and larval feeding grounds, since eggs can rely on their own resources whereas larvae must feed exogenously once their yolk-sac reserves are exhausted. Therefore, evolutionary processes would induce the selection of spawning sites not necessarily located in highly productive areas, but those whose hydrodynamic characteristics lead, once dispersal processes have taken place, to increase the spatial overlap between subsequent larval stages and their prey, and the retention of such larvae in adequate feeding areas. The size fraction of prey most relevant for the larvae to survive is expected to change as

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larger prey are incorporated into the diet as the larvae grow. Moreover, egg distribution is mainly determined by parental behavior, while larval distribution is also affected, in addition to hydrodynamics, by differential survival among different groups' eggs. Thus, the spatial and temporal match between tuna larvae and their prey at hatching would ultimately depend on the previous spatial locations of eggs, resulting in future fitness of older larval stages being influenced by earlier responses of the parents to environmental variations.

While biological variables may ultimately drive successful larval feeding and reduced predation risk during early life history stages, physical variables are indicators and precursors of egg distributions. In fact, it has been already stated that adult fish are frequently found in association with environmental and geographical physical features, presumably using them as cues for their spawning activities (Ciannelli et. al., 2015, Schabetsberger et al., 2016). On the other hand, spawning in warm water temperatures may respond to the thermal preferences of the eggs and larval stages (Schaefer, 2001; Reglero et al. 2014) and physiological constraints during early life development (Ciannelli et al. 2015). Based on these premises we propose that there is a progression of the factors that affect tuna egg and larval occurrence and abundance, from physical oceanographic features during the egg stage, to physical and biological features during the larval stage.

Tuna spawning sites have never been characterized in terms of the probability of egg occurrence, which would be the most precise method to define spawning areas, since direct information on the eggs distribution is still lacking. Therefore, the main hypotheses explaining the environmental and biological requirements characterizing tuna spawning grounds have never been evaluated using egg distribution data. Determining the spatial distribution of tuna eggs is difficult because morphological descriptions alone, useful for the identification of larvae at species level, can mislead species identification in the eggs due to strong similarities across species. Only recent developments in the use of molecular analyses make possible the identification of eggs to species level (Ward et al., 2005; Ivanova et al., 2007). Besides, the short duration of tuna egg developmental stages, never exceeding two days (Miyashita et al., 2000; Gordoa and Carreras, 2014), constrains surveys that need to cover a tight grid of stations during the spawning window. In addition, eggs are difficult to obtain from field sampling due to their highly patchy distribution. However, getting a better understanding of factors affecting tuna egg distribution and comparing them with those driving the spatial patterns of later stages can help to unveil the spawning strategies and ontogenetic habitat shifts of these species and explain differences in habitat use during early development.

In the Balearic Sea, a major spawning ground for tuna in the Mediterranean, coexisting tuna species show different spawning strategies. Atlantic bluefin tuna (*Thunnus thynnus*) has been described as being an environmental-driven spawner based on larvae being distributed according to the confluence of recent and resident Atlantic water, as observed when using longer data series in the area (e.g. Alemany et al., 2010; Reglero et al., 2012). Such water confluence results in a salinity front whose position changes within years (Balbín et al., 2014). In contrast, albacore (*Thunnus alalunga*) has been characterized as a geographically driven spawner with consistent hotspots of larvae to the northeast of the Balearic Islands when comparing interannual variability (Reglero et al., 2012). Similar trends seem to prevail in other Mediterranean areas such as the Gulf of Gabes (Koched et al., 2013). Our aim in this study is to provide for the first time egg distribution data for bluefin tuna and albacore obtained from extensive sampling in the Balearic Sea.

Not only the geographical variations in environmental conditions, but their variability throughout the water column should be taken into account for investigating tuna larval ecology. This is because there is a strong stratification of the water column during the tuna spawning season in the Balearic Sea as a consequence of a thermocline that separates two layers in the euphotic zone, the surface mixed layer (0–20 m) and the deep layer (20–70 m), characterized by clearly different nutrients and chlorophyll concentrations (Mena et al. 2016). Therefore, the role of biological variables on the spawning strategies of tuna and their relationship with the water masses need to be based on field studies that sample independently the surface mixed layer, since tuna larvae are only found within the first 20 m depth, above the thermocline and hence any sampling methodology integrating data or biological material from waters above and below the thermocline would blur the conclusions.

Our aim in this study is to provide, for the first time, egg distribution data for bluefin tuna and albacore obtained from extensive sampling in the Balearic Sea, correlating egg occurrence (presence-absence) and abundance to indicators of mesoscale activity and temperature in the area. We test the hypothesis that tuna generally spawn in warm frontal areas and corroborate the particular reproductive strategies for albacore and bluefin tuna in the area, previously stated from the larval data. Specifically, in this study we are interested in the correlations between chlorophyll and micro- and mesozooplankton biomass, as indicators of different size fractions of larval tuna prey, and the occurrence and abundance of tuna egg and larvae. A novelty of this study is that, considering the aforementioned tuna larvae vertical distribution, to accurately describe the biological and environmental habitat of both tuna eggs and larvae the plankton samples have been taken only throughout the surface mixed layer, contrastingly to previous similar studies in which plankton tows integrated the whole water column from 70 m in the open sea (Alemany et al., 2010; Reglero et al., 2012). The results from this study are expected to provide information on the consistency of the spawning strategies described for the two species based only on larval data and will improve our ability to use such patterns for short-term forecasting and long-term predictions of climate effects on tuna.

2. Material and methods

2.1. Field sampling and laboratory analyses

Sampling activities, including larvae, eggs and environmental sampling, were carried out onboard the research vessel *Ramón Margalef* from 21 June to 4 July 2012 coinciding with the spawning season of albacore and bluefin tuna in the study area. Tuna larvae were collected using standard double-oblique hauls with Bongo nets 90-cm mouth diameter equipped with 500-μm meshes and geared with General Oceanics flowmeters, covering a regular grid of 112 stations with a 10 nm separation between them. Bongo-90 catches were conducted down to approximately 30 m, throughout the mixed layer and the thermocline, whose position was determined from CTD profiles onboard. One replicate was preserved in 4% buffered formalin in seawater and the second replicate was preserved in ethanol. Once at the lab, fish larvae were sorted from the 4% seawater-buffered formalin using a stereoscopic microscope, identified and counted to the lowest taxonomic level using determination keys according to available descriptions for the area (Alemany, 1997).

A 20-cm diameter Bongo net was geared with a General Oceanics flowmeters above the Bongo-90 to sample zooplankton. One of the mouths of the Bongo-20 was fitted with a 250-μm mesh net to sample mesozooplankton and the other mouth was fitted with a 50-μm mesh net to sample microzooplankton. These samples from the 250-μm mesh size were equally divided in two aliquots using a Folsom plankton sample splitter. One sub-sample was preserved in 90% ethanol, and the other immediately frozen onboard at −20 °C. The whole sample from the 50-μm mesh size was immediately frozen onboard at −20 °C in other refrigerator but due to a technical problem the samples were lost and could not be analysed. In the laboratory, the mesozooplankton dry weight was obtained following Lovegrove, (1966) and Laíz-Carrión et al., (2013). Mesozooplankton dry weight biomass values were standardized to mg m^{-3} (mg DW m^{-3}).

In the 112 stations, coinciding with the Bongo sampling, several