



Age and growth of *Engraulis encrasicolus* (Clupeiforme: Engraulidae) in the Tunisian waters

Sana KHEMIRI^{1,3}, Adel GAAMOUR¹, François J. MEUNIER^{2,3} and Louise ZYLBERBERG³

⁽¹⁾ Institut National des Sciences et Technologies de la Mer, 28 rue 2 Mars 1934, Salammbô, Tunisie.

Tel : +216 71 735848, Fax : +216 71 735848. E-mail: sanak182000@yahoo.com

⁽²⁾ UMR CNRS 5178, Biodiversité et Dynamique des Communautés aquatiques, Département des Milieux et Peuplement Aquatiques, Muséum National d'Histoire Naturelle, CP 26, 43 rue Cuvier, 75231 Paris Cedex 05, France.

⁽³⁾ Université Pierre & Marie Curie-Paris 6, UMR CNRS 7179, Mécanismes adaptatifs : des organismes aux communautés, Case 7077, 2 place Jussieu, 75251 Paris Cedex 05, FRANCE

Abstract: Age and growth of the European anchovy *Engraulis encrasicolus*, caught in the Northern and Southern areas along the Tunisian coasts, were determined by otolithometry. Analyses of the otolith marginal zone indicate that a hyaline zone is deposited yearly from November/December to March. In both areas, the anchovies have short lives and grow fast. Their growth was almost achieved during the first year of life and no growth difference was recorded between males and females in the same area. However a different growth pattern was found between the anchovies from the North (open sea) that have on an average a statistically greater size at the same age than those from the South area (inshore coastal water). The corresponding von Bertalanffy growth equations were in the North area: $FL = 19.16(1 - e^{-0.32(t + 1.68)})$ and in the South area: $FL = 17.19(1 - e^{-0.36(t + 1.01)})$. Abiotic and/or genetic factors could be involved to explain the growth differences observed between the two areas.

Résumé : Age et croissance d'*Engraulis encrasicolus* (Clupéiforme : Engraulidae) dans les eaux tunisiennes. L'estimation de l'âge et de la croissance de l'anchois *Engraulis encrasicolus*, collecté le long des régions Nord et Sud des côtes tunisiennes, a été réalisée par otolithométrie. L'analyse de la zone marginale des otolithes d'anchois montre la formation d'une seule zone hyaline par an ; cette dernière se dépose de novembre/décembre à mars. Dans les deux régions, les anchois se caractérisent par une faible longévité et une croissance rapide notamment au cours de leur première année de vie. Dans chacune des régions, aucune différence de croissance n'a été observée entre les mâles et les femelles alors qu'une différence de croissance existe entre la région Nord et la région Sud. En effet, les anchois de la région Nord sont en moyenne statistiquement plus grands que ceux de la région Sud à âge égal. Les équations de croissance de von Bertalanffy correspondantes sont pour la région Nord : $FL = 19,16(1 - e^{-0,32(t + 1,68)})$ et pour la région Sud: $FL = 17,19(1 - e^{-0,36(t + 1,01)})$. L'implication de facteurs abiotiques et/ou génétiques pourrait expliquer la différence de croissance entre les anchois des deux régions.

Keywords: *Engraulis encrasicolus* • Tunisian coasts • Age • Growth • Otolithometry

Introduction

The European anchovy, *Engraulis encrasicolus* (Linnaeus, 1758), is wide spread in the sea and support large fisheries. It is mainly caught in the Mediterranean and Black seas but also in Eastern Atlantic areas (Fisher et al., 1987). In Tunisia, the European anchovy is of a great economic importance. Its biomass estimated by hydroacoustic surveys averaged 6000 tons (Gaamour et al., 2005). It is caught along the coasts all year round without significant seasonal differences in the catches. Nevertheless, for all the Tunisian coasts the maximum of landing is recorded in July (National Statistics). Anchovies belong to the group of small pelagic fishes that represent 33% of the overall catches along the Tunisian coasts. Since 1993 the annual fishing yields of anchovies increase from 23 to reach 450 tons in 2003 (Gaamour et al., 2005).

The European anchovies are distributed in various areas where they experience different environmental conditions that may affect their growth and cause recruitment variability (Sinovčić, 1998 & 2000). In some cases, large natural fluctuations of the biomass may induce sudden fishery collapses that are also reported for other small pelagic fishes (Schwartzlose et al., 1999). The species recruitment variability causes low resilience and thus more sensitivity to over fishing. Therefore, a rational management of *E. encrasicolus* fishery is necessary to preserve juveniles and to ensure the durability and the profitability of the exploitation. For that purpose, biological parameters (age, growth, reproduction period, size and age at first sexual maturity...) and population dynamics are required (Mills & Beamish, 1980; Panfili et al., 2002). Data are still fragmentary and important gaps exist on the anchovies of Tunisian waters. This is the first study devoted to the comparison of the anchovy growth along the Tunisian coasts.

Recent studies have shown that the morphological differences found in anchovy populations could be related either to specific genotypic adaptations (Spanakis et al., 1989; Bembo et al., 1996; Borsa, 2002; Borsa et al., 2004) or to environmental conditions adaptations (Sinovčić, 1982; Tudela, 1999). These hypotheses led us to study the growth of anchovies caught from different areas along the Tunisian coast characterized by varied hydrological regimes.

The aim of this study is to report first data on the age and growth of the anchovies in the Tunisian waters, using otolithometry.

Material and methods

Sampling was carried out during three years (2000 - 2002) in order to provide a yearly average of the studied characters (age, growth). Most of the months of these three

years were represented in the sample. Samples were collected along the Tunisian coasts in the North in the open sea (36°58'N 8°40'E-37°10'N 10°16'E), and in the South, in inshore coastal waters (35°N 11°E-33°20'N 11°40'E) (Fig. 1). These regions differ in the water depth and in hydrological parameters (Table 1). The South region is a wide shallow area of brackish water (below 50 m) characterized by high values of temperature and it is affected by variable climatic forcing (thermal front, tide...). Conversely, in the North region, the temperature of the deep-sea water (over 50 m) is lower and environmental conditions are more temperate than in the south area (Sammari & Gana, 1995).

Table 1. *Engraulis encrasicolus*. Data on water surface salinity and temperature in the North and South areas.

Tableau 1. *Engraulis encrasicolus*. Données de salinité et de température de l'eau de surface dans les régions Nord et Sud.

	North area		South area	
	Summer	Winter	Summer	Winter
Temperature (°C)	24	13.5	27.3	15
Salinity	37.5	36.6	39.3	38

In each region, anchovies were caught by mid-water trawl (hydroacoustic survey catches) and purse seine (commercial catches). For each fishing gear, the sampling periods were the same in both regions. Three thousand anchovies were sampled. For each specimen, the fork length and the total length (FL and TL to the nearest mm) were measured and the sex determined by macroscopic examination.

Otoliths (sagittae) were removed, cleaned, and preserved after drying. For age determination, *in toto* otoliths were viewed with a binocular dark-field reflected light in order to count the translucent zones. According to Panfili et al. (2002), a translucent zone corresponds to a "slow growth zone", that appeared as a dark layer whereas an opaque zone, a "fast growth zone", appeared as a white layer. Each otolith was examined by two readers. If there was a discrepancy between the readings the otolith was discarded.

The periodicity of the formation of the otolith growth increments was revealed by the marginal zone analysis (Beamish & Mac Farlane, 1987; Panfili et al., 2002). This method is based on both qualitative data that involves following the evolution of the percentage of translucent edge through time and quantitative data obtained by the monthly following of the relative marginal distance (RMD). The measures were done along a standard axis (Fig. 2) with analysing image system (Tnnc Software).

$$\text{RMD} = \text{AMD}/\text{D}$$

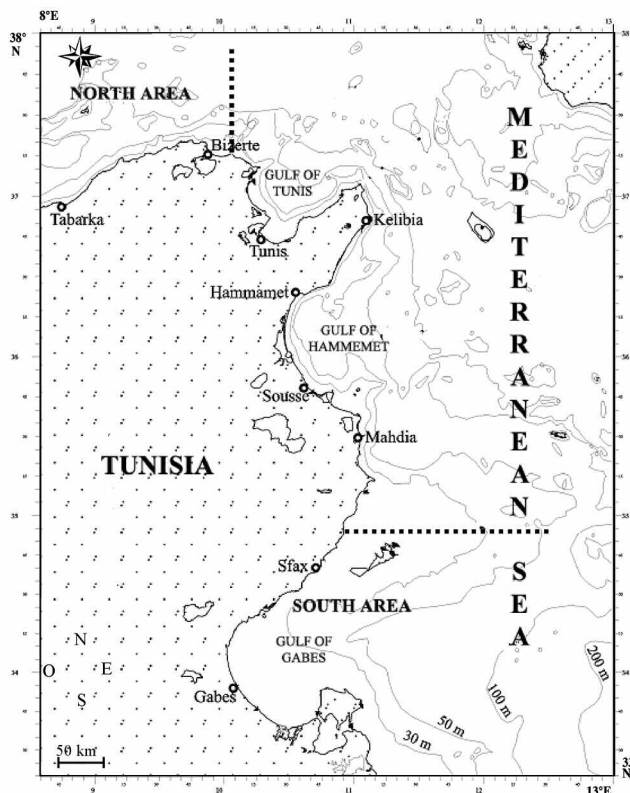


Figure 1. *Engraulis encrasicolus*. Map of the Tunisian coast showing the sampling areas (dotted lines).

Figure 1. *Engraulis encrasicolus*. Carte des côtes tunisiennes indiquant les zones d'échantillonnage (en pointillé).

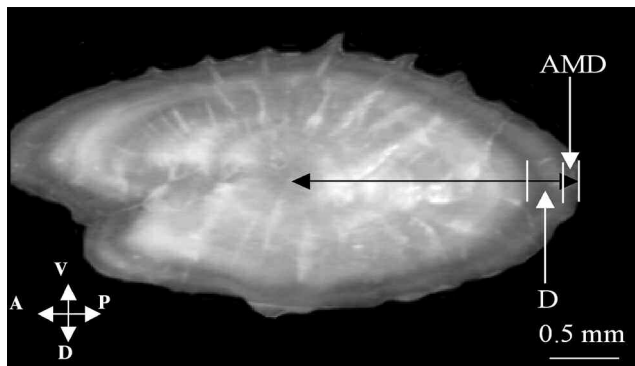


Figure 2. *Engraulis encrasicolus*. Otolith of anchovy of 11.5 fork length showing the axis of measurement (black arrow), the absolute marginal distance (AMD) and the distance separating the two last increments (D). A: anterior, P: posterior, D: dorsal, V: ventral parts.

Figure 2. *Engraulis encrasicolus*. Otolithe d'anchois d'un individu d'une longueur à la fourche de 11,5 cm montrant l'axe de mesure (flèche noire), la distance marginale absolue (AMD) et la distance séparant les deux dernières marques (D). Régions A : antérieure, P : postérieure, D : dorsale, V : ventrale.

(AMD is the distance separating the last translucent zone from the edge; D is the distance separating the two last increments).

If growth increments were formed yearly, the evolution through time of the RMD should show one peak per year, which would correspond to the formation of an opaque zone.

The age readings were carried on a sub-sample of 950 otoliths of one year average sampling and pooled within each area (343 individuals in the North area and 607 individuals in the South area). The age of each specimen was assigned, in month, by taking into account the annual formation and the total number of translucent zones, the date of capture and the theoretical birth date; 15 July was considered as a birth date (Gaamour et al., 2004). The growth model for the anchovies was established with the von Bertalanffy Model (Bertalanffy, 1938). The growth equations were calculated by the "Quasi Newton" non-linear method using the statsoft "Statistica".

The student t-test was used to compare the growth in length between males and females of anchovies and between anchovies in each of the two sampling areas. This t-test assessed whether the mean lengths (at the same age) of males and females within each area respectively for the age class 1, 2, and 3 were statistically different. In our study, we used the alpha level (risk level) of 0.05 to test the significance.

The test of the normal distribution of the anchovy lengths from the North and the South areas was performed using Shapiro-Wilk test (Shapiro & Wilk, 1965).

Results

In most cases, the otolith growth mark pattern was clear and legible; only 3% of the analysed otoliths were discarded. The monthly trend in RMD showed an apparent seasonal cycle (Fig. 3A). However it should be noted that the monthly evolution of the RMD and the percentage of translucent zones in the otoliths appeared approximately similar in the North and the South areas even if data were missing for some months, (Figs 3B, C). Thus, the analyses of the monthly evolution of the average of the RMD and the average of the percentage of translucent zones showed a cyclic phenomenon of the growth increment formation.

The RMD value increased from April until it reached a peak in August (69%) and then decreased (Table 2). Nevertheless, it remained at a high level until October. In December the RMD value dropped down and stabilized at low value until March. The highest percentage of marginal otoliths with translucent marginal zone was observed during this period. The evolution of the percentage of translucent zones showed that whatever the month was, the rate of hyaline marginal zones did not fall down 15% in the

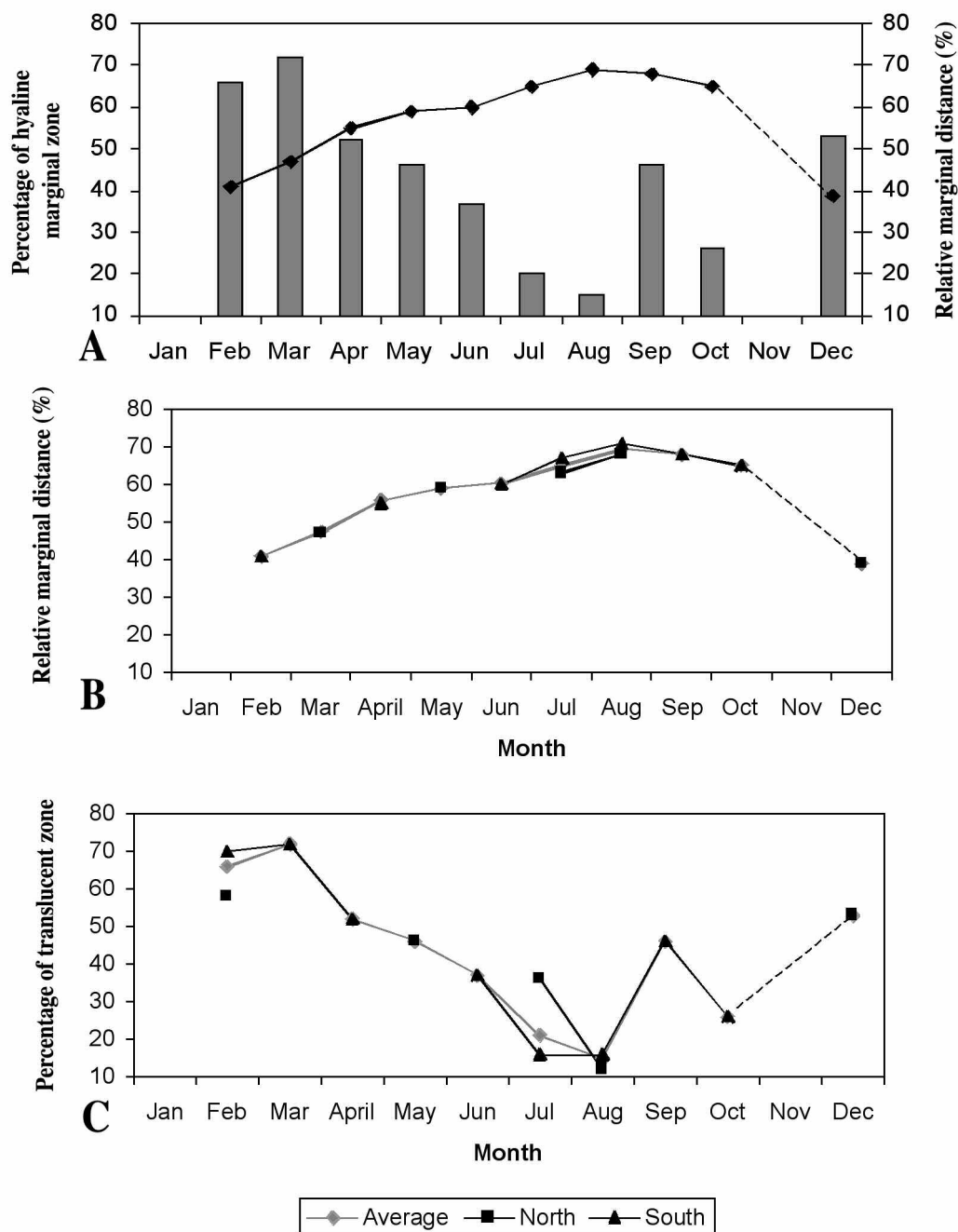


Figure 3. *Engraulis encrasicolus*. Monthly evolution of the Relative Marginal Distance (curve) and percentage of marginal translucent zone (histogram) in the otoliths (A), monthly evolution of the Relative Marginal Distance by area (B) and monthly evolution of the percentage of marginal hyaline zone by area (C).

Figure 3. *Engraulis encrasicolus*. Evolution mensuelle de la distance relative marginale (courbe) et du pourcentage de zone hyaline marginale (histogramme) dans les otolithes (A), évolution mensuelle de la distance relative marginale par région (B) et évolution mensuelle du pourcentage de zone hyaline marginale (C).

Table 2. *Engraulis encrasicolus*. Monthly evolution of the relative marginal distance and of the marginal zone of anchovy otoliths. n: number of otoliths, s standard deviation, HMZ : number of otoliths with hyaline marginal zone, OMZ: number of otoliths with opaque marginal zone.

Tableau 2. *Engraulis encrasicolus*. Evolution mensuelle de l'allongement marginal relatif et de la zone marginale des otolithes d'anchois. n : nombre d'otolithe, s : écart-type, HMZ : nombre d'otolithes avec une zone hyaline marginale, OMZ : nombre d'otolithes avec une zone opaque marginale.

Month	Relative Marginal Distance				Marginal Zone		
	Length (cm)	n	Average	s	Length (cm)	HMZ	OMZ
January	-	-	-	-	-	-	-
February	7.5-11.6	11	0.41	0.18	7.5-12.4	48	24
March	8-11	13	0.47	0.09	8-11	54	21
April	7.7-10	20	0.55	0.29	7.4-10.3	14	13
May	9.8-14.6	67	0.59	0.22	9-15.8	65	74
June	8.5-12.2	52	0.60	0.27	8.5-12.2	41	67
July	7.9-16.7	82	0.65	0.35	7.7-16.7	27	105
August	8.1-15.9	54	0.69	0.25	8.1-15.9	19	100
September	8.1-10	12	0.68	0.26	8-10	29	34
October	7.6-11.1	58	0.65	0.31	7.6-11.1	28	78
November	-	-	-	-	-	-	-
December	8.5-14.8	14	0.39	0.22	8.1-15.6	14	12

otoliths. One clearly defined peak was observed in RMD suggesting that one translucent zone was formed per year in the anchovy otoliths. This translucent zone is deposited from November/December to March whereas an opaque zone was formed from April to October/November.

Anchovies from 0 to 4 years old were present in both areas. The length frequency distributions of age showed a large range in length for each age class and an overlap between adjacent age classes (Tables 3 & 4). In the North area, the most common groups were respectively class 1 and 2. In the South area most of the population was composed of specimens belonging to age class 1.

The W values of Shapiro-Wilk test of 0.80 for the North area and of 0.79 for the South area validate the normality of the distribution of the anchovy lengths in the two areas. The student t-test showed no significant differences between males and females within each area ($p > 0.05$), so the two sexes were grouped for the growth analysis (Table 5). However significant differences ($p < 0.05$) were found in mean lengths between the two areas in the different class of ages (Table 6). Specimens from the North area were longer than in the South area in all age class. Thus, the data concerning these two areas were analysed separately.

Von Bertalanffy growth curves showed that differences in growth between the North and South areas were important since the first year of anchovy life (Fig. 4). The growth of the anchovies was almost achieved during the first year in both areas. One-year-old anchovies reached 10.9 cm in the North area and 8.5 cm in the South area, these values corresponding respectively to 56% and 50% of their maximal theoretical length.

Discussion

Our analysis of the formation of otoliths of anchovies in the Tunisian waters demonstrated that one hyaline zone is yearly formed. The progressive change from a hyaline to an opaque one probably reflects intrinsic physiological processes in anchovies as demonstrated in other teleosts (Khemiri, 2006). The formation of an opaque zone in the anchovy otoliths occurred in a period of high water temperatures along the Tunisian coasts coinciding with the well-being period of the anchovies. Conversely, the hyaline zone was formed when the water temperatures were at their lowest value corresponding to a poor condition of the anchovies (Sinovčić & Zorica, 2006). Seasonal environmental variations including changes of the water temperature and food supply seemed to be more important than physiological processes such as spawning activity to control the formation of the hyaline zone in the anchovies in the Tunisian waters. The concurrent formation of an opaque zone in spring and summer when anchovies had a high metabolism supported the hypothesis that the opaque zone was associated with a rapid growth of the fish whereas the formation of the hyaline zone was coupled with a slow growth of the fish. Our results were in accordance with other reports on the formation of the hyaline zone in species living in temperate and sub-polar latitudes (Beckman & Wilson, 1995).

Like other small pelagic teleosts (Blaxter & Hunter, 1982), anchovies are fast growing and short-lived species. The decrease in growth rate after the first year could be related to the onset of the reproductive activity occurring

Table 4. *Engraulis encrasicolus*. Length frequency distribution of the female (A) and male (B) anchovies in the South area in various ages. FL: Fork length.**Tableau 4.** *Engraulis encrasicolus*. Distribution des fréquences de tailles en fonction de l'âge des anchois femelles (A) et mâles (B) dans la région Sud. FL : Longueur à la fourche.

Month FL/age (month)	10 3	11 4	12 5	2 7	4 9	7 12	8 13	9 14	10 15	1 18	2 19	3 20	1 30	2 31	3 32	1 42	2 43	3 44
A																		
7-7.5	2																	
7.5-8	3																	
8-8.5				14	11	34		4	4									
8.5-9				5	6	33	12	9	14									
9-9.5				4	3	23	7	18	21									
9.5-10						4	4	9	4									
10-10.5						3	18	1	8		1							
10.5-11						1	9		8		1							
11-11.5							1		7		1							
11.5-12											3							
12-12.5											9				15			
12.5-13															12			
13-13.5															8			
13.5-14															11			
14-14.5															1			
14.5-15															1			
15-15.5																	1	
class	class 0: 5			class 1: 299					class 2: 15				class 3: 48			class 4: 1		
Month FL/age (month)	10 3	11 4	12 5	2 7	4 9	7 12	8 13	9 14	10 15	1 18	2 19	3 20	1 30	2 31	3 32	1 42	2 43	3 44
B6-6.5	2																	
6.5-7	2																	
7-7.5	3																	
7.5-8																		
8-8.5				16	8	10	4	4	1									
8.5-9				9	6	17	10	12	13									
9-9.5				1	2	12	12	10	20									
9.5-10						3	7	2										
10-10.5						1	8	1	4									
10.5-11							2		4		1							
11-11.5									1		1							
11.5-12											1			2				
12-12.5											4			7				
12.5-13														8				
13-13.5														6				
13.5-14														3				
14-14.5																	3	
class	class 0: 7			class 1: 200					class 2: 7				class 3: 26			class 4: 3		

during the first year of life (Gaamour et al., 2004). In both the North and South areas, the lifespan of the anchovies was, at least 4 years from age group 0 to 4. This longevity corresponds to the lifespan reported for the same species in the Adriatic Sea (Sinovčić, 2000) and in the Northwestern Mediterranean Sea (Morales-Nin & Perterra, 1990). However, according to Bailey (1992), a small fraction of

the anchovy population may reach an age of five years. The overlap observed between age groups could be attributed to the protracted reproductive period of this species (Gaamour et al., 2005) and fast growth of juveniles, which is reflected in the individual lengths of the cohort (Fréon, 1984; Sinovčić, 1998).

Our results show that anchovies from the North area

Table 5. *Engraulis encrasicolus*. Comparison of length in the age groups 1 to 4 between sexes (N : North, S : South, FL : Fork length in cm, s : standard deviation, n : number of specimens, t : t-test with $p < 0.05$, * : significant differences).

Tableau 5. *Engraulis encrasicolus*. Comparaison de la longueur entre les sexes pour les groupes d'âge de 1 à 4 (N : Nord, S : Sud, FL : longueur à la fourche en cm, s : écart type, n : nombre de spécimens, t : test t avec $p < 0,05$, * : différence significative).

Age	Fem (N) FL \pm s (cm)	n	Male (N) FL \pm s (cm)	n	t	Fem (S) FL \pm s (cm)	n	Male (S) FL \pm s (cm)	n	t
1	10.79 \pm 0.46	80	10.64 \pm 0.53	84	1.92	9.07 \pm 0.82	299	8.93 \pm 0.64	200	1.95
2	13.51 \pm 1.09	74	13.49 \pm 1.11	55	0.20	11.96 \pm 0.12	12	11.77 \pm 0.47	6	1.17
3	15.03 \pm 0.66	20	14.7 \pm 0.39	13	0.22	13.08 \pm 0.61	48	12.83 \pm 0.54	26	1.61
4	15.77 \pm 0.29	4	15.7	1	1.03	15	1	14.45 \pm 0.07	3	6.27*

Table 6. *Engraulis encrasicolus*. Comparison of length in the age groups 1 to 4 between areas (FL : Fork length in cm, s : standard deviation, n : number of specimens, t : t-test with $p < 0.05$, * : significant differences).

Tableau 6. *Engraulis encrasicolus*. Comparaison de la longueur entre les régions pour les groupes d'âge de 1 à 4 (FL : longueur à la fourche en cm, s : écart type, n : nombre de spécimens, t : test t avec $p < 0,05$, * : différence significative).

Area	North area		South area		
Age	FL \pm s (cm)	n	FL \pm s (cm)	n	t
1	10.70 \pm 0.50	164	9 \pm 0.76	499	26.35*
2	13.50 \pm 1.09	128	11.90 \pm 0.27	18	2.62*
3	14.87 \pm 0.63	33	12.99 \pm 0.59	74	11.62*
4	15.76 \pm 0.26	5	14.23 \pm 0.66	4	4.75*

(open sea) reach a greater length than those from the South in inshore coastal water. Quignard et al. (1973) also noted morphological differences between the anchovies of the lagoon and those of the offshore in Tunisia. Other studies also showed a high dispersion in the growth patterns in the anchovies depending on the regions as summarised in table 7. This dispersion could be considered, at least in part, as a consequence of the various ageing methods but most often it reflected differences in growth patterns that could be related either to variations of the environmental conditions and/or to a genetic basis.

However, in the present study, the comparison of anchovy growth in the two areas was carried out using the same methods applied to homogenous samples to avoid technical discrepancy. Thus, the growth differences might be related to the variability of the environmental conditions in the two areas. Among abiotic factors, temperature could

be considered as a limiting factor in ectotherms. A positive correlation between instantaneous growth rate and temperature was already determined for the anchovy larvae (Dulcic, 1997). Gunter (1950 in Sinovčić, 2000) showed that a high temperature resulted in a premature onset of sexual maturity. The growth became slower and finally the body size was smaller. This may explains to some extent the difference in growth observed between the two areas, since in Tunisian waters, mean temperature in summer is higher in the South area than in the North area (Sammari & Gana, 1995). The higher temperature results in a faster growth of larval and juvenile anchovies. Furthermore, Pauly (1980) using 175 fish stocks showed that L_{∞}

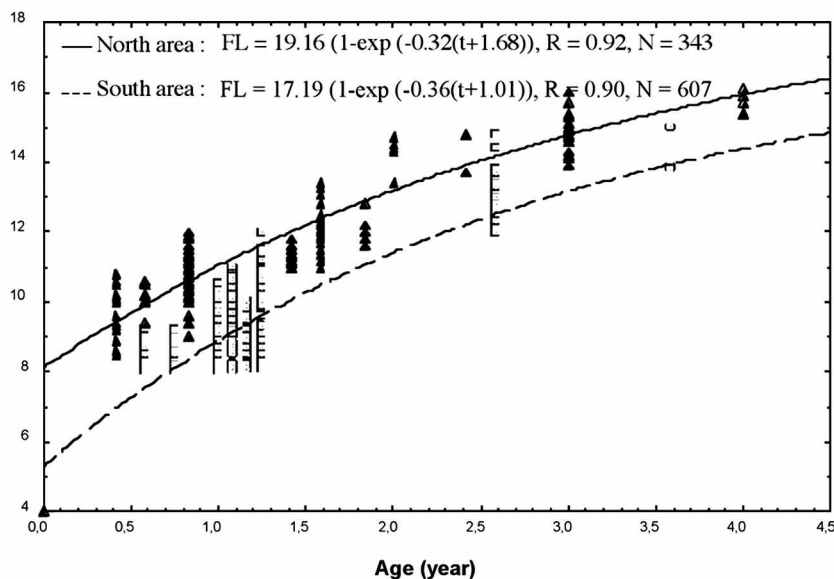


Figure 4. *Engraulis encrasicolus*. Growth curves of the anchovies in the North and South areas.

Figure 4. *Engraulis encrasicolus*. Courbes de croissance des anchois dans les régions Nord et Sud.

Table 7. *Engraulis encrasicolus*. Comparisons of the growth parameters obtained for the European anchovy in various regions (L_{∞} : asymptotic length in cm, k: growth constant, t_0 : extrapolated constant in month).

Tableau 7. *Engraulis encrasicolus*. Comparaison des paramètres de croissance des anchois dans différentes régions (L_{∞} : longueur asymptotique en cm, k : coefficient de croissance, t_0 : âge théorique du poisson en mois quand la longueur du poisson est nulle).

Area	L_{∞}	K	t_0	Method	Source
Strait of Sicily	18.6	0.3	-1.81	Otolith	Basilone et al., 2004
Gulf of Cadiz	18.95	0.9	-0.01	Frequency	Bellido et al., 2000
Gulf of Biscay	21.3	0.48		Otolith	Cendrero et al., 1981
North Adriatic sea	15.3	2.44			
Eastern Adriatic sea (juveniles)	13.2	0.82	-0.5	Otolith	Sinovčić, 2004
Adriatic sea	19.4	0.57	-0.5	Otolith	Sinovčić, 2000
North Western Mediterranean	19.1	0.34	-1.44	Otolith	Morales-Nin & Pertierra, 1990

increased as temperature decreased. Thus, the colder waters of the North area were responsible for the relatively high asymptotic length reached by the anchovies in this area.

Another factor affecting the growth of the anchovies could be productivity. Indeed, in the south area, the phytoplankton biomass is subject to stressing conditions, such as abrupt changes in the hydrological factors and/or important tidal activity. The low phytoplankton primary production found results in the low growth observed in this area. Moreover small anchovies could not travel far away to encounter better feeding conditions. Conversely, anchovies in the North area, characterised by a greater length, were able to perform wide migration towards feeding areas and store enough energy reserves to reach a great length at first maturity. Similarly the diagram established by Marchal (1991) for the round sardinella *Sardinella aurita* (Valenciennes, 1847) indicated that "two sized-types" of round sardinella were differentiated along the West African coast. The smaller type located in the Gulf of Guinea was sedentary and fed intensively only during the short productive season. The larger type found in the Northern and Southern areas (open sea) migrated all year round to follow the productive water and made important energy reserves.

Fage (1920) considered that these differences in growth, and some morphometric characteristics, allowed to distinguish two races of European anchovies, an Atlantic and a Mediterranean one. Genetic studies also showed high levels of genetic heterogeneity in anchovies (Spanakis et al., 1989; Bembo et al., 1996). Borsa (2002) and Borsa et al. (2004) analysed allozyme frequencies and Nuclar-DNA markers of anchovies collected in the Northern Adriatic (inshore) and in the Southern-central Adriatic (open sea) and distinguished two anchovy species: *Engraulis albidus* sp. and *Engraulis encrasicolus* with distinct habitats. These were widely distributed throughout the Mediterranean Sea: the open sea lineage and the inshore water lineage. These two populations showed

differences in their growth rate and maximal length.

Bembo et al. (1996), Borsa (2002) and Borsa et al. (2004), stated that the genetic differentiation between Adriatic populations of anchovies was associated with hydrological patterns (inshore-offshore). In these studies on the population structure of anchovies (Bembo et al., 1996; Borsa, 2002), the genetic differentiation was considered as a result of a restriction in the gene flow between the population of the open sea area and that of the coastal area, these two populations showing a more or less reproductive isolation.

Likewise, our results suggested that anchovies in the Tunisian waters were composed of two distinct groups: The first, located in the South area (inshore), was characterized by a low growth and a small maximal length, and the second, composed of anchovies from the North area (open sea), was characterized by a high growth and a large maximal length. The differences between the South area (shallow water) and the North area (open sea) in Tunisian waters could act to delineate the two anchovy populations. The anchovy spawning period occurred in summer concomitantly with the installation of a thermal front in the South area (Sammari & Gana, 1995) that could act as a barrier separating the spawning ground of the population of the coastal area from that of the open sea. This physical barrier could be responsible for a restriction of the gene flow between these two populations resulting in a genetic divergence. However, up to now the anchovies from these regions have not been genetically analysed, thus further studies were needed to test the hypothesis of genetic differences between anchovies from the North and the South areas. A genetic subdivision within the Tunisian water would result in a modification of the anchovy fishery-managements by incorporating stock identity.

At the present time, our results prompted to direct fishing effort to the open sea areas where large anchovies of economic interest were present.

Acknowledgements

The authors are greatly indebted to Dr Michel Laurin for constructive comments and for reviewing the English language, to Dr Othman Jarboui, Lotfi Ben Abdallah for providing samples. Special thanks to all the LASAA (Laboratoire de Sclérochronologie des Animaux Aquatiques) members for their help in image analysis.

References

- Basilone G., Guisande C., Patti B., Mazzola S., Cuttitta A., Bonanno A. & Kallianniotis A. 2004. Linking habitat conditions and growth in the European anchovy (*Engraulis encrasicolus*). *Fisheries Research*, **68**: 9-19.
- Bailey R.S. 1992. The global pelagic fish resources and its biological potential. In : *Pelagic Fish: The Resource and its Exploitation* (J. R. Burt, R. Hardy & K. J. Whittle eds), pp. 1-20. Cambridge University Press.
- Beamish R.J. & McFarlane G.A. 1987. Current trends in age determination methodology. In: *The age and growth of fish*. (R.C. Summerfelt & G.E. Hall eds), pp. 15-42. Iowa state University Press.
- Beckman D.W. & Wilson C.A. 1995. Seasonal timing of opaque zone formation in fish otoliths. In: *Recent Developments in Fish Otolith Research* (D.H. Secor, J.M. Dean & S.E. Campana eds), pp. 27-43. Columbia, SC, USA: South Carolina University Press.
- Bellido J.M., Pierce G.J., Romero J.L. & Millan M. 2000. Use of frequency analysis methods to estimate growth of anchovy (*Engraulis encrasicolus* L. 1758) in the Gulf of Cadiz (SW Spain). *Fisheries Research*, **48**: 107-115.
- Bembo D.G., Carvalho G.R., Cinagolani N. & Pitcher T.J. 1996. Allozymic and morphometric evidence for two stocks of the European anchovy *Engraulis encrasicolus* in Adriatic waters. *Marine Biology*, **126**: 529-538.
- Bertalanffy von L. 1938. A quantitative theory of organic growth (Inquiries on growth Laws II). *Human Biology*, **10**: 181-213.
- Blaxter J.H.S. & Hunter J.R. 1982. The biology of the clupeoid fishes. *Advances in Marine biology*, **20**: 1-223.
- Borsa P. 2002. Allozym, mitochondrial-DNA, and morphometric variability indicate cryptic species of anchovy (*Engraulis encrasicolus*). *Biological Journal of the Linnean Society*, **75**: 261-269.
- Borsa P., Collet A. & Durand J.D. 2004. Nuclear-DNA markers confirm the presence of two anchovy species in the Mediterranean. *C. R. Biologies*, **327**: 1113-1123.
- Cendrero O., Cort J.L. & De Cardenas E. 1981. Revision de algunos datos sobre la biología de la anchoa, *Engraulis encrasicolus* (L.) del Mar Cantabrico. *Boletín del Instituto Español de Oceanografía*, **6**: 117-124.
- Dulcic J. 1997. Growth of anchovy, *Engraulis encrasicolus* (L.), larvae in the Northern Adriatic Sea. *Fisheries Research*, **31**: 189-195.
- Fage L. 1920. *Engraulidae, Clupeidae. Report of the Danish Oceanography Expedition in the Mediterranean*, **2**: 1-136.
- Fischer W., Bauchot M. & Schneider M. 1987. Fiches FAO d'identification des espèces pour les besoins de la pêche. Méditerranée et Mer Noire. Zone de pêche 37, Révision 1. Vol. II, Vertébrés. pp. 761-1530. Rome: FAO.
- Fréon P. 1984. La variabilité des tailles individuelles à l'intérieur des cohortes et des bancs de poissons. I: Observations et interprétations. *Oceanologica Acta*, **7**: 457-468.
- Gaamour A., Khemiri S., Mili S. & Ben Abdallah L. 2004. L'anchois (*Engraulis encrasicolus*) des côtes nord de la Tunisie : Reproduction et exploitation. *Bulletin de l'Institut National des Sciences et Technologies de la Mer de Salammbô*, **31**: 17-24.
- Gaamour A., Ben Abdallah L., Khemiri S. & Mili S. 2005. Etude de la biologie et de l'exploitation des petits pélagiques en Tunisie. *MedSudMed Technical Documents*, **5**: 56-74.
- Khemiri S. 2006. Reproduction, âge et croissance de trois espèces de téléostéens pélagiques des côtes tunisiennes: *Engraulis encrasicolus*, *Sardina pilchardus* et *Boops boops*. Thèse de Doctorat de l'Ecole Nationale Supérieure Agronomique de Rennes. 194 pp.
- Marchal E. 1991. Nanisme et sédentarisme chez certaines espèces de poissons pélagiques, deux aspects d'une même réponse à des conditions défavorables. In: *Pêcheries Ouest-Africaines, Variabilité, Instabilité et Changement* (P. Cury & C. Roy eds), pp 201-207. Colloques et Séminaires ORSTOM, Paris, France.
- Mills K.H. & Beamish R.J. 1980. Comparison of fin ray and scale age determination for lake Whitefish (*Coregonus clupeaformis*) and their implications for estimates of growth and annual survival. *Canadian Journal of fisheries and Aquatic Sciences*, **37**: 534-544.
- Morales-Nin B. & Pertierra J.P. 1990. Growth rates of the anchovy *Engraulis encrasicolus* and the sardine *Sardina pilchardus* in the Northwestern Mediterranean Sea. *Marine Biology*, **107**: 349-356.
- Panfili J., De Pontual H., Troadec H. & Wright P.J. 2002. *Manual of fish sclerochronology*. IFREMER-IRD: Paris, France. 463 pp.
- Pauly D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal of the International Council for the exploration of the Sea*, **39**: 175-192.
- Quignard J.P., Hamdouni T. & Zaouali J. 1973. Données préliminaires sur les caractères biométriques des anchois *Engraulis encrasicolus* (Linné, 1758) des côtes de Tunisie et du lac Ichkeul. *Revue des Travaux de l'Institut des Pêches Maritimes*, **37**: 191-196.
- Sammari C. & Gana S. 1995. Revue de l'hydrodynamisme au large des côtes Tunisiennes. *Bulletin de l'Institut National des Sciences et Technologies de la Mer de Salammbô*, **22**: 10-31.
- Schwartzlose R.A., Alheit J., Bakun A., Baumgartner T.R., Colette R., Crawford R.J.M., Fletcher W.J., Green-Ruiz Y., Hagen E., Kawasaki T., Lluch-Belda D., Lluch-Cota S.E., Mac Call A.D., Matsuura Y., Nevarez-Martinez M.O., Parrish R.H., Roy C., Serra R., Shust K.V., Ward M.N. & Zuzunaga J.Z. 1999. Worldwide large-scale fluctuations of sardine and anchovy populations. *South African Journal of Marine Science*, **21**: 289-347.
- Shapiro S.S. & Wilk M.B. 1965. An analysis of variance test for normality. *Biometrika*, **52**: 591-611.

- Sinovčić G. 1982.** On the vertebral number of anchovy, *Engraulis encrasicolus* (L.), in the Central Adriatic. *Acta Adriatica*, **23**: 441-448.
- Sinovčić G. 1998.** The population dynamics of the juvenile anchovy, *Engraulis encrasicolus* (L.) under the estuarine conditions (Novigrad Sea-Central eastern Adriatic). *Cahiers Options Méditerranéennes*, **35**: 273-282.
- Sinovčić G. 2000.** Anchovy, *Engraulis encrasicolus* (Linnaeus, 1758): Biology, population dynamics and fisheries case study. *Acta Adriatica*, **41**: 3-53.
- Sinovčić G. 2004.** Growth and length-weight relationship of the juvenile anchovy, *Engraulis encrasicolus*, in the nursery ground (Zrmanja river estuary-eastern Adriatic Sea). *Journal of Applied Ichthyology*, **20**: 79-80.
- Sinovčić G. & Zorica B. 2006.** Reproductive cycle and minimal length at sexual maturity of *Engraulis encrasicolus* (L.) in the Zrmanja River estuary (Adriatic Sea, Croatia). *Estuarine Coastal and Shelf Science*, **69**: 439-448.
- Spanakis E., Tsimenides N. & Zouros E. 1989.** Genetic differences between populations of sardine, *Sardina pilchardus*, and anchovy, *Engraulis encrasicolus*, in the Aegean and Ionian Seas. *Journal of Fish Biology*, **35**: 417-437.
- Tudela S. 1999.** Morphological variability in a Mediterranean, genetically homogenous population of the European anchovy, *Engraulis encrasicolus*. *Fisheries Research*, **42**: 229-243.