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Size-dependent predation in piscivorous larval stages of three tuna species

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ABSTRACT

The bluefin tuna (*Thunnus thynnus*) is a heavily fished temperate tuna that spawns in the Mediterranean Sea; the area off the Balearic Islands is a key spawning area. Other abundant tunas, including albacore (*Thunnus alalunga*) and the small bullet tuna (*Auxis rochei*) spawn in the same area. The three species temporally overlap during the summer spawning period of the adults. Because they are clearly piscivorous already at very early larval stages, we expect strong interactions both in terms of a direct predator–prey relationship and as competitors for food resources. In this study, we focus on understanding the size dependent trophic interactions among the three species at the different developmental larval stages. First, we describe the environmental and biological scenarios where different size stages of the three species co-occur through the application of generalized additive model (GAM) analyses to field data collected during cruise surveys in 2004–2005. We then develop an individual based model (IBM) to evaluate inter- and intraspecific predation rates considering size structured prey and predator fields in the framework of piscivorous behaviour. The results demonstrate how predation mortality rates influence the spawning location of the three species.

Keywords: piscivorous, larvae, predation, tuna.

INTRODUCTION

The Mediterranean Sea is an important spawning area for tuna and several species coincide during the summer spawning period of the adults, among them the bluefin tuna (*T. thynnus*), which spawn primarily in June-July, the albacore (*T. alalunga*) that spawns in July-September and the bullet tuna (*A. rochei*) spawning from June to September (Alemany 1997; Macías et al 2005). The adult bluefin tuna is the most migratory of the three species

consisting of two main populations with distinct spawning areas, the Mediterranean and Gulf of Mexico, which overlap on North Atlantic foraging grounds (Block et al 2005).

Tuna larvae have some of the highest growth rates among marine species. To maintain such high growth rates they shift from a diet based on zooplankton to voracious piscivorous and cannibalistic foraging early in their life. Data on larval feeding behaviour (Uotani et al 1990; Young and Davis 1990; Miyashita et al 2001; Catalán et al 2007; Morote et al 2008) show that tuna undergo a diet shift, from a more zooplankton-oriented diet to a clearly piscivorous diet, even cannibalistic, already during the early larval stages. Therefore, the three tuna species in the Mediterranean Sea may show strong interactions both in terms of a direct predator-prey relationship and as competitors for food resources in the early life stages. To change to a piscivore the larvae need to develop their digestive system (Kaji et al. 1996) and the visual system (Margulies 1997) but also needs of prey size-dependent encounters as the intensity of piscivory/cannibalistic interactions depends on the size relationship between predators and prey (Juanes et al 2002, Claessen et al. 2000).

Here, we focus on understanding the foraging process of planktivore larvae and; on size-dependent interaction among larvae of three tuna species in terms of predator-prey relationship and competition for prey at the piscivorous stage. We perform this using a combination of field data and a bioenergetic coupled with a foraging model.

MATERIAL AND METHODS

Field data

The study site embraces the waters around the Balearic Islands. During the summer of 2004 and 2005, the Spanish Oceanographical Institute conducted two scientific surveys sampling a regular grid of about 200 stations. Larvae were collected using Bongo nets equipped with 200 μm and 333 μm meshes and flowmeters (Mod. General oceanics 230).

Oblique tows were performed down to 70 m in the open sea or down to 5 m above the sea floor at shallower stations. The larvae were classified into bluefin tuna (*Thunnus thynnus*, hereforth BFT), albacore (*Thunnus alalunga*, hereforth ALB) and bullet tuna (*Auxis rochei*, hereforth BT). The larvae were separated into stage-1 larvae, or zooplanktivorous larvae, and stage-2 larvae, or piscivorous larvae.

The biological characteristics of the larval habitats were analyzed using generalized additive models (GAMs) (Hastie and Tibshirani 1990). For each species, the response variable in the analyses was the presence/absence of “stage-1” larval stages modeled as a binomial response with a logit function related to the mesozooplankton biomass (mg dw/m³). They were also used for relating the response variable to the density (individuals /m³) of stage-1 and stage-2 of the other species.

The model

We develop a model of larval foraging capabilities and a bioenergetic model as in Urtizbera et al (unpublished) to evaluate if mesozooplankton biomass limits the larval feeding and growth at various ontogenetic stages in each of the three species. We calculate the search efficiency (clearance rates) required to obtain the potential growth rate at zooplankton densities that larva experience in the field. We simulate foraging rates of growing predator larvae feeding on growing prey larvae to assess the possibility that tuna larvae are surf-riding on a size-spectrum of younger larvae (Pope et al 1994). The parameterization of physiological and behavioral parameters is mainly from aquaculture works focused on bluefin tuna and field-derived data.

The growth rate for bluefin and albacore larvae was obtained from age-length relationships from laboratory experiments at controlled temperatures of Pacific bluefin tuna larva (*Thynnus thynnus orientalis*) reported in Miyashita et al. (2001), Sawada et al. (2005) and

Tanaka et al. (2008). An exponential relationship between age and dry weight was fitted to estimate the potential specific growth rate of Pacific bluefin tuna larvae at each temperature. Routine metabolic cost was estimated from laboratory experiments with bluefin tuna at 25 °C (Miyashita et al. 1999). The same function was used for the three species. We predict the clearance rate required for each species to achieve maximum growth rate at the temperature and prey densities that larvae experience in the field. We assume that Q_{10} is equivalent to 1.7, for larvae of *Scomber scombrus* belonging to the same family (Scombridae) (Guiguere et al. 1988).

We predict the clearance rate required for each species to achieve maximum growth rate at the temperature and prey densities that larvae experience in the field:

$$(1) \quad \beta_{zoo}(W_{t-1}, T; N_{zoo}) = \frac{\delta_t}{dw \times N_{zoo} \times Pc_{zoo}},$$

where β_{zoo} is the minimum clearance rate m³/s required to sustain the maximum growth rate at temperature T , δ is the required ingestion to sustain the maximum growth rate for each larva size (equation 2), dw is the dry weight of the mesozooplankton in mg/prey, N_{zoo} is the abundance of mesozooplankton per m³ and Pc_{zoo} is the capture probability.

RESULTS

The stage-1 and stage-2 larvae of the three species were found together in many of the sampled stations. There were some stations where the predominance of one of the stages of one species was very clear but in many cases at least two of the species were found together. Bullet tuna was the species with the widest distribution in the grid and was present in most of the stations. The grid coverage in 2004 was more complete than in 2005.

The “stage-1” of the three species was differently located. Bullet tuna was located in waters with high mesozooplankton abundances while the albacore and bluefin tuna were present mostly in low mesozooplankton waters.. The probability to have presence of BT1 increases with densities of ALB1, and viceversa. However the presence of ALB1 was not significant with mesozooplankton densities (Table 1).

We calculated the required clearance rates in order to get the potential growth rate at zooplankton densities that larvae experience in the field assuming a required ingestion of 70% of dry weight per day. The calculated clearance rates were always lower for BT compared to BFT and ALB (Fig 1). For BFT and ALB the estimated clearance rates were very similar for larval lengths below 4.5 mm for BFT and ALB and to a lesser extent to BT. In contrast, BT required lower clearance rates over the larger larval sizes compared to ALB and BFT.

We calculated the required clearance rate for small (3.5 mm) and large (6.5 mm) larvae to grow at maximum rate with the range of zooplankton densities that larvae experienced in the field (from 1 to 18 mg dw m⁻³). In both cases, the required clearance rates decreases with zooplankton densities (Fig 2). The large and small larvae require highest clearance rates at mesozooplankton densities lower than 5 mg dw m⁻³. At zooplankton biomasses below 5 mg dw m⁻³, clearance rates were up to ten times higher for 6.5 mm compared to 3.5 mm larvae.

The estimation of the specific ingestion rates for piscivorous larvae feeding on prey larvae of different size showed that the highest impact of the predatory larvae was performed on prey larvae sizes in the range of 4.5-5 mm (Figure 3). Our simulations suggest predation of larger larvae on smaller tuna larvae is possible and in general piscivory is needed to achieve the growth rates observed in nature.

DISCUSSION

We have focused on describing the potential for food competition and predator-prey interaction among tuna larvae and the oceanographical characteristics in which these interactions can occur. Based on our analyses we have identified some key biotic variables involved in presence and the distribution of tuna larvae.

We found differences in where “stage-1” of the three species occurs. BT1 shows preference for environments with high mesozooplankton abundance. The probability to have presence of BT1 increases with densities of ALB1, and viceversa. However the presence of ALB1 was not significant with mesozooplankton densities. On the other hand, BFT1 larvae occurred alone following no trend with any variables besides salinity. In the study by Alemany et al (submitted) the distribution pattern of the larvae (all developmental stages pooled together) during 2001-2005 showed a preference towards sea oceanic waters for bluefin tuna and albacore than bullet tuna which were more abundant in shallow waters nearer to the coast. This physical preference in BFT for medium saline waters we also observed in our study considering BFT1 and can be related to the spawning behavior of the adults.

Our study shows that size-dependent descriptors of larval assemblages are essential to provide information on possible competition and predation scenarios among tuna larvae and in comparison with other early-life piscivorous species. Improvements of our understanding of the larval ecology of one tuna species is achieved by including other tuna species in the assemblage’s descriptors.

Our simulations suggest that bluefin tuna and albacore larvae need to rely very much on their encounters with larval prey to survive in the low productive environments compared to bullet tuna usually found in richer environments. The three species go from a strictly zooplanktivorous feeding to a plausible piscivorous one. We found from our simulations that smaller larvae can tolerate lower mesozooplankton resource levels. In fact, minimum clearance rates for small larvae were in the range normally found for other planktivorous larvae (Sørnes and Aksnes 2004) and varied little despite the mesozooplankton biomass considered.

The three species considered in the study may follow different strategies for survival. Bluefin tuna and albacore may rely very much on their capacity for piscivory whereas bullet tuna, even if piscivore, occupy richer water masses that could be a source of mixed feeding.

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TABLE

Table 1: Based on GAM models the estimated significance of the relationship between the presence/absence of each species at stage 1 with respect to zooplankton biomass (Zoo), and to the other species: Bluefin tuna stage 1 (BT1) and 2 (BT2), albacore stage 1 (ALB1) and stage 2 (ALB2).

Variable	BT1		ALB1		BFT1	
	Dev. %	UBRE	Dev. %	UBRE	Dev. %	UBRE
~s(zoo)	11	**	1.73	0.19 ns	0.009	-0.45 ns
~s(BT1)			15.2	0.07 *	1.78	-0.46 ns
~s(ALB1)	13.7	0.22 *			5.07	-0.46 ns
~s(BFT1)	0.26	0.38ns	3.11	0.18 ns		
~s(BT2)	8*	**	5.23	0.15 *	0.09	-0.45 ns
~s(ALB2)	1.04	0.36ns	1.09	0.19 ns	0.32	-0.45 ns
~s(BFT2)	0.27	0.38ns	0.66	0.2 ns	1.16	-0.45 ns

FIGURES

Figure 1. Estimated clearance rates to get the maximum growth rate at 23.5 °C for larvae of different size feeding on mesozooplankton densities that on averages each size of larva encounter in the field. We assumed an ingestion rate of 70% of dry weight. A trend compiled for other planktivorous fish is shown for comparison (Sørnes and Aksnes 2004).

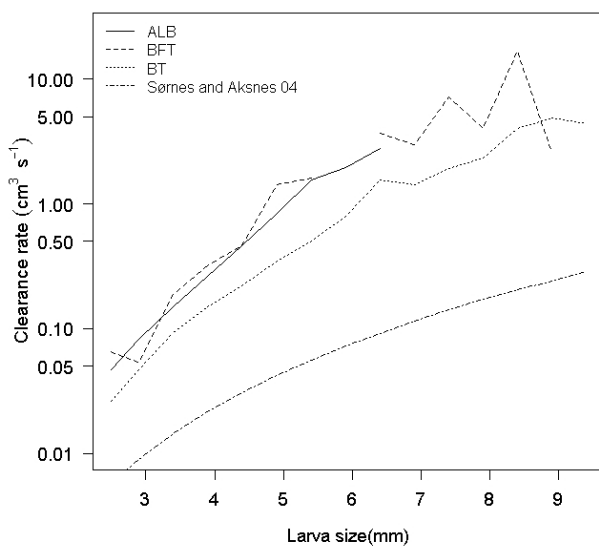


Figure 2. Required clearance rates to obtain the potential growth rate for stage-1 (average SL=3.5 mm) and stage-2 larvae (average SL=6.5 mm) at different mesozooplankton biomass and ingestion rates (0.5W, 0.7W and 1W for 50%, 70% and 100% of dry weight). Simulations are shown for bluefin tuna.

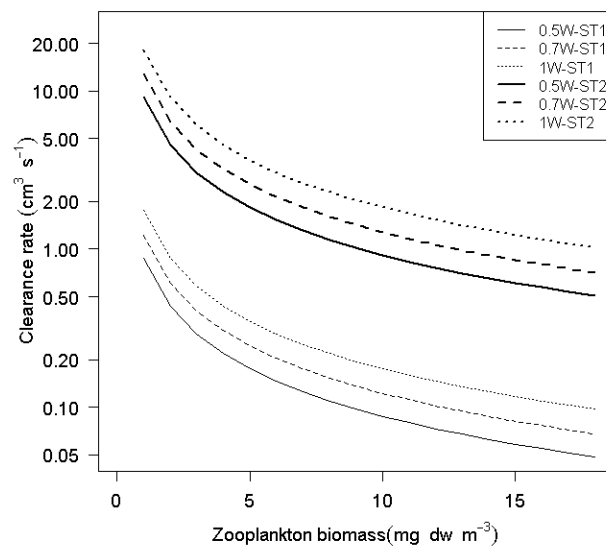


Figure 3. Estimation of specific ingestion rates for piscivorous tuna larvae feeding on prey larvae of different size assuming prey density of 0.1 prey/m³.

