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Life history traits of *Scardinius acarnanicus* (Economidis, 1991) (Pisces: Cyprinidae) in two Greek lakes (Lysimachia and Trichonis)

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Summary

Age, growth, reproduction and mortality of *Scardinius acarnanicus*, an endemic cyprinid fish from central and western Greece, were investigated in two contrasting environments, the eutrophic Lake Lysimachia and the oligotrophic to mesotrophic Lake Trichonis. Maximum ages observed were 7+ for males and 10+ for females in Lake Lysimachia and 8+ for males and females in Lake Trichonis. *Scardinius acarnanicus* grew allometrically (slope of fork length–somatic weight regressions >3) and relatively rapidly until age 2 or 3 years, then slowed at a time coincident with maturation. Total instantaneous mortality rates of fish from Lake Trichonis were higher than in Lake Lysimachia. *Scardinius acarnanicus* is a multiple spawner; monthly values of the gonadosomatic index (GSI) indicated that spawning occurred mainly in April. Mean egg diameter in Lake Lysimachia was 1.54 ± 0.2 and 1.28 ± 0.16 mm in Lake Thrichonis. In Lake Lysimachia, the population sex ratio departed markedly from 1 : 1; females were more abundant at ages >3 and the overall male : female ratio was 1 : 1.47. In Lake Trichonis, females were more abundant at ages >6; the overall male : female ratio was 1 : 1.16, not significantly different from a 1 : 1 ratio.

Introduction

Scardinius acarnanicus (Economidis, 1991) (formerly misidentified as *S. erythropthalmus*), locally called 'tseroukla', is an endemic Greek species distributed in the Acheloos River system (Acheloos River and lakes Trichonis, Lysimachia, Ozeros and Amvrakia) (Economidis, 1991; Economou et al., 1994). It is a freshwater fish closely related to the Mediterranean complex of *Scardinius* species. The genus *Scardinius* is represented in Greece by three species, the European species *S. erythrophthalmus* (rudd) and the two endemic species *S. acarnanicus* and *S. graecus* (Economidis, 1991). *Scardinius acarnanicus* has limited economic importance in Greece; consumption is restricted to a few months per year, with a monetary value of about 2.5€ per kg in the local markets.

Scardinius acarnanicus is among the most abundant cyprinids occurring in the lower reach of the Acheloos River and Etoloakarnia lakes. Despite its abundance, knowledge on the life history parameters of the fish is limited. Economidis (1991) described the distribution, Iliadou (1981, 1991) as well as Iliadou and Ondrias (1980) studied the feeding behaviour, age, morphometry and reproduction of a mixed population from lakes Trichonis and Lysimachia. Iliadou and Anderson (1998) as well as Iliadou et al. (1996) studied the morphological differentiation of the genus *Scardinius* in Greece, while Barbieri-Tseliki (1992) studied the reproductive biology in Lake Trichonis. Finally, Economou et al. (1994) reported on the larval ecology and behaviour of *S. acarnanicus* along with 14 other fish species from Lake Trichonis. The minimal amount of published information on this species may be partly because of its restricted distribution and low economic importance.

The aim of this study was to determine age structure, growth rate, mortality and reproduction of *S. acarnanicus* for Lake Lysimachia and Lake Trichonis populations and an attempt was made to compare the life history parameters in relation to the different trophic state of two nearby lakes.

Study area

The natural lakes Lysimachia and Trichonis are located at the western-central part of Greece in the region of Etoloakarnania, both belonging to the Achellos River system. Lake Trichonis (38°15′N, 21°30′E), is the largest (96.9 km^2) and deepest (maximum 58 m and average depth 30.5 m) natural lake in Greece. The physicochemical features and the status of phyto- and zooplankton classify the lake as oligotrophic to mesotrophic (Overbeck et al., 1982; Daoulas and Economidis, 1984). It is a warm monomictic lake, with water temperatures ranging from 10 to 28°C. The mean Secchi disk depth is about 9 m.

Lake Lysimachia (38°33′N, 21°30′E) has a surface area of 13.6 km^2, maximum depth of 9 m and mean depth of 3 m. It is a warm monomictic lake. The mean Secchi disk depth is <1 m. The lake was originally oligotrophic, but is now eutrophic (Petridis, 1993).

A narrow channel allows outflow of clear surface water from Trichonis to Lake Lysimachia, which in turn maintains an open connection to the sea via the Acheloos River. Sewage effluents from the town of Agrinio (population *c.* 80 000) are discharged into the northern part of Lake Lysimachia. Furthermore, the north-western part of the lake receives agricultural run-off from arable land.

Because of hypolimnion springs in Trichonis Lake in addition to hypsometric divergence, there is a water overflow from Trichonis to Lysimachia and, in turn, to the Acheloos River. As of 1961, a dam has prevented fish movements between the two lakes. Lake Trichonis was characterized by 'Project Aqua' (Luther and Rzoska, 1971) as an area of high potential research value because of its endemic diatoms, Chrysophyceae, molluscs and fishes, some of which now face extinction.

Materials and methods

Sampling was carried out every third month from December 1991 to November 1992. A gillnet with a 22 mm (knot to knot) mesh size, 100 m length and 3 m height was used to capture fish. The net was placed in both lakes from dusk until dawn with the aid of local fishermen. During spring and summer, the net was placed near the coast of the lakes; during winter the net was placed in the interior of the lakes. A total of 544 individuals from Lake Lysimachia and 137 individuals from Lake Trichonis were collected. After collection, the fish were transported to the laboratory and frozen until examined.

Fork length (FL) and total length (TL) were measured to the nearest 1 mm. Total weight (TW), and eviscerated (net somatic) weight (NW) were weighed to the nearest 0.1 g. The length–weight relationship was described by the equations: $NW = aFL^b$, $TW = aTL^b$ and $TW = aFL^b$ (NW–FL, TW–TL and TW–FL relationships, respectively), where b and a are parameters. Regressions on log-transformed data were tested for differences in slopes and intercepts between sexes and between lakes by using ANCOVA (Zar, 1999).

Age was determined from scales removed from the left side of the fish, between the posterior end of the pectoral fin and the anterior end of the dorsal fin. Six scales from each fish were cleaned in 4% sodium peroxide, rinsed with distilled water and mounted wet between microscope slides. Distances to marks and overall scale sizes were measured on one representative not regenerated scale along an axis from focus to middle of the anterior field. Marks were recognized by standard criteria (Everhart and Youngs, 1975; Bagenal and Tesch, 1978).

The relationship between FL and scale radius (R) was best described by a linear equation ($FL = (a + b)R$). FL-R regressions were tested for differences in slopes and intercepts between sexes and between lakes by using ANCOVA (Zar, 1999). The back-calculated FLs were estimated using the equation: $FL_n = a + (FL - a)R_n/R$ (where FL_n = length of the fish when annulus 'n' was formed, FL = fork length of the fish when the scale sample was obtained, R_n = radius of annulus 'n'. R = total scale radius, a = intercept of the linear regression relationship between FL and total scale radius) (Bagenal and Tesch, 1978). Mean back-calculated FLs were tested for differences between sexes and lakes using the Mann–Whitney test. To evaluate growth, back-calculated lengths at ages were fitted to the von Bertalanffy model: $L_t = L_\infty[1 - e^{-k(t - t_0)}]$ (Ricker, 1975) by using non-linear regression (Marquardt method) calculated with Fishparm computer software (Saila et al., 1988). As the growth parameters k and L_∞ are inversely correlated, the overall growth performance index $\Phi' = 2 \text{ Log } L_\infty + \text{Log } k$ (phi prime test) was employed to compare growth rates (Munro and Pauly, 1983). Growth was studied from a sample collected at the end of March 1992.

Instantaneous mortality rates (Z) were calculated for the total sampling period separately for males and females in each lake, using the length-converted catch curves (Pauly, 1983). Slopes of the regressions were tested for differences between sexes in each lake and between lakes using ANCOVA (Zar, 1999).

Natural mortality (M) was estimated using the empirical formula of Pauly (1980):

$$\text{Log(M)} = -0.0066 - 0.279\text{Log}(L_\infty) + 0.6543\text{Log}(k) + 0.4634\text{Log}(T)$$

Where, L_∞ and k are the parameters derived from the von Bertalanffy equation, and T is the mean environmental temperature, 17.25°C during this study.

The sex of all specimens was recorded by microscopic examination of the gonads. Maturity stages were determined after applying slight pressure to the abdomen of fish to extract sperm or ova for identification. Examined were 15 ovaries from Lake Trichonis and 20 ovaries from Lake Lysimachia, collected at the end of March 1992.

Absolute fecundity (F) was considered as the mean number of eggs found in the ovaries of all specimens of the species. Relative fecundity indices were calculated as $RF_{NW} = F/NW$ and $RF_{TW} = F/TW$ (where F is the number of eggs, i.e. fecundity and NW and TW are NW and TW, respectively, of each specimen in g). Fecundity was studied using the gravimetric method (Bagenal and Braum, 1978). There were no significant differences (t-test for dependent samples, $P > 0.05$) in the number of eggs or in the diameter of the egg in relation to the position of the eggs in the gonad or between the two ovaries. Therefore, from an ovary sample of each female, all eggs (mature or ripening) were counted. The relationship between the number of eggs and fish body size was expressed by the equation: $\log F = \log a + b \log X$, where F is the number of eggs per specimen, X is the FL or somatic weight of the fish, a is a constant and b is the slope (Bagenal and Braum, 1978; Elliott, 1995). The equations F-X were calculated for each lake separately and the slopes were compared using ANCOVA (Zar, 1999).

To estimate the sex ratio in the populations of each lake, the chi-square goodness-of-fit test (Zar, 1999) was used to compare the proportion of male : female specimens in each age class with the hypothetical 1 : 1 ratio.

Results

Age

The length frequency distribution of 544 fish from Lake Lysimachia and 137 from Lake Trichonis is shown in Fig. 1. Scale readings showed 10 age classes in Lake Lysimachia and 8 age classes in Lake Trichonis. The maximum length observed in Lake Lysimachia was 35.4 cm, corresponding to a 10-year-old female. In Lake Trichonis, the maximum observed length was 31.7 cm, corresponding to an 8-year-old female.

Marginal increment analysis showed that a single annulus was formed during the end of the winter of each year. Scales from fishes collected in February showed that formation of a new annual ring had begun, while April scale samples showed that the annual ring had formed.

Growth

Total length–fork length relationships. The relationships between TL and FL of the fish were calculated for each lake separately, and for males, females and sexes combined (Table 1). TL-FL regression slopes differed significantly between males ($F_{1,259} = 16.21$; $P < 0.001$) and between the two lakes when sexes were combined ($F_{1,617} = 10.32$; $P = 0.001$), whereas no significant differences were found between females ($F_{1,355} = 1.82$; $P = 0.178$) (Table 1).

Length–weight relationship. The relationships between somatic weight (NW) and FL of the fish were calculated separately for each lake and for males, females and sexes combined (Table 2). The slopes of the logarithmic equations indicated the positive allometric nature of growth ($b \geq 3$) in most cases. No statistically significant differences were found between sexes in each lake ($F_{1,259} = 0.589$, $P = 0.271$; $F_{1,355} = 0.214$, $P = 0.640$ for males and females, respectively) or between

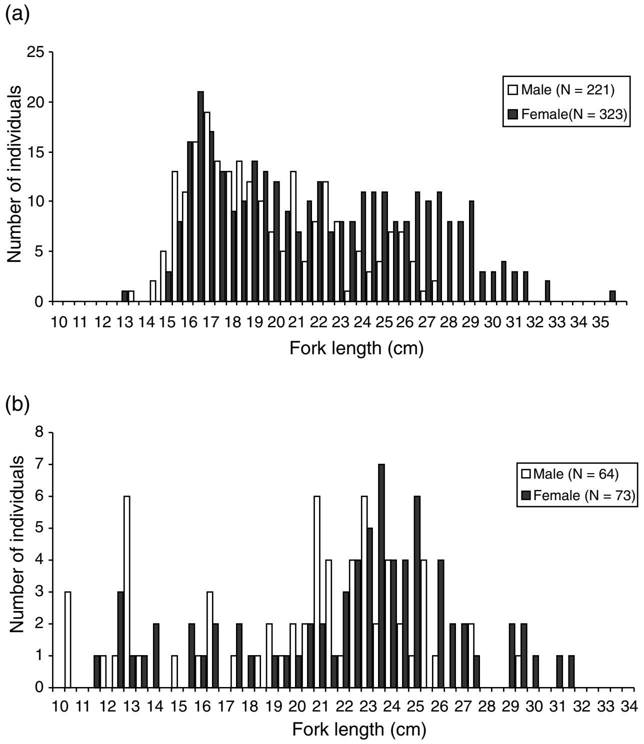

Fig. 1. Length frequency distributions for *Scardinius acarnanicus*: (a) from Lake Lysimachia, (b) from Lake Trichonis

the lakes when the sexes were combined ($F_{1,617}$ = 1.212; P = 0.271) (Table 2). Similar results were found when the relationships, TW–TL and TW–FL were studied.

Fork length–scale radius relationships. Scale radius (R, mm) was linearly related to FL (mm), indicating that scale growth was proportional to fish growth. The regressions of FL on R were estimated for males and females and for sexes combined. The slopes of FL-R regressions differed significantly between females ($F_{1,135}$ = 12.72; P = 0.0005) and between regions ($F_{1,247}$ = 8.02; P = 0.005) when sexes were combined, but no significant differences were found between males in the two lakes ($F_{1,108}$ = 0.701; P = 0.404) (Table 3). This indicates that females from Lake Lysimachia grow faster than those in Lake Trichonis, while males grow at a similar rate in the two lakes.

The mean back-calculated FLs of each age group were smaller than the observed length of the same age group at the time of capture and greater than the observed FL at the time of capture of the previous age group. Differences between back-calculated FLs-at-age and observed FLs are in the range of observed seasonal growth. There were no significant differences in back-calculated FLs between sexes in each lake and between lakes (Mann–Whitney test: P < 0.05). In Lake Lysimachia, the fish attained almost 26.8% of their maximum adult size during the first year and a sharp decline in growth was observed during the second year (13.4%) (Table 4). In Lake Trichonis, during the first year the fish reached 31.1% of their maximum adult size, 12.4% in the second year, 11.0% in the third, and 9.5% in the fourth year (Table 4).

The parameters of the von Bertalanffy growth equation were computed by using back-calculated FLs to the most recent annuli, to reduce bias in asymptotic length and growth coefficient k due to the presence of Lee's phenomenon (Table 5). Values of asymptotic FL (L_∞), growth coefficient (k), such as the overall growth performance index Φ', did not differ between sexes and between lakes.

Table 1
Relationship parameters of total length (TL) : fork length (FL) of *Scardinius acarnanicus* from lakes Lysimachia and Trichonis

Lake	Sex	Equation	95% CI of b	N	R^2	P-value
Lysimachia	Male	TL = 0.830 + 1.076 FL	1.064–1.087	194	0.99	< 0.001
	Female	TL = 0.621 + 1.087 FL	1.079–1.094	291	0.99	< 0.001
	Total	TL = 0.663 + 1.085 FL	1.079–1.091	485	0.99	< 0.001
Trichonis	Male	TL = 0.155 + 1.112 FL	1.099–1.126	68	0.99	< 0.001
	Female	TL = 0.397 + 1.098 FL	1.086–1.110	67	0.99	< 0.001
	Total	TL = 0.306 + 1.104 FL	1.095–1.113	135	0.99	< 0.001

Table 2
Relationship parameters between net somatic weight (NW) : fork length (FL), total weight (TW) : total length (TL) and total weight (TW) : fork length (FL) of *Scardinius acarnanicus* from lakes Lysimachia and Trichonis

Lake	Sex	Equation: NW = aFL^b	95% CI of b	N	R^2	P-value
Lysimachia	Male	NW = 0.0078 FL$^{3.20}$	3.14–3.25	194	0.99	< 0.001
		TW = 0.0036 TL$^{3.36}$	3.20–3.52	194	0.90	< 0.001
		ÔW = 0.0073 FL$^{3.27}$	3.11–3.42	194	0.90	< 0.001
	Female	NW = 0.0065 FL$^{3.25}$	3.21–3.28	291	0.99	< 0.001
		TW = 0.0041 TL$^{3.33}$	3.28–3.37	291	0.98	< 0.001
		TW = 0.0075 FL$^{3.26}$	3.21–3.30	291	0.98	< 0.001
	Total	NW = 0.0071 FL$^{3.22}$	3.19–3.25	485	0.99	< 0.001
		TW = 0.0039 TL$^{3.34}$	3.28–3.40	485	0.96	< 0.001
		TW = 0.0073 FL$^{3.26}$	3.20–3.32	485	0.96	< 0.001
Trichonis	Male	NW = 0.0069 FL$^{3.23}$	3.17–3.29	68	0.99	< 0.001
		TW = 0.0049 TL$^{3.26}$	3.18–3.34	68	0.99	< 0.001
		TW = 0.0049 FL$^{3.26}$	3.18–3.34	68	0.99	< 0.001
	Female	NW = 0.0063 FL$^{3.26}$	3.19–3.34	67	0.99	< 0.001
		TW = 0.0041 TL$^{3.33}$	3.24–3.43	67	0.98	< 0.001
		TW = 0.0041 FL$^{3.33}$	3.24–3.43	67	0.98	< 0.001
	Total	NW = 0.0066 FL$^{3.25}$	3.20–3.29	135	0.99	< 0.001
		TW = 0.0043 TL$^{3.31}$	3.25–3.37	135	0.99	< 0.001
		TW = 0.0044 FL$^{3.31}$	3.25–3.37	135	0.99	< 0.001

Table 3
Relationship parameters of fork length (FL) and scale radius (SR) of *Scardinius acarnanicus* from lakes Lysimachia and Trichonis

Lake	Sex	Equation	95% CI of b	N	R^2	P-value
Lysimachia	Male	FL = 5.415 + 0.251 SR	0.230–0.271	67	0.91	< 0.001
	Female	FL = 5.233 + 0.254 SR	0.243–0.263	78	0.97	< 0.001
	Total	FL = 5.287 + 0.254 SR	0.244–0.263	145	0.96	< 0.001
Trichonis	Male	FL = 5.452 + 0.261 SR	0.247–0.275	45	0.97	< 0.001
	Female	FL = 7.341 + 0.224 SR	0.210–0.237	61	0.95	< 0.001
	Total	FL = 6.710 + 0.235 SR	0.225–0.244	106	0.96	< 0.001

Table 4
Back-calculated fork lengths (cm) at age for *Scardinius acarnanicus* from lakes Lysimachia and Trichonis

	Age (years)												
Age (years)	MFLC	SD	N	1	2	3	4	5	6	7	8	9	10
Lake Lysimachia													
0													
1				8.46									
2	15.19	0.18	13	8.43	12.72								
3	17.67	0.12	80	8.41	12.68	16.33							
4	20.81	0.24	18	8.49	12.58	16.20	19.49						
5	23.80	0.29	6	8.57	12.73	16.56	19.84	22.71					
6	25.97	0.21	10	8.45	12.36	16.20	19.36	22.20	24.68				
7	28.35	0.19	10	8.27	12.40	16.22	19.40	22.16	24.61	26.89			
8	29.83	0.17	3	8.35	12.84	16.01	18.92	21.57	24.20	26.50	28.88		
9	31.40	0.15	3	8.39	12.27	15.81	18.93	21.79	24.23	26.42	28.61	30.55	
10	31.90		1	8.63	12.51	16.13	19.23	22.08	24.66	26.47	28.28	29.83	31.38
Weighted mean				8.42	12.62	16.28	19.41	22.18	24.55	26.71	28.68	30.37	31.38
SD				0.043	0.067	0.070	0.124	0.162	0.177	0.266	0289	0.182	
Annual increment				8.42	4.20	3.67	3.20	2.81	2.49	2.24	2.22	1.84	1.55
Annual increment (%)				26.83	13.38	11.69	10.20	8.95	7.93	7.14	7.07	5.86	0.95
N			144	144	144	131	51	33	27	17	7	4	1
Lake Trichonis													
0													
1	11.34	0.38	5	9.15									
2	13.31	0.17	16	9.14	12.82								
3	17.84	0.35	18	9.48	13.19	16.58							
4	21.64	0.18	20	9.72	13.86	17.46	20.31						
5	23.62	0.14	24	9.83	13.84	17.22	20.09	22.59					
6	25.50	0.22	10	9.79	13.20	16.21	19.23	21.85	24.29				
7	27.70	0.26	4	9.47	12.87	16.27	19.38	22.15	24.53	26.68			
8	29.60	0.23	3	9.10	12.92	16.67	19.70	22.26	24.65	26.73	28.65		
9	30.50	0.10	2	9.49	13.19	15.96	18.61	21.04	23.57	25.99	28.18		
10	31.67	0.33	3	9.75	13.03	16.22	19.12	21.72	23.88	25.81	27.59		
Weighted mean				9.56	13.40	16.89	19.88	22.24	24.26	26.36	28.14		
SD				0.051	0.084	0.112	0.105	0.150	0.110	0.168	0.241		
Annual increment				9.56	3.81	3.38	2.91	2.55	2.39	2.12	1.94		
Annual increment (%)				31.14	12.41	11.01	9.48	8.30	7.79	6.91	6.32		
N			105	105	100	84	66	46	22	12	8		

MFLC, mean fork length (cm) at capture; SD, standard error of MFLC; N, number of fish.

Table 5
von Bertalanffy growth parameters of *Scardinius acarnanicus* from lakes Lysimachia and Trichonis

Lake	Sex	L_∞ (95% CI)	k (95% CI)	t_0 (95% CI)	R^2	Φ'
Lysimachia	Male	40.72 (39.51–40.86)	0.139 (0.13–0.15)	−0.69 (−0.64 to 0.75)	0.99	2.36
	Female	41.06 (40.47–41.65)	0.137 (0.13–0.14	−0.66 (−0.61 to −0.70)	0.99	2.36
	Total	41.07 (40.51–41.63)	0.137 (0.13–0.14)	−0.67 (−0.72 to −0.63)	0.99	2.36
Trichonis	Male	42.84 (38.89–46.80)	0.125 (0.10–0.15)	−0.84 (−1.04 to −0.64)	0.98	2.36
	Female	39.65 (39.15–40.15)	0.134 (0.13–0.14)	−1.18 (−1.23 to −1.13)	0.98	2.32
	Total	39.10 (38.53–39.67)	0.140 (0.09–0.19)	−0.99 (−1.05 to −0.93)	0.98	2.33

Lake	Sex	Ln(N/dt) = a − Zt	Z	95% CI of Z	N	R^2	P-value
Lysimachia	Male	Ln(N/dt) = 6.48 − 0.60t	0.60	0.40–0.80	22	0.81	< 0.001
	Female	Ln(N/dt) = 5.73 − 0.34t	0.34	0.27–0.42	26	0.78	< 0.001
	Total	Ln (N/dt) = 7.05 − 0.51t	0.51	0.46–0.56	33	0.96	< 0.001
Trichonis	Male	Ln(N/dt) = 9.55 − 1.25t	1.25	0.92–1.25	17	0.90	< 0.001
	Female	Ln(N/dt) = 7.13 − 0.74t	0.74	0.48–1.01	15	0.74	< 0.001
	Total	Ln(N/dt) = 7.98 − 0.80t	0.80	0.61–0.98	17	0.92	< 0.001

Table 6
Regressions estimated for length converted catch curves for *Scardinius. acarnanicus* from lakes Lysimachia and Trichonis

Mortality

The fishing net was capable of catching specimens with a TL > 10.5 cm. This TL corresponds to specimens older than 1 year (Table 4). The slopes of the regressions differed significantly between males ($F_{1,35}$ = 4.08; P = 0.0051), females ($F_{1,37}$ = 14.54; P = 0.0004) and lakes when the sexes were combined ($F_{1,46}$ = 10.87; P = 0.001) (Table 6). The instantaneous total mortality rates from Lake Trichonis were higher than those from Lake Lysimachia, as there is no exploitation in Lake Lysimachia, Z = M. In Lake Trichonis, the natural mortality (M) was found to be 0.40 year^{-1}. The calculation of fishing mortality gave F = 0.40 year^{-1}.

Reproduction

Following the study of the gonadosomatic index (GSI), the macroscopical and histological examination of gonads showed that *S. acarnanicus* is a multiple spawner. The reproductive effort (GSI) profile and histological studies of the ovaries indicate that *S. acarnanicus* reproduction is extended and lasts from March to June, peaking in mid-April.

The slopes of the equations for fecundity (F) – FL and fecundity (F) – body weight (NW) did not differ statistically between lakes ($F_{1,31}$ = 0.959, P = 0.335; $F_{1,31}$ = 0.266, P = 0.609 for the relationships F-FL and F-NW respectively) (Table 7). The maximum absolute fecundity for Lake Lysimachia was 99 000 eggs in a female of 668.0 g NW, whereas for Lake Trichonis was 47 000 eggs in a female of 191.9 g TW.

Relative fecundity for Lake Lysimachia was RF_{NW} = 143.9 ± 33.1 eggs g^{-1} and RF_{TW} = 113.4 ± 21.7 eggs g^{-1}; relative fecundity for Lake Trichonis was RF_{NW} = 161.34 ± 51.9 eggs g^{-1} and RF_{TW} = 124.8 ± 33.5 eggs g^{-1}.

Eggs were spherical and yellowish with a homogenous yolk mass and thin perivitelline space. Mean egg diameter (95% CI) was 1.54 ± 0.2 mm (n = 20) in Lake Lysimachia and 1.28 ± 0.16 mm (n = 15) in Lake Trichonis. In Lake Lysimachia, the mean egg diameter was negatively correlated with fish size (FL or body weight), but in Lake Trichonis there was no correlation between egg diameter and fish size.

Sex ratio

Overall sex ratio for *S. acarnanicus* collected in this study was 193 males : 283 females, or 1 : 1.47 in Lake Lysimachia. A chi-square test of the sex ratio indicated statistically significant

Lake	Equation	95% CI of b	N	R^2	P-value
Relationship between fecundity (F) and fork length (FL) (cm)					
Lysimachia	$F = 0.121\ FL^{3.80}$	3.28–4.33	20	0.92	< 0.001
Trichonis	$F = 1.081\ FL^{3.22}$	1.92–4.50	15	0.69	< 0.001
Relationship between fecundity (F) and body weight (NW) (g)					
Lysimachia	$F = 0.56 \times 10^2\ NW^{1.31}$	0.95–1.31	20	0.91	< 0.001
Trichonis	$F = 0.12 \times 10^3\ NW^{1.01}$	0.69–1.32	15	0.78	< 0.001

Table 7
Relationship between fecundity (F) and fish size (fork length and body weight) of *Scardinius acarnanicus* from lakes Lysimachia and Trichonis

	Lake Lysimachia				Lake Trichonis			
Age	Male	Female	♂ : ♀	χ^2-value	Male	Female	♂ : ♀	χ^2-value
1+					3	0		3.00
2+	21	11	1 : 0.52	3.13	9	8	1 : 0.89	0.06
3+	76	87	1 : 1.14	0.74	8	9	1 : 1.25	0.06
4+	41	61	1 : 1.49	3.92	20	12	1 : 0.60	2.00
5+	27	50	1 : 1.85	6.87*	16	24	1 : 1.50	1.60
6+	25	28	1 : 1.12	0.17	5	13	1 : 2.60	3.56
7+	3	19	1 : 6.30	11.64**	2	5	1 : 2.50	1.29
8+	0	17			1	2	1 : 2.00	0.33
9+	0	7						
10+	0	3	1 : 5.00					
Total	193	283	1 : 1.47	17.02**	64	73	1 : 1.16	0.59

*P < 0.05, **P < 0.001.

Table 8
Sex ratio of *Scardinius acarnanicus* caught in lakes Lysimachia and Trichonis by age class and chi-square values of tests for a 1 : 1 ratio

deviations from 1 : 1 ($\chi^2 = 17.02$; $P < 0.001$). In Lake Trichonis, the overall sex ratio was 64 males : 73 females, or 1 : 1.16, which was not statistically different from 1 : 1 ($\chi^2 = 0.59$; $P = 0.79$) (Table 8). Of the fish exceeding 25 cm in both lakes, more than 70% were females, with the proportion of males gradually decreasing with increasing FL. Thus, sex ratio changed markedly according to fish length. A chi-square test of sex ratios for *S. acarnanicus* divided into age classes showed that females dominated the upper age classes.

Discussion

Scardinius acarnanicus is a relatively long-lived species. In Lake Lysimachia, the oldest female was estimated to be 10+ and the oldest male 7+ years of age. In Lake Trichonis, the oldest female and the oldest male were both 8+ years old. The only available data on age structure of *S. acarnanicus* came from Iliadou (1981), who studied a mixed population from lakes Lysimachia and Trichonis and estimated that the fish reach an age of 7 years. In this study, most individuals from the population of Lake Lysimachia were 3 and 4 years old, whereas in Lake Trichonis most individuals were 4 and 5 years old. In accordance with the above, Iliadou (1981) found that most individuals in a mixed population from lakes Lysimachia and Trichonis were 3 and 4 years old. In this study, the age structure pattern of *S. acarnanicus* shows more age classes of females than males in eutrophic Lake Lysimachia. Annuli form on the scales of *S. acarnanicus* from late February to April. It seems that annulus formation on the fish scales occurred before the period of increased water temperature and, for mature fish, this period coincides with the initiation of the spawning period.

The exponents of FL–somatic weight relationships (Table 2) showed that growth is positively allometric, which indicates a proportionally better weight gain in relation to growth in length. The length–weight relationships between and within lakes did not differ significantly. A similar growth pattern has been reported for Lake Trichonis by Economou et al. (1999), who studied the relationship between TL and somatic weight ($b = 3.07$ for males, $b = 3.20$ for females and 3.14 for sexes combined).

Back-calculated lengths-at-age for *S. acarnanicus* were consistently less than observed lengths-at-age for all age groups, which may be attributed to Lee's phenomenon (Ricker, 1975). As *S. acarnanicus* are not harvested commercially or recreationally in Lake Lysimachia, the presence of Lee's phenomenon in the back-calculation estimates may be due to higher mortality of larger individuals within an age class. In Lake Trichonis, where the fish population is exploited, the principal cause of Lee's phenomenon is that faster-growing fish of a year-class become vulnerable first, considering that the maximum catching power of the nets is for the largest fish. There is often a problem of underestimating age because of lost annual rings in large individuals or ignoring such cases by treating them as outliers. Such errors were avoided, as the results of age estimation from scales were validated using some otoliths from large individuals.

Von Bertalanffy growth curves fitted the data very well, as shown by the coefficient of determination ($R^2 = 0.99$ for Lake Lysimachia and $R^2 = 0.98$ for Lake Trichonis). Values for asymptotic lengths for both lakes agreed well with observed lengths. The largest specimens collected during this study were 35.4 and 31.7 cm and the calculated L_∞ were 41.06 and 42.84 cm for lakes Lysimachia and Trichonis, respectively. According to Economou et al. (1999), the largest specimen collected in Lake Trichonis had a 41.0 cm TL. These results are acceptable because asymptotic length is a regression estimate, and thus is an average that represents an average maximum length if fish live and grow according to the von Bertalanffy equation.

The fact that mortality was higher in Lake Trichonis than in Lake Lysimachia (Table 6) could be explained from the fishery status prevailing in the area. People avoid consuming fish caught in Lake Lysimachia because the lake is reported to be polluted; preference is for fish from Lake Trichonis. Consequently, fishing pressure is mainly on Lake Trichonis, and the above reflects the total instantaneous mortality rate as well as the population structure (Table 1). Natural mortality (M) for both sexes in Lake Trichonis was found to be equal to the fishing mortality (F) = 0.4 years^{-1}.

Prior to spawning, ovaries showed a bimodal distribution in the size of eggs, one with immature and the other with mature oocytes. During this study, two batches of eggs per female at least were detected. Batch spawning is undoubtedly an advantage for *S. acarnanicus*, which live in unstable and changing environments such as eutrophic lakes. It increases individual fecundity and overcomes the constraints on fecundity imposed by the volume of the abdominal cavity. Progeny are not at risk in just one reproductive event where an environmental catastrophe could destroy the entire spawning (Miller, 1979).

Fecundity of *S. acarnanicus* was positively correlated to fish size (length or weight). In fish, fecundity generally increases with fish size. Larger females may be considered as a life history strategy for supporting increased egg production. Maximum fecundity estimated (99 000 eggs in Lake Lysimachia and 47 000 in Lake Trichonis) was near the values found by Iliadou (1981) (70 000 eggs) in a mixed population from lakes Trichonis and Lysimachia. No significant differences were found for the relationships between fecundity-body size in relation to the lake. This indicates that fishes would give the same number of eggs per fish size (length or weight) in each lake.

The egg sizes did not differ significantly between the two lakes despite the fact that fishes from Lake Lysimachia were significantly larger than those from Lake Trichonis. In our study, the mean egg diameter in Lake Lysimachia was 1.54 ± 0.02, and 1.28 ± 0.16 mm in Lake Trichonis. Barbieri-Tseliki (1992) found that the mean egg diameter in Lake Trichonis was 1.4 ± 0.16 mm, and Iliadou (1981) reported that the largest diameter of the oocytes of a mixed population from lakes Trichonis and Lysimachia was 1.6 mm.

During this study, females predominated (1 : 1.45 and 1 : 1.16 males to females) in both lakes (significant in Lysimachia, non-significant in Trichonis). Females were dominant in all age groups, and the magnitude of dominance varied with increasing age (Table 6). The strategy of *S. acarnanicus*, in terms of the sex ratio, is the 'investment' in females. This strategy is characteristic of species from unstable and variable environments (Slobodkin and Rapoport, 1974; Ware, 1984; Leonardos and Sinis, 1998).

The differences obtained in age composition and mortality rates between the two populations could be explained on the basis of the different exploitation pattern (Lake Trichonis exploited, Lake Lysimachia unexploited), which affects the population structure of *S. acarnanicus*. In this sense, several environmental conditions such as primary production, water temperature, eutrophication, pollution and unstable and unpredictable conditions, especially in Lake Lysimachia, seem not to affect significantly the life history parameters of *S. acarnanicus*.

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