

On the life-history of *Barbus peloponnesius* and *Barbus cyclolepis* in Macedonia, Greece

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A b s t r a c t. Life-history parameters of *Barbus peloponnesius* and *Barbus cyclolepis* were studied in two streams in Macedonia, Greece. In *B. peloponnesius* age ranged from 0+ to 4+ in males and 0+ to 9+ in females, while in *B. cyclolepis* from 0+ to 5+ in males and 0+ to 9+ in females. In both species, after the first year of life, females exhibited longer mean lengths at age and greater maximum length than the males, while between species *B. cyclolepis* showed greater mean lengths at age and greater maximum length than *B. peloponnesius*. Total mortality rates were higher in the males of each species than in females. Significant difference in the sex ratio was found only for *B. cyclolepis* and this species population was male dominated. Gonad maturation began at the age of 1+ in males and 3+ in females of both species. Both species exhibited a protracted multi-spawning season, which started at the end of March-beginning of April and lasted until mid July. Despite differences in growth and body size, the two species are characterized by similar life-history styles: (1) similar age structure, (2) early maturation and same age at maturity, (3) males have a shorter life span, higher rate of mortality, decreased growth and smaller body size and mature earlier than the females and (4) elongated multi-spawning season, which shows a high investment in reproduction. The life-history style of the two stocks seems to be in concordance with the environmental conditions of their habitats, which are typical of the fluctuating Mediterranean streams.

Key words: *Barbus peloponnesius*, *Barbus cyclolepis*, life-history parameters, population structure, growth, mortality, reproduction

Introduction

The study of life-history styles of fish species is essential to the analysis of population performance and so to both theoretical ecology and fisheries management (Wine Miller & Rose 1992). Life-history theory deals with constraints among demographic variables and traits associated with reproduction and the way these constraints, or trade-offs, form strategies in order to maximize fitness in different kinds of environment (Adams 1980, Wootton 1990, Roff 1992, Stearns 1992, Wine Miller & Rose 1992).

Mediterranean rivers and streams are considered as highly variable ecosystems because of variations in water flow, water temperature and resource availability throughout the year and, as many authors have pointed out, environmental variability influences most of the life-history parameters of fish inhabiting these rivers and streams (Wootton 1984, Bruton 1989, Herrera & Fernandez-Delgado 1994, Fernandez-Delgado & Herrera 1995, Encina & Granado-Lorenzo 1997, Aparicio & Sostoa 1999).

Based on the life-history theory (e.g. Adams 1980, Wootton 1984, Roff 1992, Pauly 1998), one may predict that the fish populations inhabiting the fluctuating Greek streams will generally have small body size, mature at an early age, have a high investment in reproduction and probably suffer from high adult mortality.

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In this paper, life-history parameters were studied and compared between two species (*Barbus peloponnesius* Valenciennes, 1842 and *Barbus cyclolepis* Heckel, 1837), in an attempt to find differences and similarities in the strategies that the two species follow during their life cycle in two streams in Macedonia (Greece), with hydrological regimes typical of the Mediterranean streams. The geographical distribution of these two species in Greece is of particular interest (Fig. 1a). Axios River acts as a barrier, with *B. peloponnesius* present in its left (western) tributaries and *B. cyclolepis* in its right (eastern) tributaries (Economidis & Voyadjis 1985). The coexistence of these two species in the same river has never been recorded (Economidis 1989). Despite the wide distribution of the two species, there are only a few data on the life-history of *B. peloponnesius* (Šorić & Janković 1989, Šorić 1992, Lenhardt et al. 1996) and *B. cyclolepis* (Neophitou 1987, Dikov & Zhivkov 1985) and the only available information concerns basic biological traits.

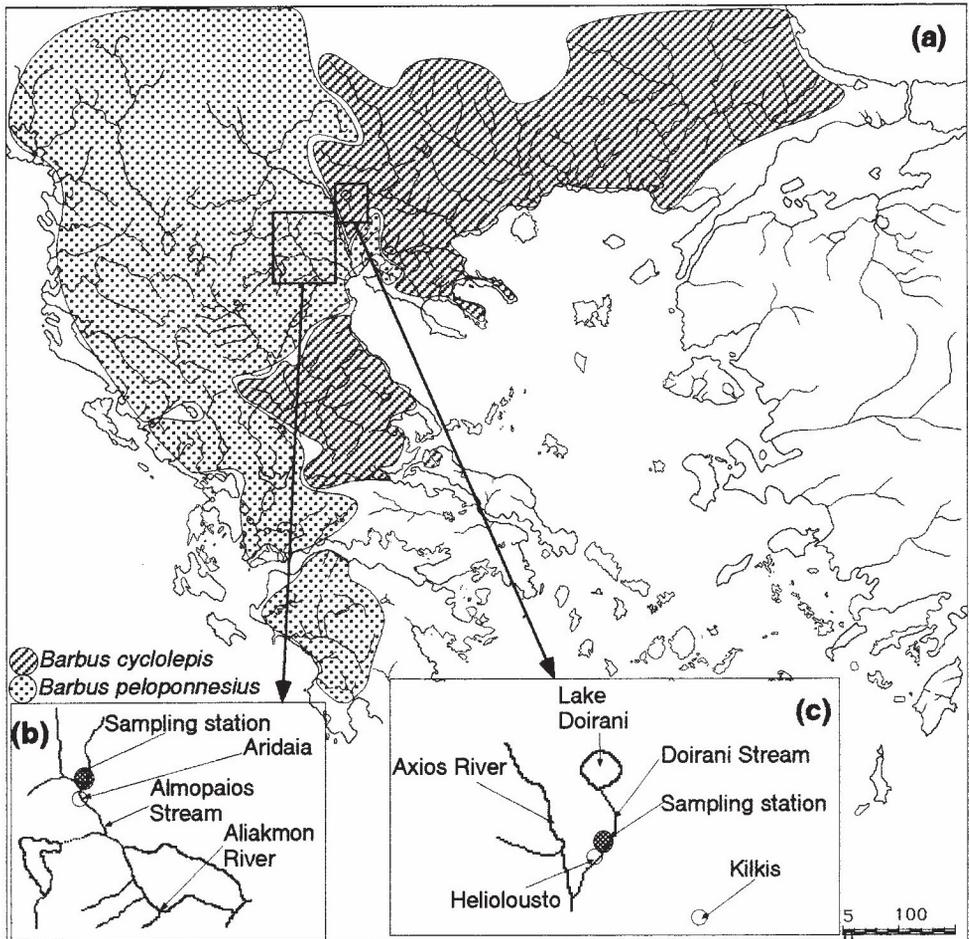


Fig. 1. (a) Distribution of *Barbus peloponnesius* and *Barbus cyclolepis* in Greece, (b) Almopaios Stream and sampling station and (c) Doirani Stream and sampling station.

Study Area

This study was carried out in Almopaios Stream and Doirani Stream, characteristic habitats for the rheophilic species *B. peloponnesius* and *B. cyclolepis*, respectively. Almopaios Stream is a tributary of the Aliakmon-Loudias River basin. The sampling station was located outside the town of Aridaia (Fig. 1b) and the depth in this section of the stream was 30–150cm. During the study period (March 1998–February 1999) the water temperature fluctuated between 9.3 °C (December) and 23 °C (July), with a mean value of 14.6 °C. Doirani Stream flows between Lake Doirani and Axios River and is considered as a tributary of the Axios River basin. The sampling station was located near the village of Heliolousto (Fig. 1c) and the depth in this section of the stream was 20–100 cm. The minimum, maximum and mean water temperature were 7.9 °C (January), 25.4 °C (July) and 15.5 °C, respectively. The hydrological cycle of the two streams is typical of the Mediterranean area, with the water flow decreasing dramatically during the summer. Especially in Doirani Stream, the flow of water almost ceases in the summer and the stream consists mainly of small pools.

Material and Methods

Specimens were electrofished monthly (in the second half of each month) between March 1998 and February 1999. The standard (*Sl*, in mm), fork (*Fl*, in mm) and total length (*Tl*, in mm) and the total (TW, in g), gonad (GW, in g) and somatic weight (SW, in g) and sex were recorded for each fish. SW was the weight of the fish after the removal of the gut and the gonad. Ages of both species were determined using scales from the left side of the body, between the lateral line and the dorsal fin. Length at age was back-calculated using the relationship between total length (*Tl*, in mm) and scale radius (SR, in micrometer units). The best fit between *Tl* and SR was exponential in both species (Table 1), so lengths at the time of annulus formation were back-calculated using Monastyrsky's equation (Francis 1990):

$$Tl_i / Tl = (R_i / R)^b$$

where Tl_i is the total length at the time of the formation of the i th annulus, Tl the total length of the fish at the time of capture, R_i the radius from the nucleus to the i th annulus, R the radius from the nucleus to the edge of the scale and b the constant derived from the Tl -SR relationship. Back-calculated lengths at age were used to calculate the von Bertalanffy growth parameters, using the non linear fitting routine of FISAT (Gaynilo et al. 1996). Growth has been described using the von Bertalanffy (1938) growth equation:

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

where L_t (in mm) is the length of fish at age t , L_∞ (in mm) is the asymptotic length, K (in yr^{-1}) is the growth coefficient and t_0 (in yr) represents the age a fish would have at zero length. Because neither K nor L_∞ have the dimensions of growth, the growth index $\phi' = \text{Log}K + 2\text{Log}L_\infty$ (L_∞ in cm, K in yr^{-1}) (Munro & Pauly 1983, Pauly & Munro 1984) was used to compare within- and between-species overall growth performances.

The condition factor (RW) was calculated using the formula (Wege & Anderson 1978):

$$RW=100 SW/SW_s$$

where SW (in g) is the observed somatic weight and SW_s (in g) the weight estimated from the SW- TL relationship.

Total mortality (Z) was calculated using the length-converted catch curve (Paily 1983, 1984a,b).

Gonad development was studied using the gonadosomatic index (GSI):

$$GSI=100 GW/SW$$

where GW (in g) is the gonad weight and SW (in g) the somatic weight. In addition, histological examination of the ovaries was conducted and oocyte size-frequency distributions were determined from histological sections, in order to provide precise assessment of the reproductive period.

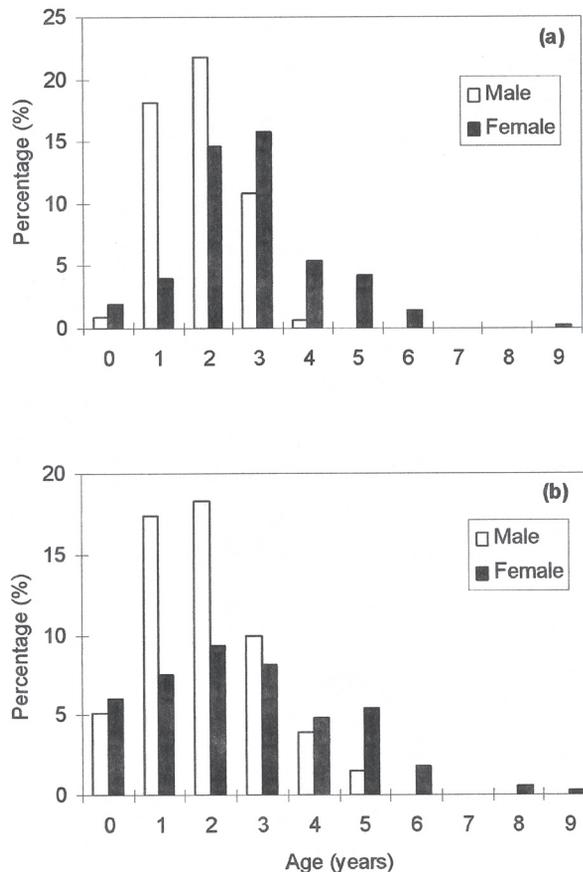


Fig. 2. Age-frequency distribution of male and female (a) *Barbus peloponnesius*, Almopaios Stream and (b) *Barbus cyclolepis*, Doirani Stream, March 1998-February 1999.

Results

Population structure, sex ratio and morphometrics

In *B. peloponnesius* age ranged from 0+ to 4+ in males and 0+ to 9+ in females, although female individuals older than 5+ were rare (Fig. 2a). The maximum *Tl* observed in males was 121 mm, in one 4+ specimen and in females 198 mm, in one 9+ individual. The sex ratio was 1.09 males : 1 female and did not differ significantly from unity ($\chi^2=0.94$, $P>0.05$).

In *B. cyclolepis* six age groups (0+ to 5+) in males and ten (0+ to 9+) in females were detected and again females older than 5+ were scarce (Fig. 2b). The maximum *Tl* observed were 163 mm in males, in one 5+ male and 244 mm in females, in one 9+ female. The population of *B. cyclolepis* was male dominated with a sex ratio of 1.28 males : 1 female, differing significantly from unity ($\chi^2=5.04$, $P<0.05$).

Morphometric relationships between *Tl-Sl*, *Tl-Fl*, *Tl-SR*, *SW-Tl* and *TW-Tl*, are summarized in Table 1. In *B. peloponnesius* significant differences between sexes were found in the *Tl-SR* relationship (ANCOVA, $F=14.23$ $P<0.05$), while in *B. cyclolepis* in the *Tl-Fl* relationship (ANCOVA, $F=6.67$ $P<0.05$). Between the two species, differences were found: (a) between males in the *Tl-Sl* and *Tl-Fl* relationship (ANCOVA, $F=6.29$, 13.55 respectively, for both cases $P<0.05$), (b) between females in the *Tl-SR*, *SW-Tl* and *TW-Tl* relationship (ANCOVA, $F=6.61$, 7.08, 4.24 respectively, for all cases $P<0.05$) and (c) finally between the total number of specimens (males+females+unsexed) in the *Tl-Sl*, *Tl-Fl* and *Tl-SR* relationship (ANCOVA, $F=8.18$, 9.80, 4.42 respectively, for all cases $P<0.05$).

Table 1. Morphometric relationships for *Barbus peloponnesius*, Almopaios Stream and *Barbus cyclolepis*, Doirani Stream, March 1998-February 1999. n, number of fish; r^2 , coefficient of determination. For all regressions $P<0.001$. For other symbols see Materials and Methods.

	<i>B. peloponnesius</i>			<i>B. cyclolepis</i>		
	Relationship	n	r^2	Relationship	n	r^2
males	$Tl = 6.448 + 1.180 Sl$	240	0.984	$Tl = 4.288 + 1.216 Sl$	187	0.988
	$Tl = 2.016 + 1.059 Fl$	240	0.994	$Tl = 0.215 + 1.088 Fl$	187	0.995
	$Tl = 14.599 SR^{0.584}$	222	0.796	$Tl = 17.787 SR^{0.594}$	187	0.871
	$SW = 9.660 * 10^{-6} Tl^{3.016}$	240	0.977	$SW = 8.539 * 10^{-6} Tl^{3.034}$	187	0.989
	$TW = 12.580 * 10^{-6} Tl^{2.989}$	240	0.967	$TW = 10.739 * 10^{-6} Tl^{3.015}$	187	0.983
females	$Tl = 6.634 + 1.179 Sl$	234	0.989	$Tl = 5.376 + 1.199 Sl$	163	0.994
	$Tl = 1.637 + 1.063 Fl$	234	0.997	$Tl = 1.398 + 1.071 Fl$	163	0.998
	$Tl = 10.787 SR^{0.691}$	202	0.864	$Tl = 16.798 SR^{0.626}$	146	0.918
	$SW = 11.379 * 10^{-6} Tl^{2.985}$	234	0.986	$SW = 7.391 * 10^{-6} Tl^{3.066}$	163	0.993
	$TW = 12.124 * 10^{-6} Tl^{3.002}$	234	0.983	$TW = 8.302 * 10^{-6} Tl^{3.071}$	163	0.992
males +	$Tl = 6.248 + 1.183 Sl$	483	0.991	$Tl = 5.161 + 1.203 Sl$	355	0.993
females +	$Tl = 1.626 + 1.063 Fl$	483	0.997	$Tl = 1.215 + 1.075 Fl$	355	0.997
unsexed	$Tl = 11.736 SR^{0.661}$	430	0.872	$Tl = 16.434 SR^{0.626}$	338	0.909
	$SW = 9.583 * 10^{-6} Tl^{3.020}$	483	0.988	$SW = 7.681 * 10^{-6} Tl^{3.057}$	355	0.993
	$TW = 10.784 * 10^{-6} Tl^{3.025}$	483	0.984	$TW = 9.129 * 10^{-6} Tl^{3.051}$	355	0.990

Table 2. Mean back-calculated total lengths (*TL*, mm) at age for *Barbus peloponnesius*, Almopaios Stream, March 1998-February 1999. n, number of fish; 95%C.I., 95% confidence intervals.

Age (yr)	n	Mean <i>TL</i> at capture	Mean back-calculated <i>TL</i> at age								
			1	2	3	4	5	6	7	8	9
males											
0+	4	57.00									
1+	77	74.81	56.06								
2+	92	93.00	57.33	79.29							
3+	46	108.54	58.28	80.86	97.34						
4+	3	114.66	52.86	76.94	93.75	105.85					
Total	222		218	141	49	3					
Mean			57.02	79.75	97.12	105.85					
95% C.I.			56.28-	78.58-	95.28-	91.09-					
			57.77	80.94	98.97	120.61					
Annual increment			57.02	22.73	7.36	8.72					
females											
0+	8	57.00									
1+	17	71.00	50.74								
2+	62	98.48	52.96	80.42							
3+	67	119.32	55.50	82.58	102.97						
4+	23	137.73	55.98	83.94	104.66	122.54					
5+	18	155.83	57.64	86.06	107.29	126.19	141.69				
6+	6	163.50	58.22	85.90	107.77	125.85	140.12	152.19			
7+	0										
8+	0										
9+	1	198.00	48.49	69.01	95.47	118.96	138.20	156.31	164.30	175.61	183.89
Total	202		194	177	115	48	25	7	1	1	1
Mean			54.57	82.39	104.17	124.25	141.17	152.78	164.30	175.61	183.89
95% C.I.			53.63-	81.13-	102.46-	121.75-	138.32-	145.42-			
			55.53	83.66	105.89	126.76	144.02	160.14			
Annual increment			54.57	27.81	21.78	20.07	16.92	11.61	11.51	11.31	8.27
males + females + unsexed											
0+	17	54.70									
1+	95	73.89	53.45								
2+	154	95.20	54.07	79.06							
3+	113	114.93	55.90	81.44	100.52						
4+	26	135.07	57.01	84.29	104.23	121.04					
5+	18	155.83	60.17	88.30	109.04	127.35	142.27				
6+	6	163.50	60.87	88.33	109.73	127.29	141.06	152.67			
7+	0										
8+	0										
9+	1	198.00	51.54	72.24	98.54	121.62	140.37	157.92	165.63	176.53	184.48
Total	430		413	318	164	51	25	7	1	1	1
Mean			54.97	81.01	102.37	124.01	141.90	153.42	165.63	176.53	184.48
95% C.I.			54.36-	80.07-	100.88-	121.26-	139.07-	146.01-			
			55.58	81.95	103.85	126.77	144.75	160.82			
Annual increment			54.97	26.03	21.35	21.64	17.89	11.51	12.21	10.89	7.95

Table 3. Mean back-calculated total lengths (*TL*, mm) at age for *Barbus cyclolepis*, Doirani Stream, March 1998-February 1999. n, number of fish; 95%C.I., 95% confidence intervals.

Age (yr)	n	Mean <i>TL</i> at capture	Mean back-calculated <i>TL</i> at age								
			1	2	3	4	5	6	7	8	9
males											
0+	17	59.52									
1+	58	85.34	66.01								
2+	61	108.81	67.24	93.96							
3+	33	129.63	72.01	99.36	117.24						
4+	13	144.61	72.57	98.20	117.19	132.60					
5+	5	157.60	73.99	99.72	118.34	133.42	146.72				
Total	187		170	112	51	18	5				
Mean			68.35	96.30	117.33	132.83	146.72				
95% C.I.			67.20-	94.67	114.64	128.80	140.10				
			69.51	97.93	120.03	136.85	153.35				
Annual increment			68.35	27.94	21.03	15.49	13.89				
females											
0+	20	56.60									
1+	25	88.72	67.20								
2+	31	108.93	65.91	92.34							
3+	27	129.00	67.93	96.62	115.88						
4+	16	154.37	73.01	102.50	122.94	139.53					
5+	18	180.94	76.70	109.72	132.59	152.70	168.04				
6+	6	195.66	80.01	111.48	135.31	156.09	170.88	183.59			
7+	0										
8+	2	234.50	88.36	117.03	143.86	163.01	182.35	199.17	215.15	226.33	
9+	1	244.00	89.09	118.78	141.05	161.38	180.28	198.07	209.41	225.76	236.29
Total	146		126	101	70	43	27	9	3	3	1
Mean			70.25	100.08	124.62	148.95	170.18	188.66	213.24	226.14	236.29
95% C.I.			68.48-	97.51	121.00	143.81	164.02	176.65			
			72.03	102.65	128.23	154.09	176.35	200.67			
Annual increment			70.25	29.82	24.53	24.33	21.23	18.47	24.57	12.90	10.14
males + females + unsexed											
0+	42	55.80									
1+	83	86.36	65.74								
2+	92	108.85	65.67	92.93							
3+	60	129.35	68.95	97.36	116.28						
4+	29	150.00	71.64	99.67	119.78	136.15					
5+	23	175.87	75.47	107.02	129.10	148.25	163.28				
6+	6	195.66	79.99	111.47	135.31	156.08	170.87	183.59			
7+	0										
8+	2	234.50	88.34	117.02	143.85	163.01	182.35	199.16	215.15	226.33	
9+	1	244.00	89.07	118.77	141.03	161.37	180.27	198.06	209.40	225.76	236.28
Total	338		296	213	121	61	32	9	3	3	1
Mean			68.22	97.49	121.16	143.96	166.43	188.65	213.23	226.14	236.28
95% C.I.			67.22-	95.98	118.70	139.72-	160.33-	176.65-			
			69.23	98.99	123.62	148.20	172.52	200.66			
Annual increment			68.22	29.26	23.67	22.80	22.46	22.22	24.57	12.90	10.14

Age and growth

Back-calculated lengths at age and annual length increments of *B. peloponnesius* and *B. cyclolepis* are shown in Tables 2 and 3, respectively. Significant differences in the mean back-calculated lengths at age between sexes were found in the 1, 2, 3 and 4 age groups in *B. peloponnesius* (t-test=4.07, 2.96, 4.87, 3.78 respectively, for all cases $P<0.05$), and in 2, 3, 4 and 5 age groups in *B. cyclolepis* (t-test=2.32, 2.93, 3.85, 3.14 respectively, for all cases $P<0.05$). In all cases, except the 1 age group of *B. peloponnesius*, females showed greater lengths at age than males. Between species, significant differences were found in all age groups, with *B. cyclolepis* showing larger mean lengths at age than *B. peloponnesius* (males: t-test=16.55, 16.61, 12.47, 6.01 for age groups 1, 2, 3 and 4 respectively; females: t-test=16.26, 13.32, 11.08, 8.69, 7.87, 4.44 for age groups 1, 2, 3, 4, 5 and 6 respectively; males+females+unsexed: t-test=22.99, 19.04, 13.44, 7.36, 6.33, 4.36 for age groups 1, 2, 3, 4, 5 and 6 respectively, for all cases $P<0.05$).

Von Bertalanffy growth parameters and ϕ' values for *B. peloponnesius* and *B. cyclolepis* are given in Table 4. In both species females showed greater values of L_∞ and ϕ' and smaller of K than the males, while *B. cyclolepis* showed greater values of L_∞ and ϕ' and smaller of K than *B. peloponnesius*.

Table 4. Parameters L_∞ (TL, mm), K (yr⁻¹), t_0 (yr) of the von Bertalanffy growth equation and growth index $\phi'=\text{Log}K+2\text{Log}L_\infty$ for *Barbus peloponnesius*, Almopaios Stream and *Barbus cyclolepis*, Doirani Stream, March 1998-February 1999. (standard error is given in parenthesis).

Species/Sex	L_∞	K	t_0	ϕ'
<i>B. peloponnesius</i>				
males	124.83 (5.07)	0.430 (0.060)	-0.414 (0.142)	1.826
females	228.24 (3.67)	0.169 (0.007)	-0.627 (0.055)	1.944
males + females + unsexed	233.94 (5.25)	0.162 (0.008)	-0.634 (0.073)	1.947
<i>B. cyclolepis</i>				
males	189.87 (5.84)	0.256 (0.020)	-0.748 (0.083)	1.965
females	354.43 (26.03)	0.112 (0.015)	-0.938 (0.173)	2.148
males + females + unsexed	354.41 (37.42)	0.112 (0.022)	-0.813 (0.236)	2.148

Condition factor

In both species the monthly mean RW values increased during spring and started progressively to decrease during summer (Fig. 3). *B. peloponnesius* showed a slight increase in September and November, while *B. cyclolepis* only in November. In late winter RW started to increase progressively.

Mortality

Z rates (Fig. 4) for males, females and males+females+unsexed were estimated at 0.79, 0.55 and 0.70 yr⁻¹ for *B. peloponnesius* and 0.70, 0.47 and 0.71 yr⁻¹ for *B. cyclolepis*, respectively. In

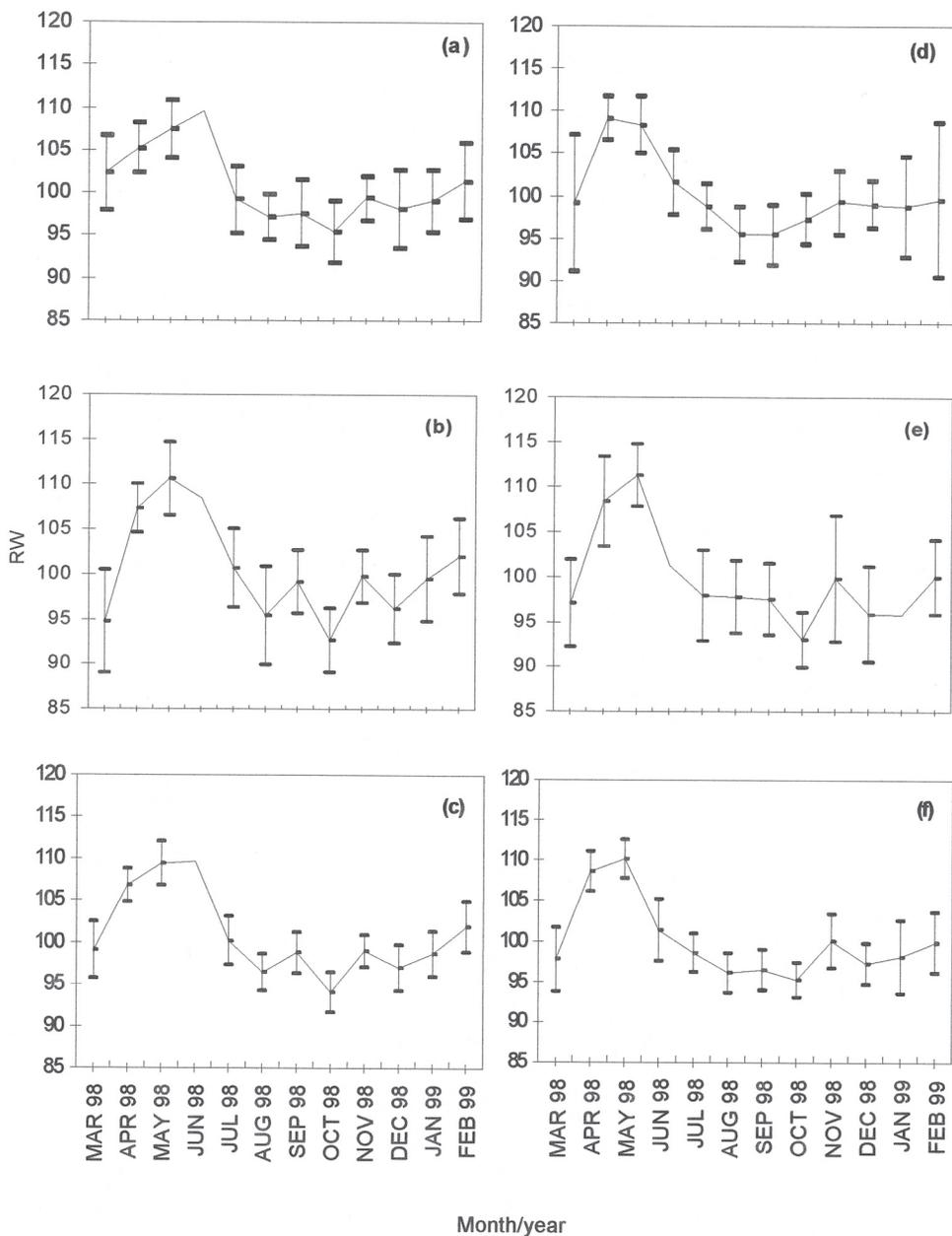


Fig. 3. Monthly variation of the mean condition factor (RW) (and 95% confidence limits for samples of five or more fish) of (a) males, (b) females, (c) males+females+unsexed *Barbus peloponnesius*, Almopaios Stream and (d) males, (e) females, (f) males+females+unsexed *Barbus cyclolepis*, Doirani Stream, March 1998-February 1999.

both species males exhibited higher mortality rates than the females. Since no directed fishery exists at present at the study areas, the length-converted catch curve estimate of Z can be accepted as an approximate estimate of natural mortality (M).

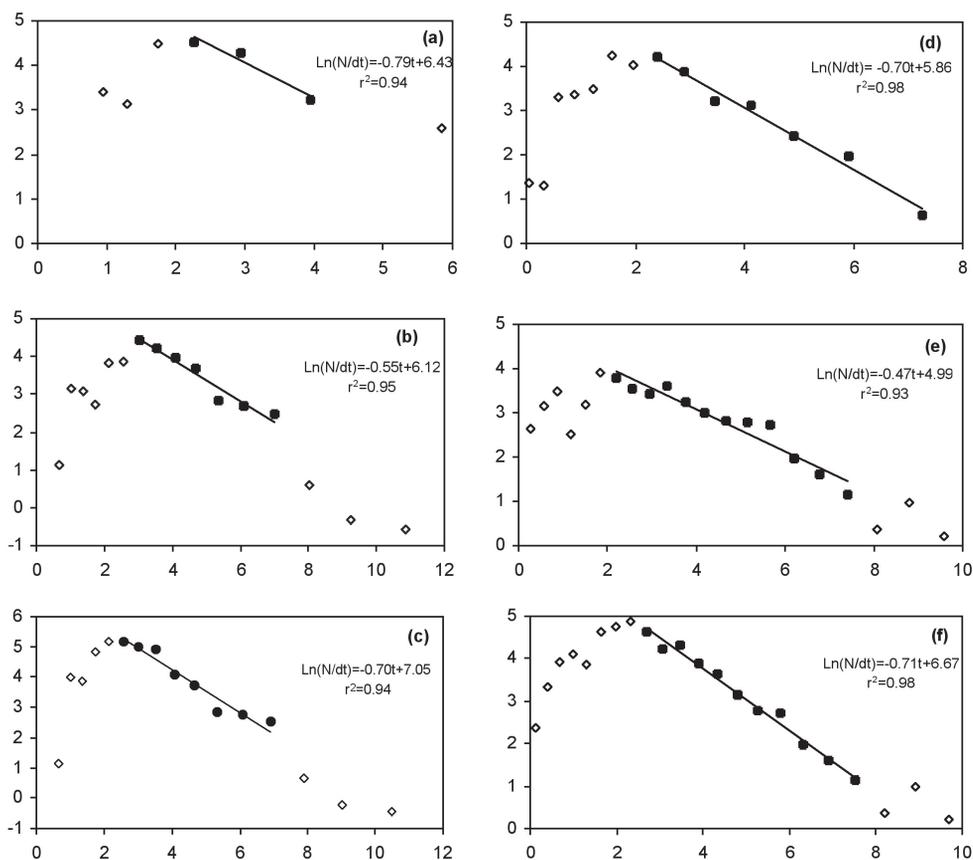


Fig. 4. Length-converted catch curves of (a) males, (b) females, (c) males+females+unsexed *Barbus peloponnesius*, Almopaios Stream and (d) males, (e) females and (f) males+females+unsexed *Barbus cyclolepis*, Doirani Stream, March 1998-February 1999. Black circles (●) represent the data used in the regression.

Reproduction

Seasonal changes of GSI for *B. peloponnesius* and *B. cyclolepis* are shown in Fig. 5. The reproductive activity of the two species throughout the year is best seen when the GSI is studied independently of sex (sexes combined) (Fig. 5c,f). It seems that in both species reproduction starts in March and is completed in August.

Histological analysis showed that the pattern of oocyte development was similar in both species. Although sampling started in March 1998, the description of oocyte development starts from September 1998, when vitellogenesis begins. In both species vitellogenesis started in September and, until February, most ovaries contained two modes of oocytes, one with previtellogenic oocytes and one with larger oocytes with yolk vesicles in the periphery of the cytoplasm (Figs 6a,b, 7a,b). In April ovaries showed a trimodal distribution (Figs 6c, 7c), which is typical of multi-spawning fish (Richard & Kestemont 1996). The first group consisted of previtellogenic oocytes, the second of oocytes with yolk vesicles

in the periphery of the cytoplasm and the third of larger oocytes with yolk globules around the nucleus and yolk vesicles in the periphery of the cytoplasm (Figs 6c, 7c). The oocytes of this last group continued to grow, their cytoplasm filled with yolk globules and after they

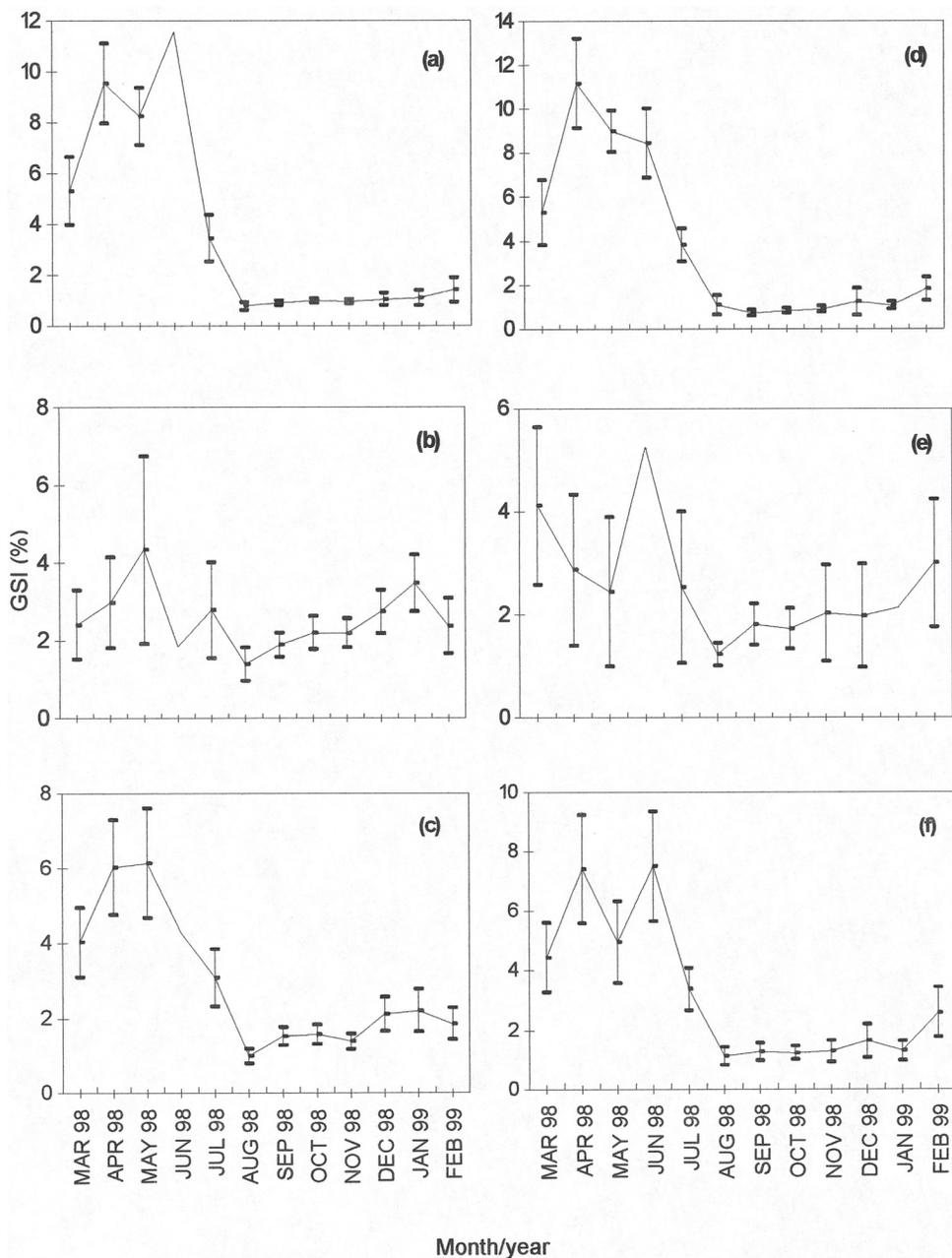


Fig. 5. Monthly variation of the mean gonadosomatic index (GSI) (and 95% confidence limits for samples of five or more fish) of (a) males, (b) females, (c) males + females *Barbus peloponnesius*, Almopaios Stream and (d) males, (e) females, (f) males + females *Barbus cyclolepis*, Doirani Stream, March 1998-February 1999.

become hydrated, they were ready to be released. This mode of oocytes represented the final maturation of the ovary (Figs 6d,e, 7d,e). In both species mature females were found from late March to late June, although in the beginning and in the end of this period only a very small number of mature females was found. In late July, a few ovaries with immature previtellogenic oocytes and oocytes in early stages of absorption were observed (Figs 6f, 7f), which clearly showed that the last individuals had already completed spawning about mid July. During July

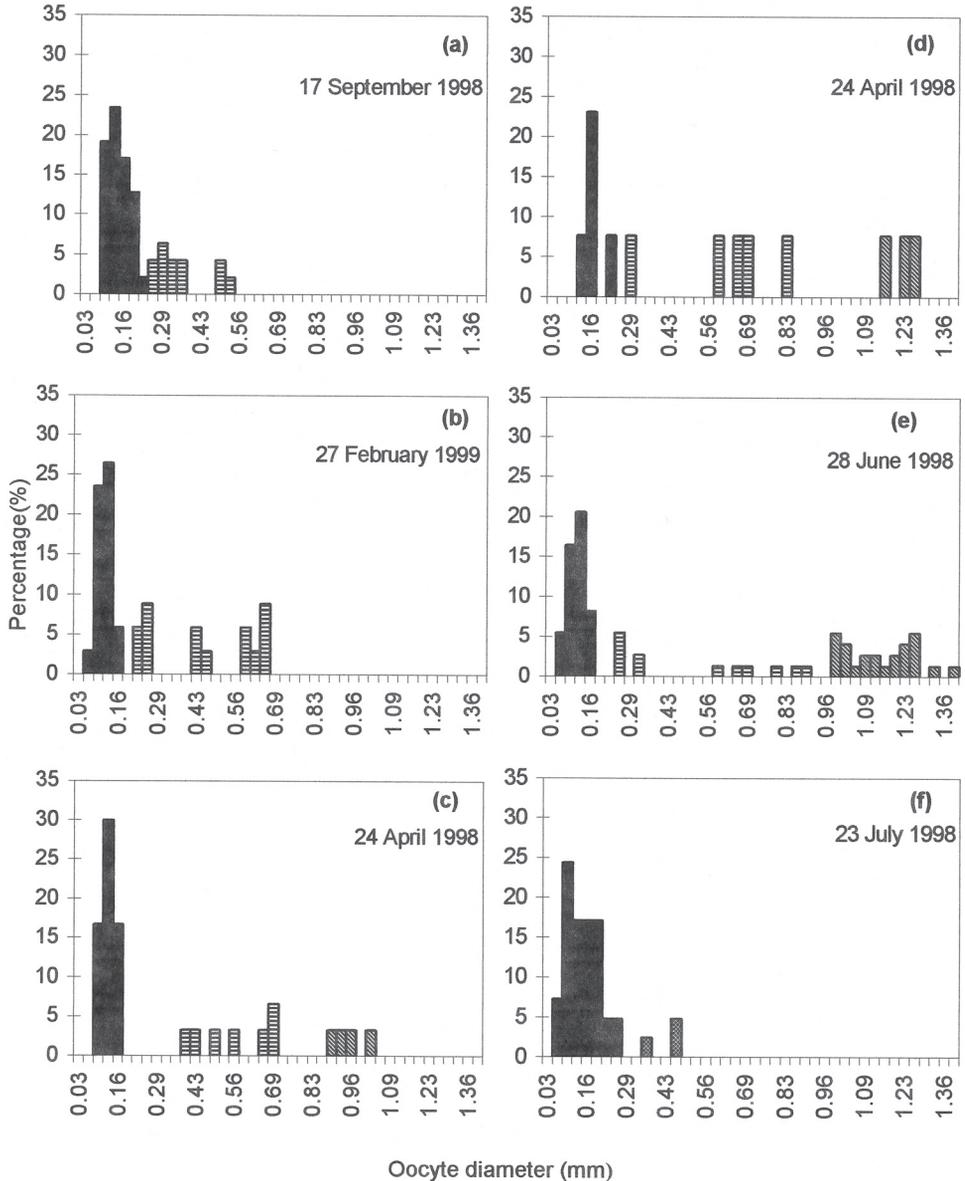


Fig. 6. Size-frequency distribution of oocytes from six (a-f) *Barbus peloponnesius* females, Almopaios Stream, March 1998-February 1999. ■, previtellogenic oocytes; □, oocytes with yolk vesicles; ▨, oocytes with yolk globules; ▩, oocytes in absorption.

and August (quiescent period) females of both species had completed ovulation and most ovaries contained only one mode of immature previtellogenic oocytes.

Mature males in both species were found from March to June. From the above it can be concluded that the reproductive period in both species starts in late March-beginning of April and lasts until mid July.

Examination of the testes showed that in *B. peloponnesius* and *B. cyclolepis* males started to mature in their second year of life (1+ age group). In both species all males in their third

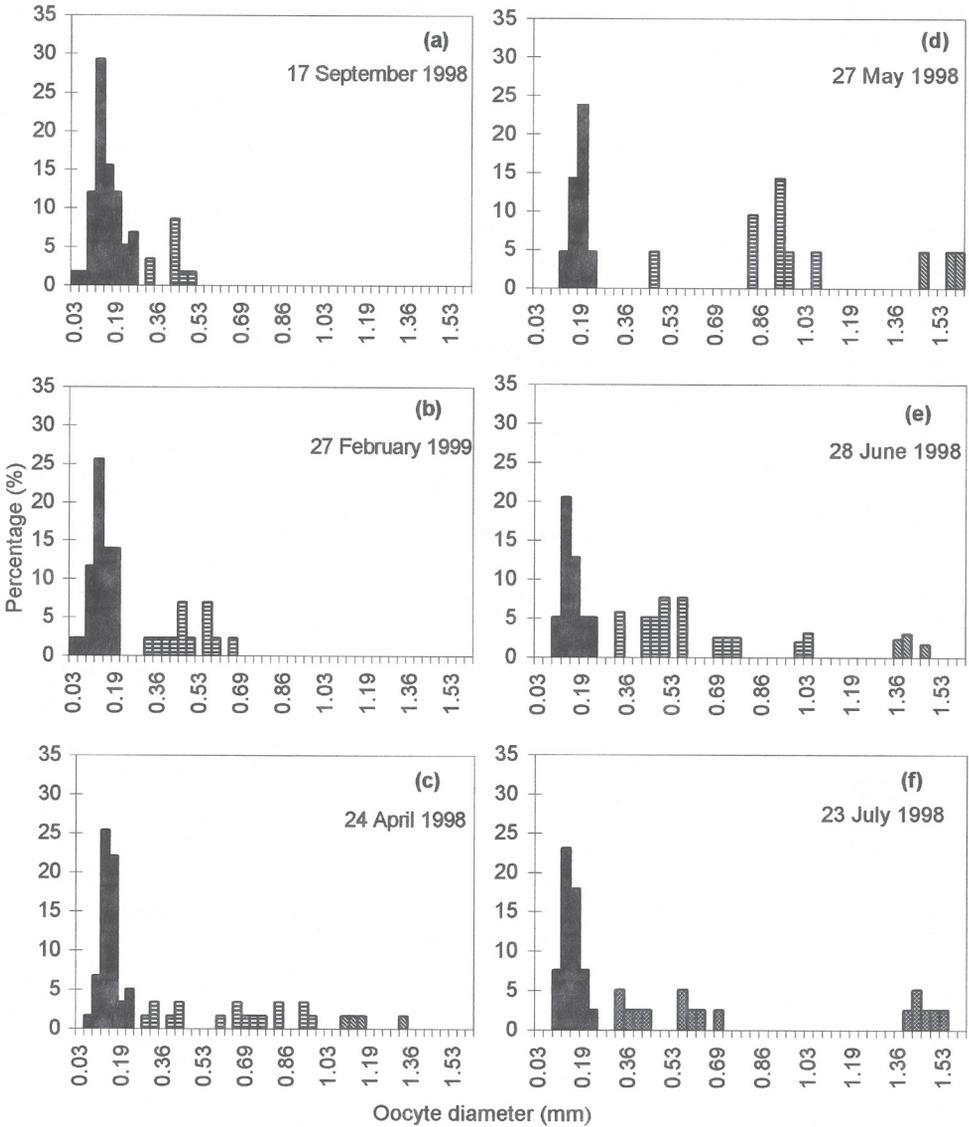


Fig. 7. Size-frequency distribution of oocytes from six (a-f) *Barbus cyclolepis* females, Doirani Stream, March 1998–February 1999. ■, previtellogenic oocytes; □, oocytes with yolk vesicles; ▨, oocytes with yolk globules; ▩, oocytes in absorption.

year of life (2+ age group) and over were mature during the reproductive period. Macroscopical and histological examination of the ovaries showed that in both species females mature at their fourth year (3+ age group). In both species all females of the 4+ age group and over were mature during the reproductive period.

Discussion

Population structure

The two species studied showed a similar age structure (Fig. 2). A similar structure was also found in other populations of *B. peloponnesius*. Šorić & Janaković (1989) and Šorić (1992) studied populations of *B. peloponnesius* in the rivers Beli Drim and Gruza (Serbia) and found that age ranged from 1+ to 5+ in males and from 1+ to 8+ in females, while Lenhardt et al. (1996), who studied the same species in the river Gradac (Serbia), found that age varied from 1+ to 4+ in males and from 1+ to 7+ in females. In all the above populations reproduction starts at the age 1+ in males and 3+ in females and the same was found for the populations of *B. peloponnesius* and *B. cyclolepis* that we studied. For *B. cyclolepis*, age ranged from 1+ to 6+ in populations of the species studied in the Dospat Dam and the river Dzerman (Bulgaria) (Dikov & Zhivkov 1985) and from 1+ to 3+ in males and 1+ to 5+ in females in Rihios Stream (Macedonia, Greece) (Nephitou 1987).

Age and growth – Mortality

The length at age estimates revealed that in both species studied, after the 1 age group, females showed greater *Tl* at age and reached a larger maximum *Tl* than the males (Tables 2, 3). Sexual maturation takes place two years earlier in the males than in the females and this may be the reason for the smaller body size of the males. In *Barbus barbuis*, Hunt & Jones (1975) found that females grew more quickly than the males after the fourth year of life and stated that this was probably the result of the earlier maturation in the males than in the females. Earlier maturation and smaller body size in males than in females is common in many fish species (Pauly 1978, 1994). This phenomenon is common in salmonids and has been attributed to the fact that body size is a less important factor for male fitness (Elliot 1994). In contrast, for females a small size at maturity probably implies large fitness costs, for example small eggs, low fecundity, small survival of the offspring and reduced access to the best spawning sites (Wootton 1984, 1990, Stearns 1992, Hagen & Rygg 1996). The opposite situation, where females are smaller and mature earlier than the males, is usually found under conditions of social structure, in which strong competition occurs among the males for access to females (Stearns 1992).

In the two species studied, males exhibited higher mortality rates than the females conspecifics (Fig. 4). According to Lien (1978), the early maturation of *Salmo trutta* males may lead to higher mortality rates because of large energy investments into spawning activities. In *Salmo salar*, early sexual maturity in males leads to an increase in natural mortality compared to immature females and males (Lundqvist et al. 1994). Similarly in another salmonid, *Thymallus thymallus*, males were found to have higher natural mortality rate than the females and this was attributed to the larger amount of time and energy males spent at the spawning sites (Witkowski & Kowalewski 1988, Hagen & Rygg 1996). In the same

Table 5. Mean back-calculated total lengths (T_l , mm) at age, von Bertalanffy growth parameters L_∞ (T_l , mm), K (yr^{-1}), t_0 (yr) and growth index $\phi' = \text{Log}K + 2 \cdot \text{Log}L_\infty$ for *Barbus peloponnesius* and *Barbus cyclolepis* from different areas.

Mean back-calculated T_l at age									L_∞	K	t_0	ϕ'	Area	Reference	
1	2	3	4	5	6	7	8	9							
<i>B. peloponnesius</i>															
47	83	111	138	158	176	192	209	294	0.149	-0.188	2.109	River Beli Drim (Serbia)	Šorrić & Jančković 1989		
52	85	117	140	163	186	201	215	317	0.138	-0.292	2.141	River Gruza (Serbia)	Šorrić & Jančković 1989		
55	81	102	124	142	153	166	177	234	0.162	-0.634	1.947	Almopatos Stream (Greece)	present study		
<i>B. cyclolepis</i>															
54	90	129	152	167	180	219	0.293	0.071	2.148	River Dzerman (Bulgaria)	Dikov & Zhivkov 1985				
92	125	187	241	257	261	339	0.266	-0.060	2.485	Dospal Dam (Bulgaria)	Dikov & Zhivkov 1985				
68	97	121	144	166	189	213	226	236	0.112	-0.813	2.148	Doirani Stream (Greece)	present study		

* Von Bertalanffy growth parameters and ϕ' values were estimated by the author based on the back-calculated lengths at age data from the references using the non linear fitting routine of FISAT (Gaynillo et al. 1996).

Table 6. Maximum observed total lengths (*Tl*, mm) for *Barbus peloponnesius* and *Barbus cyclolepis* from different areas.

Species	max <i>Tl</i>	Area	Reference
<i>B. peloponnesius</i>	223	River Beli Drim (Serbia)	Šorić & Janković 1989
<i>B. peloponnesius</i>	225	River Gruza (Serbia)	Šorić & Janković 1989
<i>B. peloponnesius</i>	260	River Gradac (Serbia)	Lenhardt et al. 1996
<i>B. peloponnesius</i>	180	River Nedas (Greece)	Economou et al. 1999
<i>B. peloponnesius</i>	172	Mirtia Stream (Greece)	Economou et al. 1999
<i>B. peloponnesius</i>	130	River Selinous (Greece)	Economou et al. 1999
<i>B. peloponnesius</i>	210	River Vouraikos (Greece)	Economou et al. 1999
<i>B. peloponnesius</i>	265	Aoos Reservoir (Greece)	Economou et al. 1999
<i>B. peloponnesius</i>	198	Almopaios Stream (Greece)	present study
<i>B. cyclolepis</i>	210	River Dzerman (Bulgaria)	Dikov & Zhivkov 1985
<i>B. cyclolepis</i>	294	Dospat Dam (Bulgaria)	Dikov & Zhivkov 1985
<i>B. cyclolepis</i>	260 *	Rihios Stream (Greece)	Neophitou 1987
<i>B. cyclolepis</i>	244	Doirani Stream (Greece)	present study

* Fork length

species, the higher natural mortality rate of the males has been attributed to their higher activity, which probably makes them more vulnerable to predation and exploitation (Holčík & Žitňan 1972). In the present study, the reproductive period is the same for the males and the females in both species and no fishery exists in the study areas. In the two species that we studied, although it is not known if males spent more energy in spawning activities and if this investment outweighs the energy cost of oogenesis of the females, it seems that the early maturation of the males leads to a large energy investment in reproduction early in life, which limits the growth and probably results in small body sizes, higher mortality rates and reduced longevity.

B. peloponnesius in Almopaios Stream showed smaller mean *Tl* at age and smaller maximum *Tl* in comparison with other populations of the same species that were studied in the rivers Beli Drim and Gruza in Serbia (Šorić & Janković 1989) (Tables 5, 6). Generally in freshwater fishes, as the latitude decreases, mainly due to higher temperature, reproduction lasts for a longer period of time (Mann et al. 1984). The reproductive period in the population of the River Gruza lasts for 2½ months, from June to mid August (Šorić 1992), while southern, in the population of Almopaios Stream, lasts about 3–3½ months. Burt et al. (1988) stated that when environmental conditions allow an elongated reproductive period, smaller body sizes and more than one spawnings per reproductive period are in favour and fish invest more energy in reproduction, which limits the growth. Another possible explanation for the reduced growth of the Almopaios Stream population, in comparison with the populations studied in the rivers Beli Drim and Gruza, is the reduced water flow during the summer droughts in Almopaios Stream. This probably results in intense aggregations of fish and possible competition for food and space (Vila-Gispert & Moreno-Amich 2001). In addition, water temperature rises during the summer droughts, which results in oxygen depletion, imposing adverse ecological conditions on fish that could limit the growth (Herrera et al. 1988, Herrera & Fernandez-Delgado 1992, Pires et al. 1999). Also, the higher water temperatures that prevail at lower latitudes result in an increase in the metabolic rate and the feeding rate of fish (Wootton 1984, Pauly 1994, 1998). Pauly (1998)

suggested that, if metabolic rates increase with temperature and growth is limited by respiratory metabolism, one might expect that fish living in warmer waters will be smaller than their counterparts that live in colder waters. This may be another reason for the smaller body sizes that our population showed in comparison with the populations of the rivers Beli Drim and Gruza. It is possible that during the summer in Almopaios Stream, high water temperatures increase the metabolic needs of the fish, but these needs cannot be satisfied, probably due to the adverse environmental conditions mentioned above, resulting in a decrease in growth and in an increase in mortality.

According to Economidou et al. (1999), in other streams in Greece the maximum *TL* of *B. peloponnesius* rarely exceeds 200 mm, although in the Aaos Springs reservoir (Northwest Greece) the largest specimen had a *TL* of 265 mm (Table 6). A population of *B. peloponnesius* has adapted successfully in this artificial lake and this is only one of the few cases where the species is found in lakes. Although no data are available on the age and growth of the species in the reservoir, it is believed that the reservoir offers a more stable environment compared with the high environmental variability of the seasonal Greek streams.

B. cyclolepis in Doirani Stream showed greater maximum *TL* in comparison with a population of the same species studied in the river Dzerman in Bulgaria (Dikov & Zhivkov 1985) (Table 6), although the ϕ' value was the same for the two populations (Table 5), and thus their overall growth performance seems to be the same. In contrast, the population from Doirani Stream exhibited smaller mean *TL* at age and smaller maximum *TL* in comparison with a population studied in the Dospat Dam in Bulgaria (Dikov & Zhivkov 1985) (Tables 5, 6). As mentioned above, the reason for this is probably that a reservoir is a more stable environment, which offers higher trophic resources favouring fish growth and survival.

Between the two populations that were studied, *B. cyclolepis* showed increased growth, longer mean *TL* at age and larger maximum *TL* than *B. peloponnesius* (Tables 2, 3, 4). Taken into consideration that the two populations live in streams with similar environmental conditions, have the same reproductive period, life span, similar age structure and mature at the same age, the increased growth and larger body size of *B. cyclolepis* seems to be of genetic basis. This is supported by the fact that specimens with *TL* larger than 260 mm were found in Rihios Stream (Macedonia, Greece) (Neophitou 1987) and Dospat Dam (Bulgaria) (Dikov & Zhivkov 1985).

Condition factor

The condition factor showed similar annual cycles in the two species studied (Fig. 3). Although reproduction started in April, RW showed the highest values from April to June, probably due to favourable environmental conditions that prevail during spring. The condition factor showed a similar annual cycle, with the highest values in spring and the lowest in summer, in populations of *Barbus sclateri* that were studied in streams in south Spain (Herrera et al. 1988, Herrera & Fernandez-Delgado 1992, Encina & Granada-Lorenzo 1997). The decrease of the condition factor during the summer can be attributed to the severe droughts that prevail during the summer in the Mediterranean area, which produce unfavourable conditions for fish survival (Herrera et al. 1988, Herrera & Fernandez-Delgado 1992, Pires et al. 1999, Vila-Gispert & Moreno-Amich 2001) and the depletion of energy storage which is associated with spawning activities and high metabolic demands during this period (Encina & Granada-Lorenzo 1997). A slight increase in the condition factor in autumn was found in *B. cyclolepis* and *B. pelopon-*

nesius in the present study (Fig. 3) and the same was observed in *B. sclateri* by Herrera et al. (1988) and Herrera & Fernandez-Delgado (1992). These authors attributed this increase to the arrival of rain and the consequent increase in water flow in the streams during the autumn.

Reproduction

The populations of *B. peloponnesius* and *B. cyclolepis* showed an elongated multi-spawning season that lasted about 3–3½ months (Figs 5,6,7). The streams in the Mediterranean region can be considered as highly variable ecosystems mainly because of variations in water flow, water temperature and resource availability throughout the year (Herrera & Fernandez-Delgado 1994, Fernandez-Delgado & Herrera 1995, Encina & Granado-Lorenzo 1997, Aparicio & Sostoa 1999). This environmental variability may cause unpredictable mortality rates in fishes that inhabit an environment like this (Herrera & Fernandez-Delgado 1992). An elongated reproductive period with more than one spawning per season offers significant advantages in these fluctuating environments. First of all, multiple spawning increases individual fecundity and thus the number of offspring produced during the reproductive period, which compensates for the high mortality rates often observed in fluctuating environments as mentioned above (Wotton 1984, Herrera & Fernandez-Delgado 1992, 1994). Moreover, it reduces the chances that a population will become extinct due to recruitment failure during periods with unfavourable environmental conditions, as the reproductive effort is spread over a longer period of time (Weddle & Burr 1991, Herrera & Fernandez-Delgado 1992, 1994, Rinchar & Kestemont 1996). Finally, in streams where the number of spawning sites is limited, multiple spawning may reduce competition for these sites by partitioning their use in time (Rinchar & Kestemont 1996). As many authors have pointed out, multiple spawning is as a common reproductive tactic in barbels in fluctuating Mediterranean streams (Herrera & Fernandez-Delgado 1992, Pizzul et al. 1994, Torralva et al. 1997, Economou et al. 1999).

Life-history style

The populations of the two species that were studied, despite differences in growth and body size, are characterized by similar life-history styles: (1) similar age structure (individuals older than 5+ were very rare) which shows a short life span, (2) early maturation and same age at maturity, (3) males have a shorter life span, higher rate of mortality, decreased growth and smaller body size and mature earlier than the females and (4) elongated multi-spawning season, which shows a high investment in reproduction. The Mediterranean streams can be considered as quite unstable and variable ecosystems and this is probably the main factor that affects and determines the life-history styles of the two populations studied. The similarities in the life-history parameters of the two species are probably an expression of phenotypic plasticity of the species as they adapt to habitats with similar environmental conditions. Based on the characteristics mentioned above, *B. peloponnesius* and *B. cyclolepis* seem to tend to an altricial (generalist/r selected) life-history style, which is consistent with the life-history theory. An altricial (generalist/r selected) species will have a life-history style that is characterized by high energy investment in reproduction, small body size, low age at maturity, high rate of

unpredictable mortality and short life span and is more likely to be found in fluctuating or harsh environments (MacArthur & Wilson 1967, Balon 1979, Adams 1980, Bruton 1989).

B. peloponnesius and *B. cyclolepis* can be considered as highly successful species. Both species can survive under unfavourable and harsh environmental conditions and in many riverine systems in Greece these are the only species present (Economou et al. 1999, Economidis et al. 2000). In more stable and predictable riverine systems, larger maximum lengths are observed, while in the more unstable and seasonal small streams small body sizes are in favour (Economou et al. 1999).

As mentioned earlier, the geographical distribution of these two species in North Greece is of particular interest. One characteristic complexity of this distribution appears in the streams southeast of Axios River (see Fig. 1a), where *B. peloponnesius* seems to penetrate into the region of *B. cyclolepis* (Economidis 1989). The coexistence of the two species in the same river has never been recorded and it seems that *B. peloponnesius* displaces *B. cyclolepis* in this area. Although, it has not been investigated so far if these two species can hybridize naturally, one may suggest that the two species are competitive to each other, which is supported by their similar life-history strategies, and this maybe the reason for the fact that their coexistence in the same river has never been recorded.

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