SCIENTIA MARINA 71(2)
June 2007, 347-354, Barcelona (Spain)
ISSN: 0214-8358

Diet of larval albacore *Thunnus alalunga* (Bonnaterre, 1788) off Mallorca Island (NW Mediterranean)

IGNACIO ALBERTO CATALÁN[1], FRANCISCO ALEMANY[1], ANA MORILLAS[1] and BEATRIZ MORALES-NIN[2]

[1]IEO-Centre Oceanogràfic de Balears, Moll de Ponent s/n, CP 07015, Palma de Mallorca, Illes Balears, Spain. E-mail: ignacio.catalan@ba.ieo.es
[2] Grupo de Oceanografía Interdisciplinar, Institut Mediterrani d'Estudis Avançats, UIB/CSIC, 21 Miguel Marques, CP 07190, Esporles, Illes Balears, Spain

SUMMARY: These are the first data on the feeding of larval albacore (*Thunnus alalunga* Bonnaterre, 1788) in the Mediterranean. Specimens were gathered from day-time bongo-hauls conducted over the SW Mallorcan (Balearic Islands) shelf-slope. Ninety eight percent of 101 individuals ranging from 2.65 to 9.4 mm standard length (SL) contained 1 to 15 prey items per gut. Mean number of prey/gut was 3.55 ± 2.19 (SD). A positive correlation was found between larval SL and the number of prey/gut. The analysis of frequency of occurrence (F), numerical frequency (N), weight frequency (W) and the Index of Relative Importance (IRI) showed a dominance of copepodites and nauplii in the smallest size-class. As larvae grew, cladocerans and Calanoida copepodites dominated the diet, and cladocerans and copepodites were important in F, N and W. Piscivory was observed after notochord flexion and was important in terms of W. A positive correlation between mean prey size and both SL and lower jaw length (LJL) was observed. The niche breadth (S) did not vary with LJL, but the raw prey size range did. Larger copepodites, the absence of nauplii and the incorporation of fish larvae and a larger number of cladocerans in the diet accounted for the increase in mean prey size through increased larval size.

Keywords: *Thunnus alalunga*, larvae, Mediterranean, feeding, niche breadth.

RESUMEN: DIETA DE LAS LARVAS DE ALBACORA *THUNNUS ALALUNGA* (BONNATERRE, 1788) EN AGUAS DE MALLORCA (MEDITERRÁNEO NW). – Se ofrecen los primeros datos sobre la dieta de las larvas de albacora (*Thunnus alalunga* Bonaterre, 1788) en el Mediterráneo. Los especímenes se obtuvieron de pescas diurnas con bongo sobre la plataforma-talud al SW de Mallorca (Islas Baleares). El 98% de 101 individuos de entre 2.65 y 9.4 mm de longitud estándar (LE) contuvieron entre 1 y 15 presas por digestivo. La media de presas por larva fue de 3.55 ± 2.19 (DE), existiendo una correlación positiva entre el número de presas en el tubo digestivo y la LS. Los índices de frecuencia de ocurrencia (F), frecuencia numérica (N), frecuencia en peso (W) y el Índice de Importancia Relativa (IRI) mostraron un predominio de copepoditos y nauplius en larvas pequeñas, disminuyendo en importancia a lo largo del crecimiento en detrimento de cladóceros y copepoditos de Calanoida, que fueron importantes en F, N y W. Se observó piscivoría, importante en W, a partir de la flexión de la notocorda. Se detectó una correlación positiva entre el tamaño medio de las presas y tanto la LS como la longitud de la maxila (LJL) de las larvas. La amplitud del nicho alimentario (S) no varió con la LJL, aunque el rango total del tamaño de las presas sí lo hizo. El aumento de talla de los copepoditos, la desaparición progresiva de mauplius y la incorporación de larvas de peces y más cladóceros explica el aumento de la talla media de las presas a lo largo del crecimiento larvario.

Palabras clave: *Thunnus alalunga*, larvas, Mediterráneo, alimentación, amplitud de nicho.

INTRODUCTION

The topical "growth-mortality" hypothesis (Hare and Cowen, 1997) assumes that faster-growing or larger-at-age fish larvae have their survival promoted, which potentially influences the strength of recruitment (Anderson, 1988). Variability in growth rates can be attributed to density-dependent mechanisms (Sheperd and Cushing, 1980), differences in temperature (Pepin, 1991) or to the availability of

potential food (Ramirez *et al*., 2004) among others. However, larval fish feeding is species-specific, and even within the same genus there are large differences in feeding habits (e.g. Young and Davis, 1990). Therefore, species-specific dietary data are necessary to further interpret changes in recruitment, either in correlational or individual-based modelisation schemes.

The Balearic Islands (NW Mediterranean) have been recognised as an important spawning ground for several tuna species including northern Atlantic bluefin (*Thunnus thynnus* L.) and albacore (*Thunnus alalunga* Bonnaterre, 1788) (Duclerc *et al*. 1973; Dicenta *et al*. 1975, 1983; Dicenta, 1977; Alemany, 1997). This fact could be attributed to the preference shown by some oceanic migratory pelagic fishes to spawn around islands (Miller, 1979; Leis *et al*., 1991). The Balearic sea constitutes the transitional area between southflowing surface Mediterranean Waters (SMW) and surface water masses of recent Atlantic origin (AW) which reach the archipelago from the south. Therefore, the confluence of both water masses and their interaction with the Balearic islands result in frontal areas, eddies, meanders and filaments (Millot, 1994; Pinot *et al*., 2002) that act as intangible structures that regulate production and retention and that are used by pelagic species to spawn and develop.

Despite some evidence of migrations between the Atlantic and the Mediterranean (Arrizabalaga *et al*., 2002), the Mediterranean albacore populations constitute a genetically differentiated stock (Lopez-Rodas *et al*., 2002; Viñas *et al*., 2004; Nakadate *et al*., 2005) that up until now have not been as intensively exploited as Atlantic stocks. Reported landings in past decades have usually fluctuated between 2000 and 4000 tons, with a maximum of 4866 tons in 2001 (Anon., 2004), most of them captured by Italian and Greek fleets. In the Spanish Mediterranean the albacore is seasonally targeted by the Spanish fleets by bait boats and trollers coming from Atlantic ports and by Mediterranean surface longliners, as well as some local artisanal and game fisheries (De la Serna *et al*., 2002), with total mean annual landings of around 300 tons. Due to the lack of data from the albacore Mediterranean fisheries this stock has never been assessed (Anon., 2001, 2004). However, the depletion of the bluefin tuna stock could lead to shifts in the preferences of fishermen, and albacore could also become a main target species in Mediterranean tuna fisheries during the next decades. Little is known about the biology and ecology of the Mediterranean albacore populations, and studies focusing on larval stages are even scarcer. The Balearic sea constitutes a suitable place to carry out this kind of study, since high concentrations of albacore larvae have been reported in the area (Alemany *et al*., 2006). Reproduction in the Mediterranean occurs from July to September (Padoa, 1956), with maximum values in August (Padoa, 1956; Alemany, 1997; Alemany *et al*., 2006).

There are few data on the physiological ecology (*sensu* Govoni (2005)) of albacore early stages. Albacore growth and condition have been studied within the Balearic Islands annual tuna larvae surveys (García *et al*., 2003; 2006), but there are no data on the feeding of early stages for this species in the area. Existing studies on the feeding ecology of larval albacore in the Indian Ocean show a diet predominantly consisting of Cyclopoida (*Corycaeus* sp., *Farranula* sp.) copepods, nauplii and cladocerans (Young and Davis, 1990). These authors found significant differences in the feeding ecology of three tuna species, and suggested that albacore larvae select corycaeids over calanoids. The present study offers the first data on the diet of albacore early stages from early pre-flexion to post-flexion stages in the Mediterranean to contribute to the understanding of survival and recruitment processes of this species, which constitutes a relevant part of the pelagic ecosystem.

MATERIAL AND METHODS

Specimens of early stages of *T. alalunga* were collected during daytime in a small grid of stations over the shelf-slope zone at the East of Mallorca island in August 1996 on a single day, and were preserved in 4% seawater-buffered formalin. Methods of collection and description of larval distribution and abundance are described elsewhere (Alemany *et al*., 2006). Specimens were selected from only two close stations as they showed high larval abundances and a sufficient range of larval sizes. A random sample of 100 individuals was first explored to search for population size structure (mean standard length (SL) = 4.71 mm, standard deviation (SD) = 0.64, Min = 3.5 mm, Max = 6.5 mm). Subsequently, the size range of larvae selected for analysis was widened to include a similar number of larvae in all

the size-ranges, ending up with 101 larvae analysed (Table 1).

Larvae were coded and stained for five seconds in 1% blue-methylene and five seconds in 1% acid fuchsin (to aid in identifying the gut contents), cleared in 70% ethanol and measured in pure glycerine under a stereo-microscope. Standard length (precision = 0.05 mm) was measured from the tip of the snout to the end of the notochord in pre-flexion larvae, and to the hypural crease in post-flexion larvae. The lower jaw length (LJL, precision = 0.025 mm) measured as the length of the lower maxilla is given as a functional proxy of mouth width, as the latter was difficult to measure in poorly preserved larvae. No correction for larval shrinkage was performed.

The gut was first excised with a microscalpel and teased open with 0.1 and 0.2 mm tungsten needles. All food was observed in the looped gut section, not the first portion of the stomach, so this work refers generally to gut contents. Gut fullness was estimated on a scale from 1 to 5, where 1 = empty; 2 < half full; 3 = half full; 4 > half full; 5 = full. Prey were identified to the lowest possible taxonomic level, counted and measured along the longest and widest axes (precision = 12.5 μm). For copepods, prosome length, width and total length were taken. Prey was classified into broad categories and an estimate of dry weight for each individual was obtained from length-dry weight relationships. Literature values were used for Cyclopoida (Satapoomin, 1999), Calanoida and general copepoda (Uye, 1982), nauplii (Schmitt, 1986) and some cladocerans (*Podon* sp. and *Penilia avirrostris*, Uye (1982)). The cladoceran *Evadne spinifera* constituted over 95% of all cladocerans in the gut. As no literature data exists for weight estimation of this species, 5 groups of 4% formalin-preserved 15-22 *E. spinifera* each (mixed males and non-gravid females) were built to obtain a dry weight per mean body size estimate. The specimens were individually measured along the longest axis including the spine. Visible salt crystals and dirt were removed from each individual under the binocular microscope. Each group was rinsed in 1ml distilled water, filtered into pre-weighed Whatman (GF/C) filters and weighted to the nearest 1 μg in an electronic microbalance after 24 h at 60°C plus 24 h in a desiccator. The linearised length-weight regression for *E. spinifera* was Log_{10} DW = 0.8605 (± 0.126, SE) + 3.741 (± 0.751, SE) Log_{10}L, r^2_{Adj} = 0.89, DF = 1,4, $p<0.05$, where DW = dry weight (μg) and L= body length (μm). For the scarce fish larvae that appeared, one was clearly identified as *Auxis rochei* and the rest had a *Cyclothone* sp. head shape. Standard lengths were derived from the crystalline radius-SL relationships obtained from our own collections. The DW for *A. rochei* was estimated using data from A. García (unpublished), and a conservative DW of 15 μg was assumed for each of the other larvae, following existing minimum DW values for eel-shaped larvae (e.g. Houde and Schekter, 1983). The weight of a small fraction of unidentified prey (3-6% of each larval size class) that could be numbered but not measured was estimated using its relative volume (%) with respect to the total prey volume (100%) in each stomach, and

TABLE 1. – Percentage frequency of occurrence (F) and percentage of the index of relative importance (%IRI) for the main prey categories analysed. Values for numeric and weight percentages are depicted in Figure 1. Calanoida and Cyclopoida are mainly copepodite stages. Errors are ± 1 standard deviation.

SL	class: 2.6-3.9 mm		class: 4-4.9 mm		class: 5-5.9 mm		class: 6-9.4 mm		range: 2.65-9.4 mm	
N	26 larvae		32 larvae		28 larvae		15 larvae		Total = 101 larvae	
Mean SL	3.61 ± 0.30		4.42 ± 0.29		5.42 ± 0.25		6.56 ± 0.92		4.81 ± 1.08	
Mean LJL	0.59 ± 0.09		0.79 ± 0.11		1.04 ± 0.09		1.44 ± 0.29		0.90 ± 0.31	
Fullness	3.54 ± 1.03		4.24 ± 0.94		4.66 ± 0.75		4.47 ± 0.67		4.21 ± 0.97	
Prey category	F	%IRI	F	%IRI	F	%IRI	F	%IRI	F	%IRI
Copepoda										
Calanoida (CA)	30.77	31.62	46.88	28.78	64.29	29.99	60.00	37.82	49.50	35.26
Cyclopoida (CY)	26.92	23.03	50.00	17.68	53.57	8.55	40.00	4.90	43.56	12.03
Nauplii (N)	19.23	11.71	31.25	12.17	21.43	2.36	-	-	20.79	4.91
Unid. copepodites (UCO)	38.46	26.69	50.00	25.12	25.00	1.96	20.00	2.14	35.64	9.92
Cladocera (CL)	11.54	6.76	31.25	15.83	71.43	56.83	73.33	49.18	43.56	36.99
Fish larvae (FL)	-	-	-	-	3.57	0.27	20.00	5.81	3.96	0.77
Decapod larvae (DL)	-	-	3.13	-	-	-	6.67	0.16	1.98	0.02
Unidentified prey (UP)	3.85	0.20	6.25	0.42	3.57	0.03	-	-	3.96	0.10
Total number of prey items	59		115		115		63		352	
Mean no. of prey per stomach	2.36 ± 1.47		3.71 ± 1.90		4.11 ± 1.83		4.73 ± 3.31		3.55 ± 2.19	

the downscaled average dry weight for that stomach was assigned. A category classified as "remains", which was formed by gut contents that were either part of numbered prey (but that could not be ascribed to a particular category) or that could not be numbered, was not taken into consideration for calculations. This category came to an average of 17% in relative volume of the gut contents, with no clear relationship to size class.

Percentage frequency of occurrence in the stomachs (F), percent number (N) and percent weight (W) was calculated for each prey category and larval size-class, and an index of relative importance (IRI) for each prey category calculated as IRI = F*(N+W), and converted to a percentage (%IRI). Due to the different information provided by each index (Cortés, 1997), all indices are given in the results section.

A Kruskall-Wallis test was used for analysing potential differences in gut fullness. Numbers of prey per larva was analysed with linear regression analyses. Relationships between larval body measurements (SL and LJL) and prey mean length and mean width (both $\log_{10}$ transformed), as well as the calculation of niche breadth (S, as a measure of increment in prey size through larval growth (following mostly Pearre (1986) and Pepin and Penney (1997))) were explored. For prey size vs larval size analyses, size-class intervals were built for fish larvae (0.2 mm intervals for SL and 0.05 mm for LJL), in order to obtain a sufficient number of prey per size-class and a minimum of 20 larval size-classes. Means and standard deviations of $\log_{10}$-transformed values of prey length and width were calculated for each larval size-class. Linear regression analysis (weighted by the number of prey per size-class) was used for exploring prey size to larval size relationships. The niche breadth was calculated by regressing the $\log_{10}$-transformed SD of prey width against larval LJL (number of prey used as weights). In addition, variation of length and weight of separate prey categories vs broader larval size classes was visually explored using means and 95% confidence intervals.

RESULTS

Feeding incidence

All specimens examined had either identifiable prey (98% of the larvae) or remains in their guts. Gut fullness was relatively high, averaging 4.21, which corresponded to an average of 3.55 prey/gut (Table 1). The lowest mean fullness was observed in larvae ranging from 2.6 to 3.9 mm SL, with an average of 2.36 prey/gut. The only significant difference in gut fullness was observed between this group of small larvae and the rest of the size groups ($H = 24.5$, $p<0.001$). The number of identifiable prey ranged from 1 to 15; the latter was observed in a larva of 7 mm SL. There was a slight but significantly positive correlation between the average number of prey/larva and SL ($r^2 = 0.10$, $DF = 97$ $p<0.01$).

Diet composition

The most important feeding categories as determined by %IRI were, with decreasing importance, cladocerans (mainly *E. spinifera*), calanoid and cyclopoid copepodites, unidentified copepoda, nau-

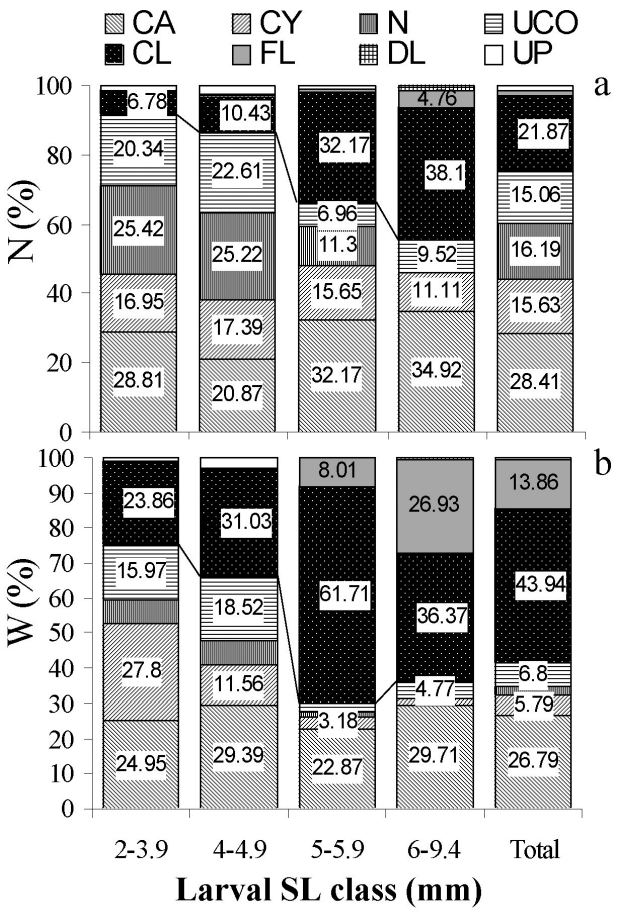

FIG. 1. – Variation of numeric frequency (a) and weight frequency (b), both in percentages, of the main prey categories through SL classes of larval *T. alalunga*. Codes for prey categories as in Table 1. Straight lines connect the accumulated N or W of copepodites plus nauplii (column areas below the line). The rightmost column summarises values for all larvae.

plii (mainly copepod nauplii), fish larvae (mainly *Auxis* sp. and unidentified), unidentified prey and decapod larvae (Table 1). The identifiable copepods included, in order of importance, Calanoida copepodites (including *Ctenocalanus* sp., *Clausocalanus* sp., *Paracalanus* sp., *Euchaeta* sp.,) and Cyclopoida copepodites (including *Corycaeus* sp., *Farranula* sp., *Oithona* sp., *Oncaea* sp.). Unidentified copepods included basically copepodites. The amount of unidentified but numbered prey was low, generally < 5% in F, N and W (Table 1, Fig. 1).

There was a clear change in diet composition with larval SL. Copepoda decreased in importance (%IRI, Table 1) with larval length, mainly as a result of a decreasing trend in N (from >90% to ca. 55%) and W (from >75% to 30-40%) (Fig. 1). Within Copepoda, Calanoida copepodites tended to increase in F with larval length, whilst nauplii sp. disappeared from the diet in larvae ≥6 mm (Table 1, Fig. 1). In small larvae, nauplii constituted an important fraction of the diet in terms of N and F, but not in W. As larvae grew, the decrease in copepod stages in the diet was replaced mainly by cladocerans and a few fish larvae, which were particularly important in terms of W (Fig. 1). Cladocerans increased in F with larval SL from about 10% to ca. 70% (Table 1), which was paralleled by an increase in N and W (Fig. 1). Piscivory was detected in albacore larvae in individuals ≥5 mm SL, coinciding with the beginning of the notochord flexion, which began in larvae of 5-5.5 mm SL. Fish larvae were not important in terms of %IRI or N but amounted to ca. 30% in F and W in larvae > 6 mm SL.

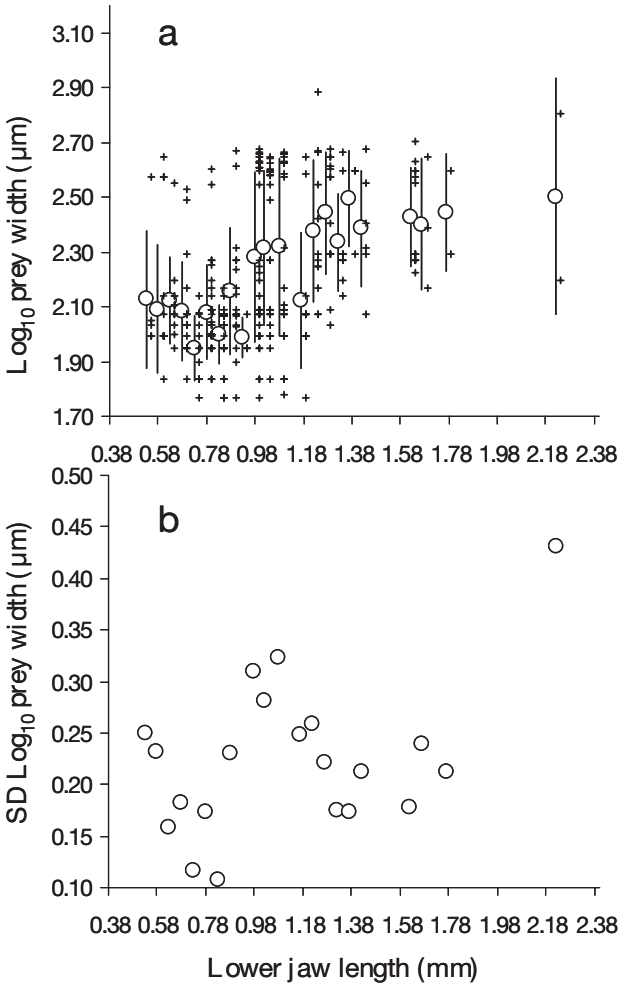

FIG. 2. – a) Raw data (dots), means (circles) and standard deviation (lines) of prey width in relation to larval LJL classes; b) Niche breadth in relation to larval *T. alalunga* LJL classes. Raw data are shifted slightly to the right to facilitate visualisation.

Relationship between prey and predator size

The LJL was linearly related to SL by LJL = –0.4055 (± 0.039, SE) + 0.272 (± 0.008, SE) SL, r^2_{Adj} = 0.920, DF = 1,100, p < 0.0001. Weighted regressions showed positive relationships between larval SL and LJL vs the average prey log_{10}length or log_{10}width (Table 2) although niche breadth did not change significantly with larval mouth size (Table 2, Fig. 2). Nauplii and cladocerans showed similar lengths regardless of predator size. Cladocerans were generally significantly larger and wider than copepodites, and were present in the diet already in the smallest larvae (Fig. 3). The increase in average prey length and width was due to the increase in mean size of calanoida, cyclopoida and unidentified copepodites, plus the incorporation in the diet of fish

TABLE 2. – Weighted regression parameters and statistics for relationships between larval SL and LJL (mm) vs prey length and width (µm). SE is 1 Standard Error. DF are degrees of freedom. S is niche breadth.

Predictor	Dependent variable	Intercept (SE)	Slope (SE)	R^2 Adj.	DF	p
SL	Mean Log_{10}prey length	1.809 (0.094)	0.156 (0.018)	0.79	1,19	<0.001
SL	Mean Log_{10}prey width	1.610 (0.096)	0.118 (0.019)	0.67	1,19	<0.001
LJL	Mean Log_{10}prey length	2.093 (0.071)	0.520 (0.070)	0.72	1,21	<0.001
LJL	Mean Log_{10}prey width	1.809 (0.070)	0.408 (0.068)	0.62	1,21	<0.001
LJL	S	0.156 (0.052)	0.068 (0.051)	0.04	1,21	0.194

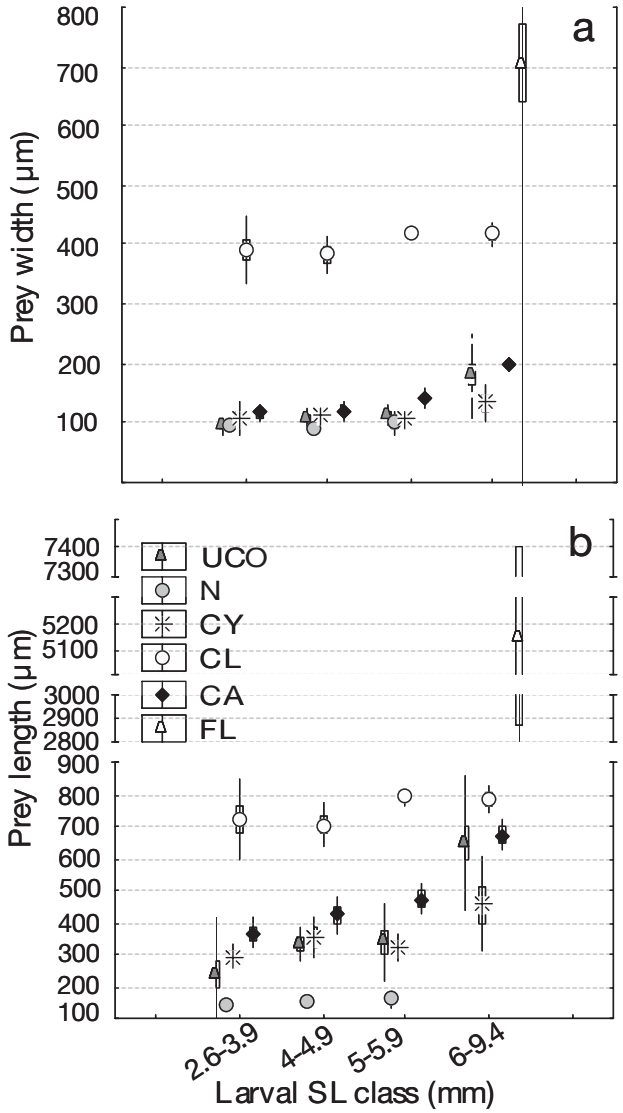

FIG. 3. – Mean prey width (a) and length (b) of the main prey categories in relation to SL of *T. alalunga*. Bars are ± 95% confidence intervals, and inner rectangles are ± 1 Standard Error.

larvae and the higher abundance of cladocerans in larger larvae coupled with the exclusion of nauplii from the diet (Fig. 3).

DISCUSSION

Feeding incidence found in albacore larvae can be considered high compared to data on the same species and stages in the Indian Ocean, where only 55% of larvae collected during the daytime contained food (Young and Davis, 1990). These authors found a positive correlation between feeding incidence and larval length. In the present study, larger larvae tended to have more prey items in their guts than smaller larvae, which can be related to a higher feeding activity with larval growth and/or to a higher gut capacity. In addition, the mean number of prey per gut was higher in our study than in Young and Davis (op. cit.), who attributed the low feeding incidence to low food abundance in the area. In the present study, this assumption could not be tested as microzooplankton samples were not available. However, the high fullness detected in our samples suggests that the relationship between empty stomachs and food abundance found in albacore larvae by Young and Davis (op. cit.) may be real, and that regurgitation is not a major problem in the collection of this species.

The numerical dominance of Copepoda and the progressive substitution of nauplii by increasingly larger copepodites in larger larvae, as found herein, is a generalised pattern in many marine fish larvae (Hunter, 1981). Similarly-sized cladocerans (Fig. 3), mainly *E. spinifera*, were observed in all larval length classes. In young larvae, this may result from a combination of a relatively large mouth and advanced visual and swimming capabilities. Several authors have shown that some tuna larvae have a preference for corycaeids (Cyclopoida), including albacore (Young and Davis, 1990) and bluefin tuna (Uotani *et al*., 1990), a behaviour that opposes the general calanoid selection observed in larvae of several fish species (Pepin and Penney, 1997). In the present study, the percentage number of Cyclopoida (mainly corycaeids) varied little through larval size, although their frequency of occurrence and weight contribution tended to decrease. It is not likely that the fraction of unidentified copepodites masked a possible increase in corycaeids, because the percentage of unidentified copepodites tended to decrease in larger larvae (Table 1). Due to the lack of microzooplanton data, it is not possible to further interpret the relationship between prey in the environment and in the guts. The piscivory observed in albacore larvae was not observed by Young and Davis (op. cit.) off NW Australia for a similar SL-range. However, they observed piscivory in other co-occurring larval tuna of slightly larger sizes, like *Thunnus macoyii* and *Katsuwonus pelamis*. The present work thus describes for the first time this phenomenon in larvae of this species. Piscivory is, however, a common feature of larvae of many tuna and related species, and has even been recorded in first feeding individuals (Shoji and Tanaka, 2001; Kaji *et al*., 2002). It should be stated that although the estimates of DW are only approximations, the main interpre-

tations are probably correct, as the relative differences in weight among the main prey items (small copepods, nauplii, cladocerans, fish larvae) holds in all the literature that has been revised. Moreover, some new estimates of DW that have been made (i.e. for *E. spinifera*) are fully consistent with mean values of DW given in the literature (Walve and Larsson, 1999) for this species. For fish larvae, DW estimates are conservative thus W values for ingested fish larvae might be higher than reported herein.

The higher mean prey size at increasing values of larval LJL or SL, and the lack of significance in the relationship between niche breath and larval size is a common feature in many species of marine fish larvae (Pepin and Penney, 1997; Sabatés and Saiz, 2000). The importance of calculating the niche breadth (basically the amplitude of the prey size spectrum when $\log_{10}$-transformed values are used) resides in the hypothesis that a wider niche breadth implies increased survival capabilities, as a wider range of prey types/sizes may be exploited by the larger larvae (Houde, 1997). However, both the lower and upper limits of the prey size range increased as larvae grew, which suggests that some components of the diet are selected against, perhaps due to their size (nauplii and small copepodites). This is in accordance with a relatively invariant niche breadth along larval growth. Nevertheless, the observation of ingested species-specific prey sizes (untransformed, Fig. 3) shows that larvae around 6 mm SL start ingesting other fish larvae. This widens the size-range of raw data enormously and indicates an ontogenetic shift in diet potentially associated with the energetic requirements of the early stages of tuna. In this respect, albacore has been found to grow rapidly (García *et al*., 2006), and high energy and protein input may be crucial for survival at the juvenile stage.

ACKNOWLEDGEMENTS

The authors would like to thank the personnel participating in the CORY surveys. F. Baldó and V. Oresland are thanked for their early comments on the methodology. This work is a result of the project D.G. XIV UE Biological studies 95/73.

REFERENCES

Alemany, F. – 1997. *Ictioplancton del Mar Balear*. PhD thesis, Univ. de les Illes Balears.

Alemany, F., S. Deudero, B. Morales-Nin, J.L. Lopez-Jurado, J. Jansa, M. Palmer and I. Palomera. – 2006. Influence of physical environmental factors on the composition and horizontal distribution of summer larval fish assemblages off Mallorca island (Balearic archipelago, western Mediterranean). *J. Plankton Res*., 28: 473-487.

Anderson, J.T. – 1988. A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. *J. Northwest Atl. Fish. Sci*., 8: 55-66.

Anon. – 1996. Report of the Final Meeting of the ICCAT Albacore Research Program . Sukarrieta, Vizcaya, Spain, 1-8 June 1994. *Collect. Vol. Sci. Pap. ICCAT*., 43: 1-395.

Anon. – 2001. The SCRS Report of the albacore assessment of ICCAT (Madrid, España, 9 a 15 octubre de 2000). *Collect. Vol. Sci. Pap. ICCAT*, 52(1): 1283-1390.

Anon. – 2004. 2003 ICCAT albacore stock assessment session. *Collect. Vol. Sci. Pap. ICCAT*, 56(4): 1223-1311.

Arrizabalaga, H., López-Rodas, V., Ortíz de Zárate, V., Costas, E. and A. González-Garcés. – 2002. Study on the migrations and stock structure of albacore (*Thunnus alalunga*) from the Atlantic ocean and the Mediterranean based on conventional tag-release-recapture experiences. *Collect. Vol. Sci. Pap. ICCAT*., 54(5): 1479-1494.

Cortés, E. – 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Can. J. Fish. Aquat. Sci*., 54: 726-738.

Dicenta, A. – 1977. Zonas de puesta del atún (*Thunnus thynnus* L.) y otros túnidos en el Mediterráneo occidental y primer intento de evaluación del stock de reproductores de atún. *Bol. Inst. Esp. Oceanogr*., 234: 109-135.

Dicenta, A., Piccinetti, C. and G. Piccinetti-Manfrin. – 1975. Observaciones sobre la reproducción de los túnidos en las islas Baleares. *Bol. Inst. Esp. Oceanogr*., 204: 27-37.

Dicenta, A., C. Franco and A. Lago de Lanzós. – 1983. Distribution and abundance of the families Thunnidae and Mullidae in the Balearic Waters. *Rapp. Comm Int. Mer. Médit*., 28: 149-153.

De la Serna, JM, J Valeiras, E Alot and D Godoy. – 2002. El atún blanco (*Thunnus alalunga*) del Mediterráneo Occidental. *Collect. Vol. Sci. Pap. ICCAT*., 55(1): 160-165.

Duclerc, J., Sacchi, J., Piccinetti, C., Piccinetti-Manfrin, G., Dicenta, A. and M. Barrois. – 1973. Nouvelles données sur la reproduction du thon rouge (*Thunnus thynnus* L.) et d'autres espèces de thonidés en Méditerranée. *Rev. Trav. Inst. Pêches Marit*., 37: 163-176.

García, A., F. Alemany, P. Velez-Belchi, J.L. López Jurado, M. de la Serna, C. González Pola, J.M. Rodríguez and J. Jansá. – 2003. Bluefin tuna and associated species spawning grounds in the oceanographic scenario of the Balearic archipielago during June 2001. *Collect. Vol. Sci. Pap. ICCAT*., 55(1): 138-148.

García, A., D. Cortés, T. Ramírez, R. Fehri-Bedoui, F. Alemany, J.M. Rodríguez, A. Carpena and J.P. Álvarez. – 2006. First data on growth and nucleic acid and protein content of field-captured Mediterranean bluefin (*Thunnus thynnus*) and albacore (*Thunnus alalunga*) tuna larvae: a comparative study. *Sci. Mar.,* 70S2: 67-78.

Govoni, J.J. – 2005. Fisheries oceanography and the ecology of early life histories of fishes: a perspective over fifty years. *Sci. Mar*., 69(Suppl. 1): 125-137.

Hare, J.A. and R.K. Cowen. – 1997. Size, growth, development, and survival of the planktonic larvae of *Pomatomus saltatrix* (Pisces: Pomatomidae). *Ecology*, 78: 2415-2431.

Houde, E.D. – 1997. Patterns and consequences of selective processes in teleost early life histories. In: M.D. Chambers and E.A. Trippel (eds.), *Early life history and recruitment in fish populations,* pp. 173-196. Chapman and Hall, London.

Houde, E.D. and R.C. Schekter. – 1983. Oxygen uptake and comparative energetics among eggs and larvae of three subtropical marine fishes. *Mar. Biol*., 72: 283-293.

Hunter, J.R. – 1981. Feeding ecology and predation of marine fish larvae. In: R. Lasker (ed.), *Marine fish larvae: morphology, ecology, and relation to fisheries,* pp. 34-77. Washington Sea Grant Program, Seattle.

Kaji, T., M. Kodama, H. Arai, M. Tagawa and M. Tanaka. – 2002. Precocious development of the digestive system in relation to early appearance of piscivory in striped bonito *Sarda orientalis* larvae. *Fish. Sci.,* 68: 1212-1218.

López-Rodas,V., Arrizabalaga, H., Nieto, B, González-Garcés, A. and E. Costas. – 2002. Use of lectins to characterise genetic

variability and geographic differentiation in natural population of *Thunnus alalunga* (Bonn. 1788). *Collect. Vol. Sci. Pap. ICCAT*, 54(5): 1495-1507.
Millot, C. – 1994. Models and data: a synergetic approach in the western Mediterranean Sea. In: P. Malanotte-Rizzoli and A.R. Robinson (eds.), *Ocean Processes in Climate Dynamics: Global and Mediterranean Examples,* pp. 407-425. Kluwer, Amsterdam.
Nakadate, M., J. Viñas, A. Corriero, S. Clarke, N. Suzuki and S. Chow. – 2005. Genetic isolation between Atlantic and Mediterranean albacore populations inferred from mitochondrial and nuclear DNA markers. *J. Fish Biol*., 6: 1545-1557.
Padoa, E. – 1956. Divisione Scombriformes, Uova, larve e stadi giovanili di Teleostei. In: *Fauna Flora Golfo Napoli*, pp. 548-572.
Pearre, S. – 1986. Ratio-based trophic niche breadths of fish, the Sheldon spectrum, and the size-efficiency hypothesis. *Mar. Ecol. Progr. Ser*., 27: 299-314.
Pepin, P. – 1991. Effect Of Temperature And Size On Development Mortality And Survival Rates Of The Pelagic Early Life History Stages of Marine Fish. *Can. J. Fish. Aquat. Sci*., 48: 503-518.
Pepin, P. and R.W. Penney. – 1997. Patterns of prey size and taxonomic composition in larval fish: are there general size-dependent models? *J. Fish Biol*., 51: 84-100.
Pinot, J.M., J.L. López-Jurado and M. Riera. – 2002. The CANALES experiment (1996-1998). Interannual, seasonal and mesoscale variability of the circulation in the Balearic Channels. *Progr. Oceanogr*., 55: 335-370.
Ramírez, T., D. Cortés, A. García and A. Carpena. – 2004. Seasonal variations of RNA/DNA ratios and growth rates of the Alboran Sea sardine larvae (Sardina pilchardus). *Fish. Res*., 68: 57-65.
Sabatés, A. and E. Saiz. – 2000. Intra- and interspecific variability in prey size and niche breadth of myctophiform fish larvae. *Mar. Ecol. Progr. Ser*., 201: 261-271.
Satapoomin, S. – 1999. Carbon content of some common tropical Andaman Sea copepods. *J. Plankton Res*., 21: 2117-2123.
Schmitt, P.D. – 1986. Prey size selectivity and feeding rate of larvae of the northern anchovy, *Engraulis mordax* Girard. *CalCOFI Rep*., XXVII: 153-161.
Sheperd, J.G. and D.H. Cushing. – 1980. A mechanism for density-dependent survival of larval fish as the basis of a stock-recruitment relationship. *J. Cons. int. Explor. Mer*., 39: 160-167.
Shoji, J. and M. Tanaka. – 2001. Strong piscivory of Japanese Spanish mackerel larvae from their first feeding. *J. Fish Biol*., 59: 1682-1685.
Uotani, I., T. Saito, K. Hiranuma and Y. Nishikawa. – 1990. Feeding habit of bluefin tuna *Thunnus thynnus* larvae in the Western North Pacific Ocean. *Nipp. Suis. Gakka.,* 56: 713-717.
Uye, S. – 1982. Length-weight relationships of important zooplankton from the Inland Sea of Japan. *J. Oceanogr. Soc. Jap*., 38: 149-158.
Viñas, J., Alvarado-Bremer J.R. and C. Pla. – 2004. Inter-oceanic genetic differentiation among albacore (*Thunnus alalunga*) populations. *Mar. Biol.,* 145: 225-232.
Walve J. and U. Larsson. – 1999. Carbon, nitrogen and phosphorus stoichiometry of crustacean zooplankton in the Baltic Sea: implications for nutrient recycling. *J. Plankton Res*., 21: 2309-2321.
Young, J.W. and T.L.O. Davis. – 1990. Feeding ecology of larvae of southern bluefin, albacore and skipjack tunas (Pisces: Scombridae) in the eastern Indian Ocean. *Mar. Ecol. Progr. Ser*., 61: 17-29.

Scient. ed.: J.J. Govoni.
Received October 17, 2006. Accepted January 22, 2007.
Published online May 23, 2007.