

Age, growth and mortality of a semi-isolated lagoon population of sand smelt, *Atherina boyeri* (Risso, 1810) (Pisces: Atherinidae) in an estuarine system of northern Greece

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Summary

Age, growth and mortality of the sand smelt, *Atherina boyeri* (Risso, 1810), were studied in the Vistonis estuarine system in northern Greece from February 1989 to August 1990. Overall male : female sex ratio was 1 : 2.5, statistically different from unity. Total lengths ranged between 13 and 105 mm. Age determination based on scale readings showed that the population comprised five age-groups. Sand smelt grew allometrically ($b = 3.22$) and rapidly during the first year, achieving 60% of their growth. Growth parameters of the population were: $L_{\infty} = 116.97$ mm, $K = 0.35$ year⁻¹ and $t_0 = -0.99$ years. Growth index ϕ' was 3.69 of all individuals studied. The mean growth index was significantly lower for the Mediterranean lagoon ($\phi' = 3.73$, SD = 0.1) than for Atlantic populations ($\phi' = 3.92$, SD = 0.06). Total mortality rate was $Z = 1.29$ year⁻¹ and natural mortality $M = 0.95$ year⁻¹. Males had a lower life span than females, the latter dominating length classes >60 mm. Exploitation rate of the studied population was $E = 0.26$, suggesting that stock size might increase and generate improved possibilities for exploitation.

Introduction

The Boyer's sand smelt, *Atherina boyeri* (Risso 1810), is a small, short-lived euryhaline teleost fish principally inhabiting coastal and estuarine waters, including coastal lagoons, over a wide salinity range from freshwater to hypersaline conditions. The species is distributed throughout the Mediterranean and adjacent seas, as well as the north-east Atlantic from the Azores to the north-west coast of Scotland (Henderson and Bamber, 1987). There is evidence that most fish remain in the vicinity of spawning areas, resulting in semi-isolated populations each with a characteristic morphology and life history (Henderson et al., 1988). Some authors (Bamber and Henderson, 1988) also consider that *A. boyeri* is at the threshold of a speciation phenomenon. Moreover, there is biochemical evidence that distinguish some Mediterranean *A. boyeri* lagoon populations when compared with marine populations (Focant et al., 1991, 1992). Kottelat (1997) suggested that the species could be divided into two distinct taxa: lagoonal (*A. boyeri*) and marine (*A. mochon*). Based on biometric investigations, Trabelsi et al. (2002) proposed including the atherinids living in the lagoon environment in a separate new species (*A. lagunae*). In western Greece, a mitochondrial DNA study on eight different *A. boyeri* populations (Klossa-Kilia et al., 2002) showed significant diversity between the marine and lagoon populations.

Life-history aspects of *A. boyeri* have been studied at various locations of the western Mediterranean and Atlantic coasts of Europe (Castel et al., 1977; Marfin, 1982; Palmer and Culley, 1983; Henderson and Bamber, 1987; Fernandez-Delgado et al., 1988; Creech, 1992; Andreu-Soler et al., 2003). In the eastern Mediterranean, sand smelt populations have been studied only in Israel (Bardawil Lagoon: Gon and Ben-Tuvia, 1983); in the Adriatic (Boscolo, 1970); and in Trichonis Lake in western Greece (Leonardos, 2001); and Mesolongi and Etolikon lagoons (Leonardos and Sinis, 2000); there is no information regarding populations in northern Greece. In Greece, sand smelt has become the most important commercial species for some inland waters (e.g. the Vistonis estuarine system in northern Greece and Lake Trichonis in western Greece) over the past two decades, when exploitation of recently established populations began. Intensive commercial exploitation of the Vistonis estuarine system sand smelt began in 1990. *A. boyeri* are collected from late October until late November and catches usually represent >50% of the total fish production of the lake. Catches fluctuated between 95 tonnes in 1990 and 285 tonnes in 1999, representing the most commercially valuable resource of this estuarine system (Koutrakis, 2000). This is the first study of the semi-isolated *A. boyeri* population of the Vistonis estuarine system in northern Greece.

This paper attempts to use age and sex structure, growth, condition, mortality and exploitation rates of *A. boyeri* populations in the Vistonis estuarine system to determine better management practices for sustainable use of this localized fishery resource. The data presented are compared with other available data from estuarine systems at various locations in the Mediterranean and the Atlantic coasts of Europe.

Study area

The study took place in the Vistonis Lake and the Porto Lagos Lagoon. Lake Vistonis is a shallow eutrophic lake (average depth 2 m) that covers approximately 4000 ha. Ouzounis and Giannakopoulou (1984) reported that the lake has high concentrations of toxic substances (pesticides and fertilizers from agricultural run-off), problems with dissolved oxygen, high pH values and very low transparency. Differences in salinity values divide the lake into two parts: the northern upstream part is affected by freshwater inflow, and the more saline southern part, due to propagation of sea water through Porto Lagos Lagoon and directly from the Vistonikos Gulf

(Thracian Sea, Northern Aegean Sea) through a narrow (5-m) 1.5-km long artificial channel. Porto Lagos is a micro-tidal (tidal range <0.30 m during spring tides) shallow coastal lagoon with northerly winds prevailing during summer and southerly winds during winter. Porto Lagos is connected to Lake Vistonis by three channels (50-m long and 25-m wide) and to the Vistonikos Gulf through a 600-m long and 60-m wide channel (Koutrakis et al., 1995).

At the northern end of the channels connecting the two systems grill screens (10 mm width between grills) prevent adult fishes from moving between the Porto Lagos Lagoon and Lake Vistonis, but allow the entrance of juveniles and small-size fish species. The grill screens are opened between January and April each year, allowing adult fish to move between the systems. Market-size individuals of commercially important species are harvested during their migration to the sea at an especially designed permanent entrapment device situated in one of the channels connecting the lake with the lagoon.

Materials and methods

Samples of sand smelt were collected on a monthly basis from February 1989 to August 1990. A bag seine net (mesh size 3 mm knot-to-knot, 10 m length, 1.2 m height) was hauled at the southern part of Lake Vistonis and the Porto Lagos Lagoon. Each haul covered an area of approximately 250 m². The design of the fishing gear allowed for catch of all sand smelt length classes (Leonardos and Sinis, 2000). Sampling was carried out in three replicates at the same time of day at the end of each month. Individuals were preserved in 4% neutralized formalin solution prior to examination. During sampling, temperature (°C), salinity (measured using the Practical Salinity Scale) and pH were measured. Surface water temperature ranged between 0.5 and 21°C in winter and between 16 and 30.5°C in summer; average water temperature for the sampling period was 17.5°C. Salinity ranged between 7.1 and 33.5 and pH between 7.4 and 8.5.

Specimen total (TL), fork (FL) and standard (SL) lengths, the latter as defined by Holčík et al. (1989), were measured to the closest 0.1 mm. Total body weight (*W*) was measured to the closest 0.01 g. Sex was macroscopically identified in the samples. Sex ratio was determined monthly and the chi-squared test (Zar, 1999) was used to determine whether the sex ratio varied from 1 : 1. Length–weight relationship was described using the logarithmic form of the formula: $W = a \times TL^b$, where *W* is total weight, TL the total length, *a* the intercept of the regression line and *b* the regression coefficient. The length–weight relationship was calculated for the entire sample and for each sex separately. Length–weight regressions were tested for differences in slopes and intercepts between sexes using analysis of covariance (Zar, 1999). The statistical package Statistica was used for statistical analysis (Statsoft, Inc., 1996).

The relationship between body length and weight can also be expressed with the condition factor index, which describes the condition of a population (Le Cren, 1951). The Fulton condition factor (CF) was estimated for all specimens used in the present study, according to the equation: $CF = 10^5 \times (W/TL^3)$ (Le Cren, 1951).

Age was determined using scales taken from the left flank, along the line of the silver stripe between the posterior end of the pectoral fin and anterior end of the dorsal fin. Scales were cleaned and placed between two slides for age determination.

Total radius of the scales and radius of each annual ring were measured as the smallest distance from the centre of the scale to the distal edge. The relationship between total length (TL) and total scale radius (*R*) was examined for all individuals and for each sex separately. TL–*R* regressions were tested for differences in slopes and intercepts between sexes using analysis of covariance (Zar, 1999).

The back-calculated total lengths were determined using the equation:

$$TL_n = a + (TL - a) \times \left(\frac{R_n}{R}\right),$$

where TL_n is the total length of the fish when annulus '*n*' was formed, R_n is radius of the annulus '*n*', *R* is total scale radius, and *a* is intercept of the linear regression relationship between total length and total scale radius on the length axis (Francis, 1990). Estimates of theoretical growth in length were obtained by fitting the von Bertalanffy growth function (VGBF) to the mean length at age data. The VGBF is expressed as:

$$L_t = L_\infty(1 - e^{-K(t-t_0)}),$$

where L_∞ is the asymptotic length, *K* is the growth coefficient (year⁻¹) and t_0 is the theoretical age for $L_t = 0$. Growth parameters were estimated iteratively using the statistical package Statistica (Statsoft, Inc., 1996). Mean data were used in order to assign equal weight to each age.

Overall growth performance of a species can be interpreted by the growth index $\phi' = \log(K) + 2 \log(L_\infty)$, which can also be used for comparing growth rates among species (phi prime test; Munro and Pauly, 1983). Estimated growth parameters of different lagoon and marine populations of sand smelt were used to construct an auximetric double logarithmic plot of the parameter *K* against the corresponding estimate of asymptotic length L_∞ . Such a plot was recently proposed for comparison of within- and between-species growth performances (Pauly, 1998).

The cumulated catch curve

$$\log_e(Nc) = a + \frac{Z}{K} \log_e(L_\infty - L)$$

proposed by Jones and Van Zalinge (1981) was used to estimate total mortality rate (*Z*). *Nc* is the cumulative number of fish of length *L* and above, L_∞ is the asymptotic length, *K* is the growth coefficient and Z/K is the slope of the curve, which was developed from the length–frequency distribution. Natural mortality (*M*) was estimated using the empirical formula of Pauly (1980):

$$\log(M) = -0.0066 - 0.279 \times \log(L_\infty) + 0.6543 \times \log(K) + 0.4634 \times \log(T),$$

where L_∞ (cm) and *K* are the growth parameters and *T* (°C) is the mean water temperature. The exploitation rate was estimated using the equation: $E = F/(F + M)$, where *F* is the fishing mortality and *M* is the natural mortality (Ricker, 1975). Total and natural mortality were estimated for all individuals and for males and females separately.

Results

Population structure

A representative subsample of 350 specimens was used for sex ratio determination, 246 of which were sexually identified throughout the year. Overall sex ratio between males and females was 1 : 2.5, which is significantly different from unity

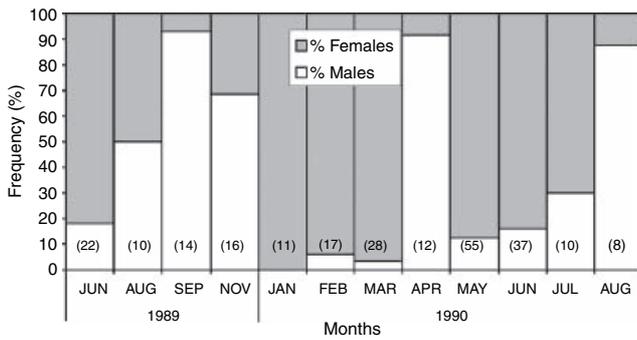


Fig. 1. Relative sex ratio (%) in catches of sand smelt *A. boyeri* in Vistonis estuarine system from June 1989 to August 1990 (horizontal axis = months when samples were caught; number of fish caught per month in brackets in each month column)

($\chi^2 = 23.01$ at $P < 0.05$). The ratio between males and females varied throughout the sampling period (Fig. 1). Males dominated during late summer months and autumn; females

dominated from January to May, which coincided with the spawning period. There was an exception in April when the percentage of males was high; this was attributed to the low numbers of fish caught during this month. Females dominated in the length classes above 60 mm TL.

Length frequency of the sand smelt samples varied between 13 and 105 mm TL. Recruitment of juvenile fish to the sampled population occurred in May and June, as shown in the monthly length frequency distribution (Fig. 2). From an examination of the gonads, the sand smelt spawning period in Vistonis Lake seems to occur from March to June. This conclusion is confirmed by the presence of sand smelt eggs in fyke nets during this season.

Age

Age determination and back-calculation analysis was determined from 761 fish. The annulus ring appeared as a thick dark zone. Appearance of the annulus ring occurred in February and March. A total of five age groups was

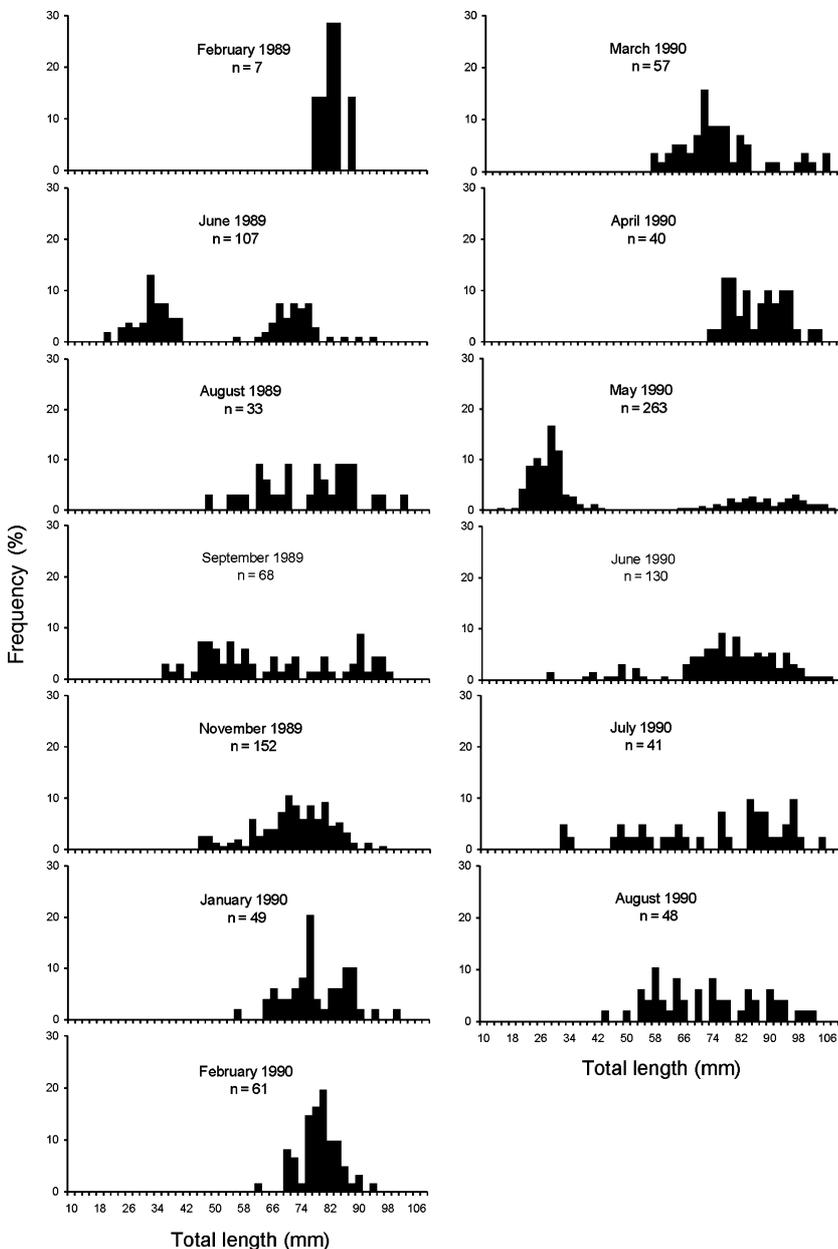


Fig. 2. Monthly length–frequency distribution of sand smelt *A. boyeri* (n = 1056) collected in the Vistonis estuarine system during the study period February 1989 to August 1990

Table 1
Back-calculated total lengths (mm) at age and standard deviation in parenthesis, for *A. boyeri* (n = 761) from Vistonis Lake and Porto Lagos Lagoon

Age (years)	MOTL	n	BCTL (per age)			
			1	2	3	4
0	45.71 (7.72)	56				
1	68.52 (5.93)	317	59.14 (4.17)			
2	83.3 (5.66)	331	60.53 (3.48)	75.68 (4.59)		
3	97.57 (3.81)	56	62.24 (2.92)	78.80 (3.30)	90.29 (3.93)	
4	100	1	58.27	74.98	85.03	97.17
Weighted mean			60.04 (3.88)	76.13 (4.56)	90.19 (3.96)	97.17
Annual increment			60.04	16.09	14.07	6.97
% annual increment			61.78	16.55	14.47	7.17

MOTL, mean observed total lengths; BCTL, back-calculated total lengths.

represented in the catches (Table 1). Maximum TL observed was 105 mm, corresponding to a 3-year-old fish. Only one fish of age 4+ years with a TL of 100 mm was found.

Growth

Relationship between total length and somatic weight for all individuals is described by the equation: $W = 2 \times 10^{-6} TL^{3.22}$ ($r^2 = 0.98$, $n = 1056$) and shows positive allometric growth for the estuarine system sand smelt population. No significant differences between sexes ($F = 0.000037$, $P = 0.99$) were found.

The Fulton condition factor (CF) varied from 0.53 (February 1990) to 0.63 (August 1990). Variation of the condition factor showed an increase in growth rate during summer months and a decrease during February, May and September (Fig. 3).

Relationships between total (TL), fork (FL) and standard (SL) length from all individuals used in the present study are described by the linear equations: $FL = 0.94TL - 0.77$ ($r^2 = 0.99$), $SL = 0.86TL - 1.01$ ($r^2 = 0.99$), $SL = 0.91FL - 0.29$ ($r^2 = 0.99$).

Slopes of the regressions between TL and total scale radius (R) showed that there are no significant differences between sexes (females: $TL = 10.203 + 8.06R$, $r^2 = 0.82$; males: $TL = 18.849 + 7.07R$, $r^2 = 0.76$, $F = 1.50$, $P = 0.22$). The linear regression relationship for all individuals of the sample used for ageing was: $TL = 5.743 + 8.4469R$ ($n = 761$, $r^2 = 0.879$). Intercept 'a' (=5.743) of the latter equation was used to back-calculate lengths-at-age.

Mean back-calculated total lengths-at-age showed rapid growth during the first year of life (61.78%) and a sharp

decline in growth in the following years (Table 1). The mean back-calculated total lengths of each age group were smaller than the observed lengths. The von Bertalanffy growth parameters were estimated as: $L_{\infty} = 116.97$ mm, $K = 0.35 \text{ year}^{-1}$, $t_0 = -0.99$ years for all individuals used for ageing; $L_{\infty} = 166.54$ mm, $K = 0.16 \text{ year}^{-1}$, $t_0 = -1.90$ years for females, and $L_{\infty} = 128.09$ mm, $K = 0.26 \text{ year}^{-1}$, $t_0 = -1.64$ years for males. Back-calculated lengths-at-age were very close to predicted lengths.

The ratio between maximum recorded length (L_{max}) and asymptotic length (L_{∞}) was 0.897. Growth index ϕ' was 3.69 for all individuals. The mean growth index was significantly lower (t -test, $t = -3.34$, $P < 0.05$) for the Mediterranean lagoon ($\phi' = 3.73$, $SD = 0.1$) than for Atlantic populations ($\phi' = 3.92$, $SD = 0.06$) (Table 2). In the auximetric plot, the $\log K - \log L_{\infty}$ relationships were linear with slopes -2.6 for the Mediterranean and -1.9 for the Atlantic populations (Fig. 4). The relationship was not significantly different from 0 ($P > 0.1$) when values from all areas were pooled together in the analysis.

Mortality

Total mortality for all individuals used for ageing was $Z = 1.29 \text{ year}^{-1}$. Slopes of the curves (Z/K) showed that values for females ($Z/K = 6.11$) and males ($Z/K = 5.85$) are significantly different ($F = 457$, $P < 0.05$). Total mortality for males was higher ($Z = 1.54 \text{ year}^{-1}$) than for females ($Z = 0.97 \text{ year}^{-1}$). Natural mortality (M) for all individuals was estimated as 0.95 year^{-1} , for females as 0.51 year^{-1} and for males as 0.76 year^{-1} . Fishing mortality for all individuals was calculated as $F = 0.34 \text{ year}^{-1}$. Exploitation rate of the population was calculated as $E = 0.26$.

Discussion

Overall sex ratio showed dominance of females, attributable to female dominance in length-classes above 60 mm TL, which indicates that most male sand smelt die at a younger age than females, as is the case in other populations (Castel et al., 1977; Gon and Ben-Tuvia, 1983; Leonardos and Sinis, 1999; Andreu-Soler et al., 2003). Moreover, females dominate the samples during spring months, which coincides with the spawning season as was also observed in the Adriatic (Boscolo, 1970), Bristol Channel (Creech, 1992) and Mesolongi and Etoliko lagoons (Leonardos and Sinis, 2000). This could be attributed to a trend of sand smelt individuals to form sexually unequal shoals, as observed by Creech (1992), and may

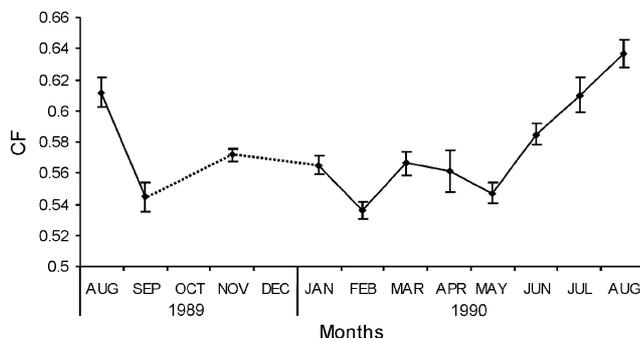


Fig. 3. Monthly mean Fulton condition factor (CF) distribution of sand smelt *A. boyeri* specimens (n = 1056) collected in the Vistonis estuarine system sampling period August 1989 to August 1990

Table 2

Growth parameters and ageing methodology for males (M) and/or females (F) of sand smelt *A. boyeri* from lagoon and estuarine populations of Mediterranean and Atlantic coasts of Europe

Area	Method	Sex	L_{∞}	K	L_{max}	t_{max}	ϕ'	Reference
Mediterranean								
Present study (northern Greece)	S	M, F	116.97	0.35	105	4	3.69	
Mesolongi and Etolikon Lagoons (western Greece)	S	M,F	115.79	0.24	103	3	3.51	Leonardos and Sinis, 2000
Trichonis Lake (western Greece)	S	M,F	112.40	0.42	109.53	4	3.72	Leonardos, 2001
Mar Menor (Spain) ^a	S	M	87.95	0.91	93.37	3	3.85	Andreu-Soler et al., 2003
Mar Menor (Spain) ^a	S	F	90.80	0.81	100.82	3	3.82	Andreu-Soler et al., 2003
Roussillon Leucate Lagoon ^b	S	M	83.74	0.85	81.40	2	3.78	Marfin, 1982
Roussillon Leucate Lagoon ^b	S	F	93.20	0.80	88.38	2	3.84	Marfin, 1982
Roussillon Canet Lagoon ^b	S	M	77.27	0.72	73.26	1	3.63	Marfin, 1982
Roussillon Canet Lagoon ^b	S	F	78.22	0.85	83.73	2	3.72	Marfin, 1982
Roussillon Bourdigou Lagoon ^b	S	M	93.36	0.59	88.38	2	3.71	Marfin, 1982
Roussillon Bourdigou Lagoon ^b	S	F	93.67	0.79	96.52	2	3.84	Marfin, 1982
Atlantic								
Oldbury-upon-Severn – Gloucestershire ^b	LD	M,F	105.97	0.63	101.17	3	3.98	Palmer and Culley, 1983
Aberthaw Lagoon – Bristol Channel ^b	LD	M,F	99.80	0.81	109.31	2	3.97	Creech, 1992
Guadalquivir River Estuary ^c	LD	M,F	89.81	1.19	84.33	2	3.91	Fernandez-Delgado et al., 1988
Bassin d'Arcachon ^b	LD	M,F	135.92	0.50	105.8	2	3.85	Castel et al., 1977

^aThe growth parameters were estimated from FL at age converted to TL according to equation of the present study.

^bThe growth parameters were estimated from SL at age converted to TL according to equation of the present study.

^cThe growth parameters were estimated from FL at age converted to TL according to the equation given by the author.

L_{∞} , asymptotic length; K , growth coefficient; L_{max} , maximum reported length; t_{max} , maximum reported age; ϕ' , growth index; S, scales; LD, length distribution.

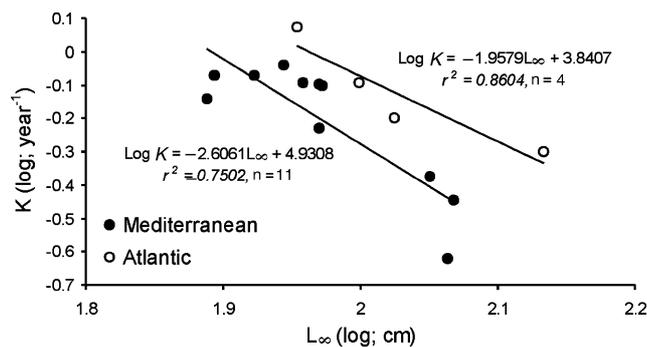


Fig. 4. Auximetric plot of L_{∞} and K for sand smelt from lagoon and estuarine populations of Mediterranean (dark circle) and Atlantic coasts of Europe (open circle) mentioned in Table 2. Equation for each area is given in the graph

indicate occurrence of small-scale reproductive migrations of males and females. It has been shown that females, especially in extreme environmental conditions, have a higher survival rate than males (Leonardos and Sinis, 1999). Many species have developed strategic mechanisms for the protection of female individuals; these mechanisms may be expressed in the form of selective predation of males, with higher survival rates, greater longevity and greater endurance of females to environmental stress (e.g. extreme temperatures, hypoxia, starvation) and higher mortality rates of males during the spawning period (Leonardos and Sinis, 1999).

There is a probability of overwintering mortality. The September length-frequency distribution has a large span, with individuals ranging from 36 to 97 mm. This distribution changes from January onward, with 36–50-mm classes absent from the sample until April. In May the first juveniles of the year again appear in the catchable population. It is thus probable that the smaller and generally later-spawned individuals enter their first winter before being able to store sufficient fat. They thus carry greater risk of starvation, which can lead to increased mortality during the cold winters of

northern Greece. First winter size-dependent sand smelt mortality was reported by Markevich (1977) for the Aral Sea. Markevich (1977) stated that sand smelt cease to feed at temperatures below 8°C. Similarly, Henderson et al. (1988) noted that sand smelt do not grow during the winter and that approximately 47% of an English Channel 0-group late-spawning population died during the winter because they could not store enough energy to survive.

The mean condition factor decreases toward the end of the reproduction period (May); thereafter, sand smelt gradually recover their condition, reaching higher condition factor values during the summer (August) when there is plenty of food available in the lake. After a decrease in September, another smaller increase of condition factor is observed in November which is essential for winter survival. This decreases again during winter (February) because of decreased food intake and low temperature. In general, the observations regarding the sand smelt condition factor in the present study are similar to reports by other authors (Marfin, 1982; Fernandez-Delgado et al., 1988; Andreu-Soler et al., 2003) who reported two peaks during the year. While the allocation of energy to reproduction, growth and stored fat varies among sand smelt populations, seasonality fixes the order within the year in which each of these activities must occur. This is because reproduction must occur near the beginning of the growing season if the young are to develop and lay down sufficient reserves to survive their first winter (Henderson and Bamber, 1987).

It has been shown that sand smelt populations vary greatly in longevity and maximum size attained. These attributes were related to physical factors in the habitat, such as salinity and temperature (Henderson and Bamber, 1987). A comparison with other sand smelt populations shows that age 4+ year old fish reported in the present study are among the oldest in studies of the Mediterranean and Atlantic coasts of Europe. Five age-groups were found only in Trichonis Lake (Leonardos, 2001) which is another recently colonized ecosystem, and in the Black Sea (Markevich, 1977).

The L_{\max} to L_{∞} ratio is an important parameter in the context of life history theory (e.g. Stergiou, 2000). The L_{\max}/L_{∞} ratio for a data set of 74 Hellenic marine fish species ranged between 0.56 and 1.34, with a mean value of 0.90 (Stergiou, 2000). The computed value for sand smelt in the Vistonis estuarine system falls within the reported range and very close to the mean value. Comparison of K and L_{∞} from different lagoon populations in the Mediterranean and the Atlantic coast of Europe, despite differences in methodology and data quality, showed that the growth patterns were different. The auximetric plot revealed that the relationship between $\log K$ and $\log L_{\infty}$ was not significant when values from all studies were used. However, the relationship was significantly negative for the Mediterranean and the Atlantic lagoon populations separately, with slopes close to -2 , which is equal to the value that Pauly et al. (1998) have empirically estimated for a large data set.

A comparison within Greek regions showed that the *A. boyeri* population in the Vistonis estuarine system reached higher back-calculated lengths at each age-class than the populations in Trichonis Lake (Leonardos, 2001) and Mesolongi-Etolikon lagoons (Leonardos and Sinis, 2000). The Vistonis estuarine system sand smelt had a higher growth rate during the first year, achieving a difference of 10 mm compared with same-age individuals in the other two areas. This can be attributed to the fact that the growing season of juveniles coincides with the season of high food availability in the lake and to the low competition of sand smelt juveniles, which feed predominantly on zooplankton (Ferrari and Rossi, 1983). Most of the Mugilidae species (*Liza ramada*, *L. aurata*, *Chelon labrosus*), which are the other abundant fish resources of the estuarine system, end their recruitment in the estuarine population in June–July (Koutrakis et al., 1995). At the range of 20–55 mm (SL) these species have a mixed diet consisting of animal and plant material; thereafter, they become almost exclusively vegetarian (Albertini-Berhaut, 1973).

Higher total mortality (Z) and natural mortality (M) for males suggest that the higher survival rate of females may be due to mechanisms developed for perpetuation of the species. Gulland (1971) suggested that a fish stock is optimally exploited at about $E = 0.5$. Later, Pauly (1987) and Patterson (1992) reported that exploitation rates below 0.4 suggest the tendency toward stock recovery and can be used as a guideline for the sustainable exploitation of small pelagic species, while exploitation rates below 0.3, as is the case of the Vistonis estuarine system sand smelt, suggest that stock size may increase. This rate thus gives very good perspectives of population exploitation, as was verified the following years. Indeed, with no increase in the fishing effort, as individuals are harvested during their migration to the sea, sand smelt catches rose to 178–285 tonnes in subsequent years.

The high degree of sand smelt plasticity allows adaptation of life history responses to variable environmental parameters characteristic of coastal and lagoonal habitats; the sand smelt is thus pre-adapted for the exploitation of novel and vacant niches (Henderson and Bamber, 1987). This is probably the case in the Vistonis estuarine system. During the 1980s, salinity in the southern part of the lake increased due to intrusion of seawater and limited freshwater inflow (Babajimopoulos and Antonopoulos, 1992). As a result, many freshwater species that feed on zooplankton and benthic organisms (e.g. *Alosa vistonica*, *Cyprinus carpio*) moved towards the northern part of the lake, leaving vacant

niches in the southern part. These were probably soon occupied by sand smelt; thus an abundant semi-isolated population was formed, allowing for the first commercial exploitation of this population in 1990. This type of colonization can produce ideal conditions for selection to local conditions and random genetic drift (Henderson and Bamber, 1987), thus it is not surprising that the species displays great variability in morphological and meristic characteristics among different populations (Chrisafi et al., 2001).

In conclusion, sand smelt males in the considered population showed reduced longevity and reached smaller L_{∞} than did females. It appears that the life history tactic of this semi-isolated lagoon population is to 'invest' in females. These life history tactics are common in variable, unstable and/or highly productive environments (Fernandez-Delgado et al., 1988). Therefore, management practices of this localized population should focus on protection of female spawners and on the areas with subtidal filamentous reed, which is used for spawning (Henderson et al., 1988). The study of the marine population of sand smelt in the North Aegean will allow for comparisons between lagoon and marine populations. Moreover, the study of the Vistonis estuarine population, as it is presently exploited, will allow an evaluation of current management practices.

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