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First study of the life cycle of *Pisidium tenuilineatum* Stelfox, 1918 (Bivalvia, Sphaeriidae)

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The sampling of molluscan communities in the French Upper Rhône has permitted describing the life cycle of *P. tenuilineatum*. This small bivalve gives birth to two or three generations per year that emerge from May to September. The presence throughout the year of gravid individuals and newborns suggests that each individual reproduces several times during its lifetime (iteroparity) of one to two years. In European *Pisidium* this reproduction strategy has only been observed in populations of *P. conventus* living in deep zones of lakes. However, it does not appear to endow *P. tenuilineatum* with any particular advantage since it is most usually represented by only small populations.

Key words: Bivalvia, Sphaeriidae, *Pisidium*, life cycle, life strategy, Rhône river, France.

INTRODUCTION

Pisidium tenuilineatum Stelfox, 1918 (fig. 1), a western Palaearctic clam, belongs to the subgenus *Odhneripisidium* Kuiper (1962a, b, 1981). In rivers it is found from the medium rhithron, where it reaches its optimum, to the potamon. It is relatively sensitive to biodegradable pollution (Mouthon, 1996, 1999). *Pisidium tenuilineatum* is considered as rare in most European countries. Nonetheless, it is more common in France where its frequency in rivers (447 stations sampled from 1977 to 1992) reaches 23.5%. Usually however, the species occurs at low population densities (Mouthon, 1994).

The life traits of *Pisidium* have been summarized by Holopainen & Hanski (1986). However, these data above all concern the species of the subgenus *Pisidium* s.s. Pfeiffer, 1821, *Cyclocalyx* Dall, 1903, and *Neopisidium* Odhner, 1921. On the contrary, the life cycles of the representatives of the subgenus *Odhneripisidium*, *Pisidium moitessierianum* Paladilhe, 1866, and the Asian *P. annandalei* Prashad, 1925, have been the subject of only very few studies (Holopainen, 1979; Morton, 1986) while that of *P. tenuilineatum* remained unknown. In this paper we analysed for the first time the life cycle of the latter bivalve from sampling performed in the framework of the study on the dynamics of molluscan populations of the Upper Rhône.

MATERIAL AND METHODS

Molluscan communities were collected monthly from September 1996, in the reservoir of Villebois located on the Upper Rhône, between Lake Geneva and the city of Lyon, approximately 80 km downstream from Génissiat Dam (fig. 2). The construction of the Villebois Dam (height: 9.7 m) has formed a 28 km long reservoir which supplies the hydropower station of Porcieu-Amblagnieu. Current velocity in the reservoir is generally lower than 0.50 m/s and water turnover occurs in less than 24 hours (Compagnie Nationale du Rhône data). Apart from flushing periods, the water-level fluctuations of the reservoir do not exceed 0.50 m.

	P. tenuilineatum Upper Rhône (this study)	*P. moitessierianum* Lake Pääjärvi (Holopainen, 1979)	*P. annandalei* Hong Kong (Morton, 1986)
Range of annual water temperature (°C)	2.1-22.8	1-20	13-34
Maximum shell length (mm)	2.35	1.8	4.0(1)
Minimum shell length (mm)	0.6	0.6	-
Minimum mature size (mm)	1.1	1.0	1.5
Minimum parent size with shelled larvae (mm)	1.275	-	2.0
Maximum larvae size (mm)	0.775	0.6	0.8
Number of shelled larvae/parent (max / mean)	21 / 7.6	7 / -	- / 7.17
Number of generations/year	2 to 3	1	3
Life span	1 to 2 years	2 years	4 months

(1) However, in a population in China most individuals have died by 3.5 mm.

Table **1**. Life cycle data for *Odhneripisidium* species.

Two sectors were selected, the first on the right bank at four stations and the second on the left bank at two stations. The samples were taken at depths from 0.50 to 1.5 m using a rectangular hand-net (25×18 cm, 315 µm mesh); the total area sampled was 1.5 m^2. The samples were fixed on-site in 12% neutralised formaldehyde and sieved at 315 µm in the laboratory. Only during the period from June 2001 to March 2003 it was possible to obtain a sufficiently high number of individuals to study the life cycle of this species. For the list and densities (number m^{-2}) of *Pisidium* species collected in the Verbois reservoir, see Appendix 1. All specimens were identified by the author and are available in his collection.

The shell length (SL, largest anterior-posterior dimension across the valves) of individuals was measured with an eye piece micrometer at 40× under a binocular microscope, and assigned to size classes of 0.05 mm width. The resulting histograms were analysed using Bhattacharya's (1967) graphical method available in the FiSAT software distributed by FAO-ICLARM (Gayanilo et al., 1996), which allows separating each length-frequency distribution into Gaussian components, i.e. the identification of generations from continuous histogram data, using Gaussian curve-fitting algorithms. For each generation, the mean size of the individuals, their number and the standard deviation were established. All the individuals measured were dissected to establish the number of larvae in the marsupium. Gravid individuals with only eggs or (and) larvae before shell formation on the one hand, and shelled larvae on the other hand, were counted. The larvae were separated into two size classes: < and >0.25 mm. Only larvae with SL close to 0.25 mm were effectively measured, whereas the smaller or longer ones were assigned to one or the other size class.

Discharge rates at Pont de Groslée, situated 8 km upstream from the Villebois Reservoir were supplied by the CNR. Physico-chemical data were recorded upstream from the nuclear power plant of Creys-Malville by EDF, the French electricity company and by the Cemagref. This power plant was decommissioned in 1998.

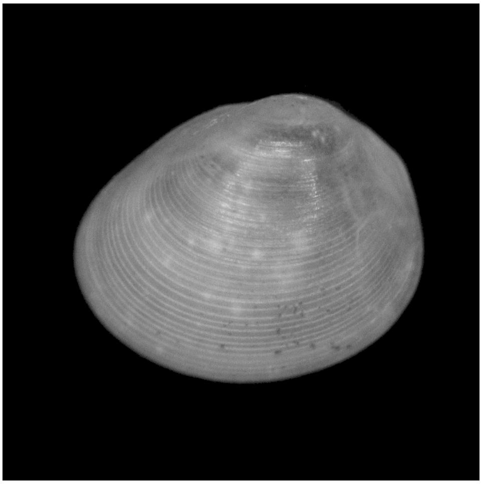

Figure **1**. Shell of *Pisidium tenuilineatum*, length 1.85 mm. Photograph by G. Le Goff.

RESULTS

Environmental variables.-- According to Pardé (1925), the hydrological regime of the Rhône at Pont de Groslée is characterized by high waters in spring and summer due to the melting of snow in the Alps and brief floods from October to January (pluvial influence). Nevertheless, the hydropower schemes built on the Upper Rhône during the last sixty years have radically altered the natural flow rhythms of the water (Bravard, 1987). The peak flows were generally accompanied by an abrupt fall in water temperature owing to the addition of cold water from melting snow and also to flushing in the Génissiat Dam (fig. 3). Maximum temperatures reached 22.8°C in August 2001 and 21.7°C in July 2002 while minimum temperatures do not fall lower than 2.1°C. The waters of the Rhône are alkaline, rich in minerals, in particular calcium (conductivity ranging from 234 to 390 µS cm^{-1} and Ca^{++} from 48 to 62 mg L^{-1} during the period studied) and well oxygenated except in summer, although minima do not fall below 5.4 mg L^{-1}.

Life cycle.-- The life cycle of *Pisidium tenuilineatum* is described using histograms of frequencies and the results supplied by Bhattacharya's method (figs 4, 5). In June 2001, three generations were present. The first (Early generation) was composed of young individuals most probably born during spring 2001 (G01E). Between July and August they grew rapidly to reach a size close to that of the individuals of the second generation born in 2000 (G00). Consequently, from August it was possible to distinguish only one generation (G00+G01E) whose abundance increased significantly (fig. 6). This generation disappeared in August 2002, when its mean size was 2.08 mm. The second generation consisting of the oldest individuals born in 1999 or in 2000 (G99-00?) disappeared in August 2001 (mean size: 1.95 mm). During this month, a new generation (Late generation - G01L) appeared (mean size: 0.81 mm). Its growth was very slow from August to April 2002 (0.17 mm) but increased strongly from April to October (0.98 mm), to remain stable until March 2003.

In 2002 three generations appeared. The first (G02E) was born in May (mean size: 1.00 mm). The fall in mean size of the individuals of G01L from July to August (6.32 vs 5.69 mm) and the considerable increase in its numbers (46 vs 107 ind. 1.5 m^{-2}, fig. 5) shows that

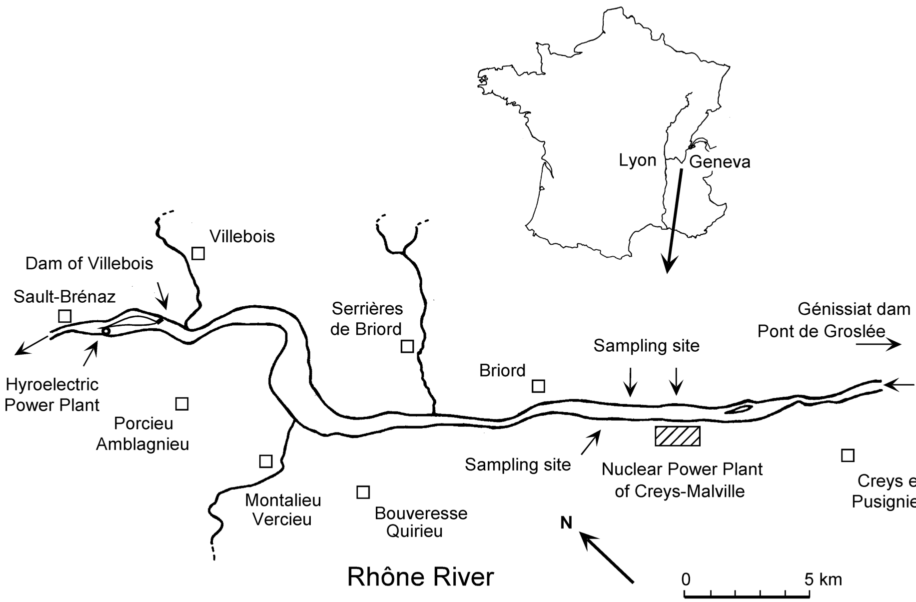

Figure **2**. Location of the *Pisidium* collection sites in the Villebois Reservoir (Upper Rhône).

the bivalves of G02E grew rapidly to reach the same size as those of G01L. From August only one generation was distinguished (G01L+G02E). A second and then a third generation ($G02L_1$ and $G02L_2$, respectively) appeared successively in August and September (mean size: 0.97 and 0.96 mm, respectively). The size of the individuals of $G02L_1$ increased from 0.58 mm from August to October. By contrast, that of the bivalves of $G02L_2$ hardly varied until March 2003. The size of gravid individuals in June and July varied from 1.25 to 2.25 mm, indicating that it was the bivalves of generations G00+G01E and G01L+G02E that contributed to the formation of $G02L_1$ and $G02L_2$.

Parents contain eggs or (and) larvae before shell formation or shelled larvae all year round (fig. 7A, B). However, litter size (number of shelled larvae/parent) varied from one season to another; it was maximal in winter and minimal in summer (fig. 7 C). Consequently the constant presence of juveniles in the population was observed, immature individuals (SL<1.1 mm) representing from 8.8 to 57.9% of the population (mean: 30.1±12.7% for the period studied, 33.2±11.9% for 2002). The reproductive and growth features of the *P. tenuilineatum* population are given in table 1.

DISCUSSION

In the French Upper Rhône *P. tenuilineatum* gives birth to two or three generations per year that appear from May to September. The presence of gravid individuals and newborns throughout the year suggests that each individual reproduces several times during its life span (iteroparity) which lasts from one to two years. The mean temperature was higher by 1.9°C between the sampling campaigns of August and September 2001 and those of 2002 (16.9 vs 18.8°C), thereby permitting the rapid growth of the juveniles (Δ=1.53

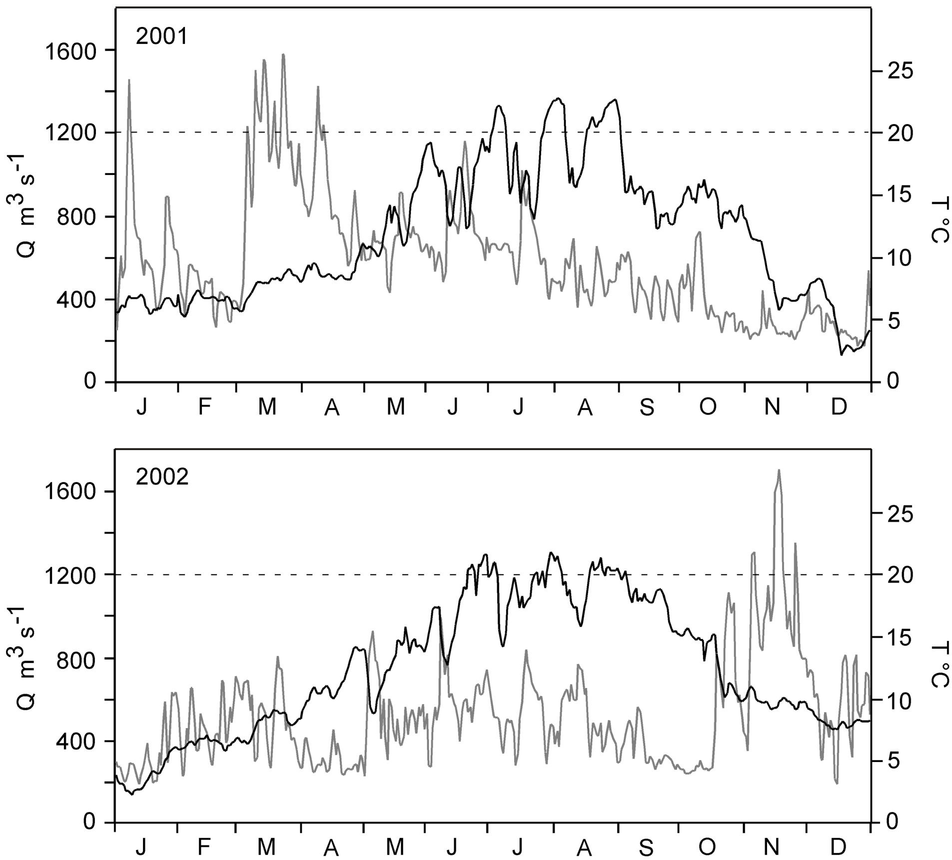

Figure **3**. Daily discharge rate at Pont de Groslée (CNR data, grey lines) and daily temperatures upstream from the Creys-Malville nuclear power plant (EDF data, bold lines) of the Upper Rhône.

mm) in 2002 and the appearance of an additional generation (G02L$_1$) in comparison to 2001. This observation shows that in the absence of unfavourable hydraulic and heat conditions (melting snow and dam flushing at Génissiat) that limit the growth of juveniles, especially in May and June, the number of generations produced may have been higher (4-5 vs 2-3).

Pisidium species usually incubate shelled larvae between spring and autumn but in *P. amnicum* the incubation period begins in the summer of the first year and stops in the spring or summer of the following year. They are semelparous or iteroparous, generally produce one to three generations per year and live from four months to four years (Holopainen & Hanski, 1986; Bailey & Mackie, 1986; Hornbach & Cox, 1987; Araujo et al., 1999). However, in the Saône, a large lowland river, *Pisidium subtruncatum* Malm, 1855, gives birth to five generations per year (Mouthon, 2005). Table 1 summarizes the life cycle data of the two other *Odhneripisidium* species, viz. *Pisidium moitessierianum* and *P. annandalei*, which are both semelparous. In the former parturition starts in July; it only produces one generation per year and lives two years (Holopainen, 1979). In the latter, which inhabits subtropical regions, shelled larvae were observed in spring (from April to June), in

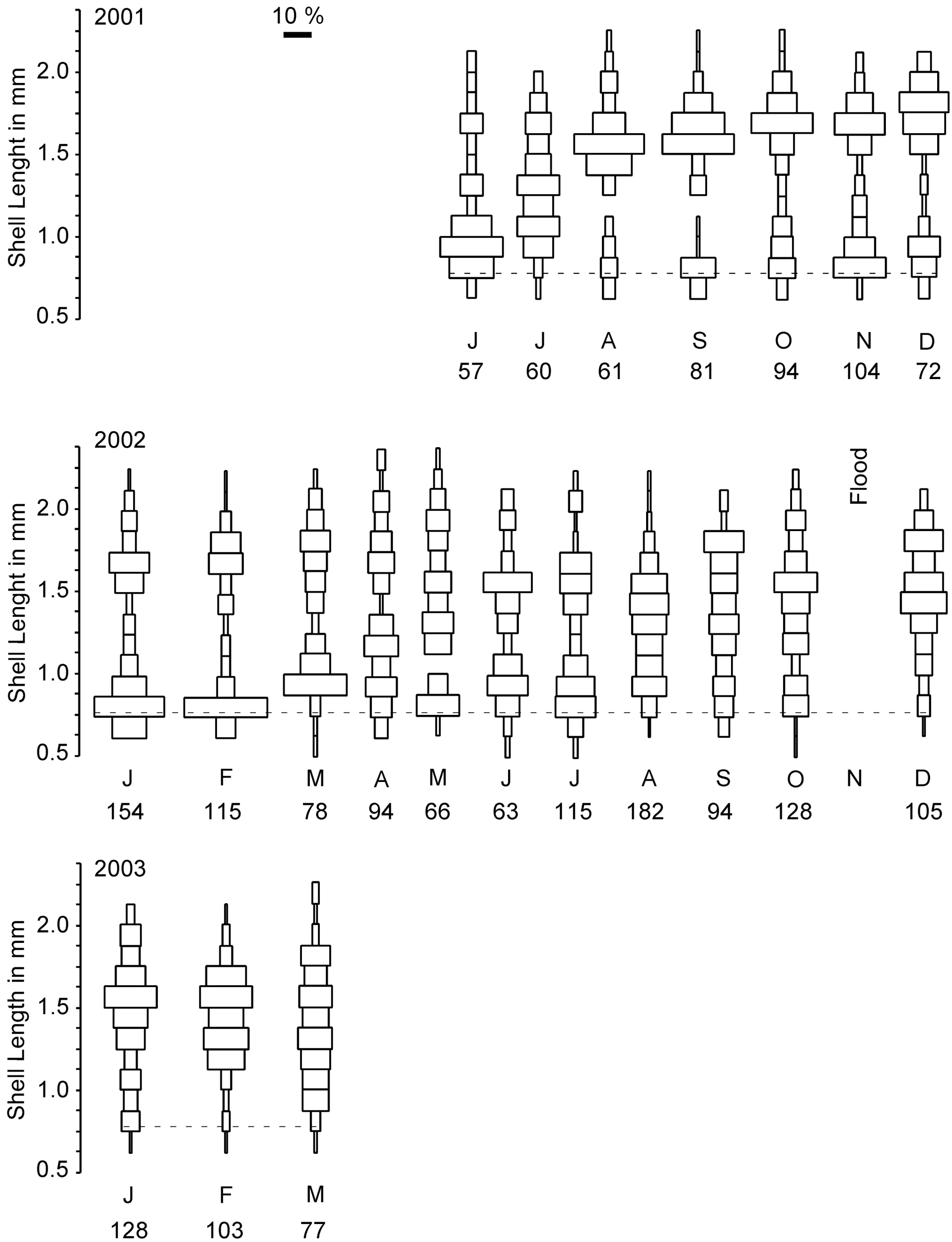

Figure **4**. Shell length-frequency diagrams of *Pisidium tenuilineatum* from Upper Rhône. Dashed horizontal line shows the maximum size at birth (0.775 mm). Sample numbers are indicated under each month.

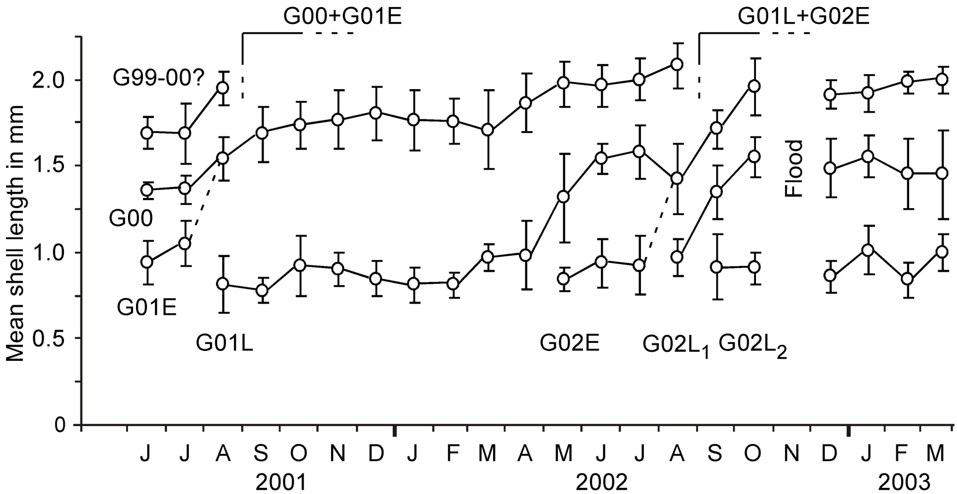

Figure **5**. Mean generation shell length (open circles) in monthly samples of the Upper Rhône *Pisidium tenuilineatum* population. Vertical bars are standard deviations.

summer (August and September) and in winter (December and January); it produces three generations per year and lives for four months (Morton, 1986). Although very few studies are available, the life strategies of the three species of the subgenus *Odhneripisidium* appear to be very different.

In *P. tenuilineatum* in the French Upper Rhône incubation of shelled larvae continues throughout the year. Up to now this reproduction strategy has only been observed in *Pisidium conventus* Clessin, 1877, living in the deep zones of lakes where the temperature remains low throughout the year (Meier-Brook, 1970; Holopainen, 1979) and in a population of *Pisidium clarkeanum* Nevill, 1871, (subgenus *Afropisidium* Kuiper, 1962a), from Hong Kong (Morton, 1986). The ability to produce young throughout the year has also been mentioned in North American populations of two Sphaeriidae, viz. *Sphaerium fabale* (Prime, 1851), and *Musculium lacustre* (Müller, 1774) by Mackie (1979) and in populations of the gastropod *Potamopyrgus antipodarum* (Gray, 1843) from New Zealand, Australia and Europe (Fretter & Graham, 1962; Winterbourn, 1970; Schreiber et al., 1998). Regarding the latter there is no doubt that continuous recruitment has been one of the causes of the high densities recorded and has contributed to the success of this invasive species (Dorgelo, 1987).

This mode of reproduction (a continuous reproductive effort) permits rapid adjustment of a population to variations in environmental conditions and should provide *P. tenuilineatum* with an advantage over the other species of *Pisidium*, particularly in sections of rivers belonging to the medium rhithron which constitutes its optimal habitat (Mouthon, 1999). In spite of this, *P. tenuilineatum* is very rarely the dominant species. In France, of several hundred stations sampled since 1977, only the upper reach of the Gapeau, a small river on the Mediterranean coast, was colonised by populations of *Pisidium* dominated by *P. tenuilineatum*. At one of these stations, its density reached 337 individuals per m^2, representing 69.9% of the entire *Pisidium* population (Mouthon, 1994).

A positive relation exists between parent size or, more precisely, total gill area (Guralnick, 2004) and larvae number in *Pisidium* (Ladle & Baron, 1969; Meier-Brook, 1970;

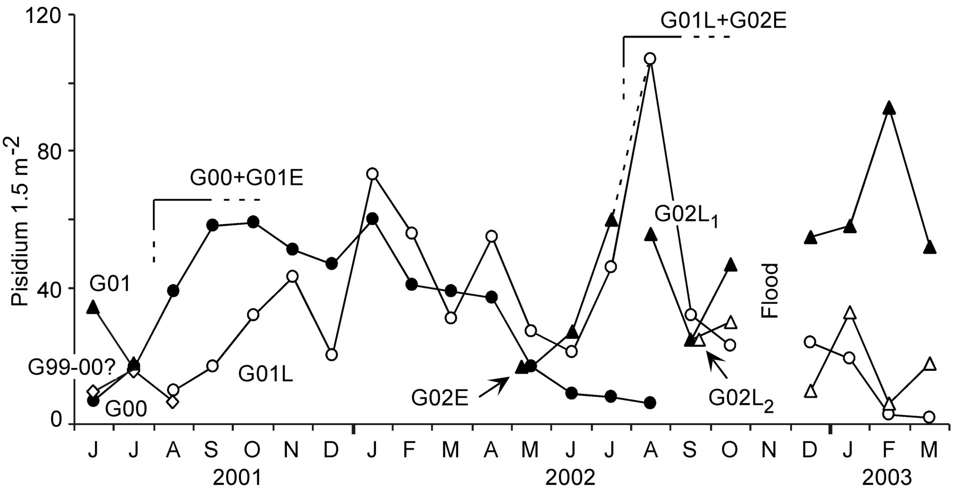

Figure **6**. Seasonal variations in the density of every generation of the Upper Rhône *Pisidium tenuilineatum* population.

Holopainen, 1979; Holopainen & Jónasson, 1983; Holopainen et al., 1997; Araujo et al., 1999). Consequently the small size of *P. tenuilineatum* could explain its low numbers. However, *P. moitessierianum*, which is even smaller, sometimes reaches high densities in the potamon, where it is frequently the dominant species (Meier-Brook, 1975; Mouthon, 1999). For example, in the Verbois reservoir, on the left bank of the Rhône, it represented 67.5% of the *Pisidium* population during the period 1997-2006 (mean density ± SE: 1524.4±140.4 individuals per m^2).

The persistence of *P. tenuilineatum* populations is ensured by continuous recruitment, but the populations rarely reach densities as high as those of most other *Pisidium* species. The potential causes of this situation are the effects of environmental and (or) demographic factors (competition, predation, etc.), and high reproductive costs. Further studies are required (1) to explain why *P. tenuilineatum* usually represents only a small proportion of the *Pisidium* populations, in contrast to *P. moitessierianum*, and (2) to determine whether this reproductive strategy reflects phenotypic plasticity or genetic differentiation.

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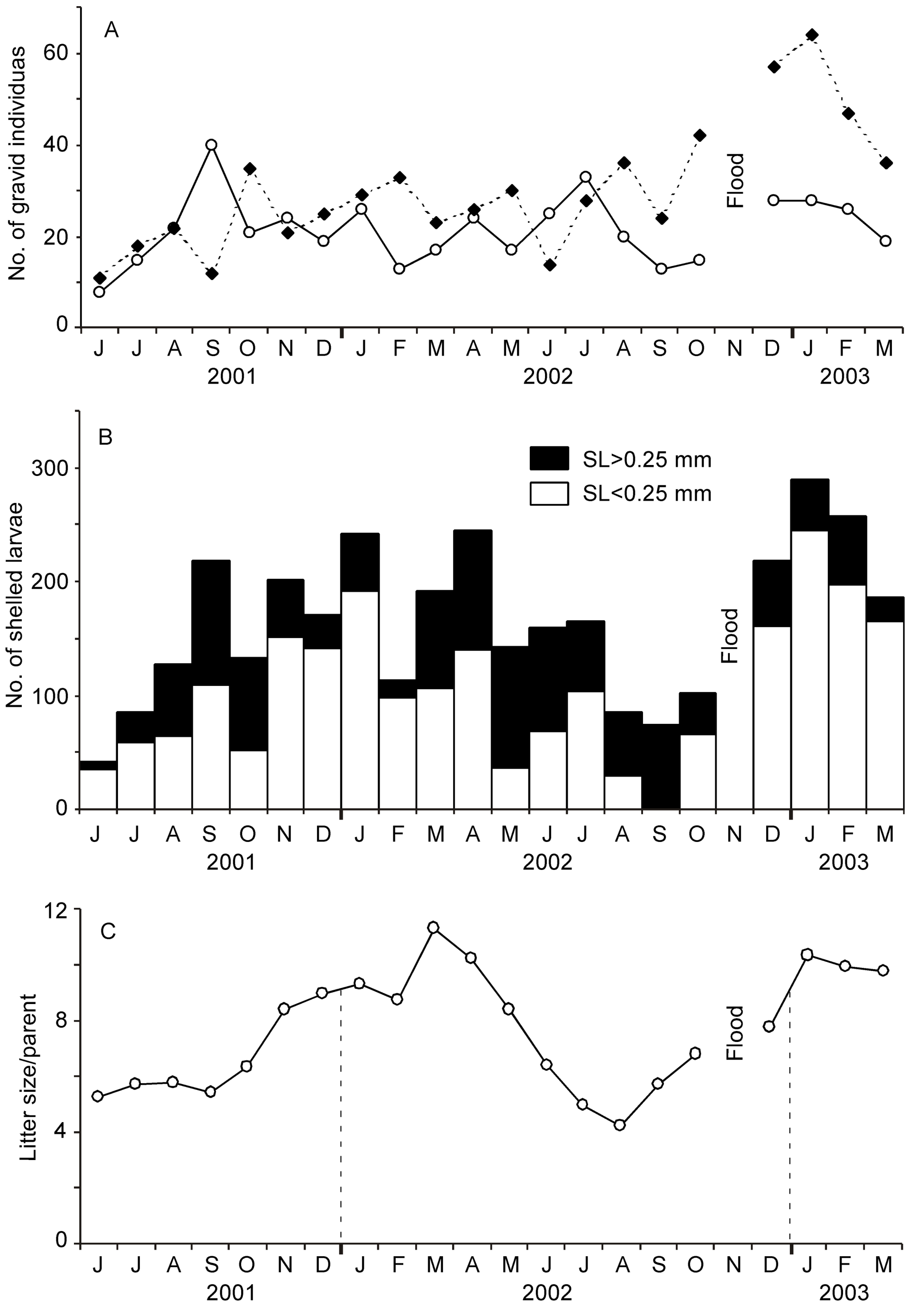

Figure 7. **A**. Number m^{-2} of gravid individuals with eggs or (and) larvae before shell formation (dotted line) and with shelled larvae (bold line). **B**. Number of shelled larvae incubated. **C**. Variations in the litter size (numbers of shelled larvae/parent)

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Appendix **1**: Densities (number m-2) of *Pisidium* species sampled in Villebois reservoir (Upper Rhône) from June 2001 to March 2003. (Sampling was not possible in November 2002 during flood period).

	Right bank							Left bank						
	P. amnicum (Müller 1774)	*P. casertanum* (Poli 1791)	*P. henslowanum* (Sheppard 1823)	*P. moitessierianum* Paladihle 1866	*P. subtruncatum* Malm 1855	*P. tenuilineatum* Stelfox 1918	*P. supinum* Schmidt 1851	*P. amnicum* (Müller 1774)	*P. casertanum* (Poli 1791)	*P. henslowanum* (Sheppard 1823)	*P. moitessierianum* Paladihle 1866	*P. subtruncatum* Malm 1855	*P. tenuilineatum* Stelfox 1918	*P. supinum* Schmidt 1851
2001														
June	8	127	13	348	300	35	0	4	98	110	1752	862	52	536
July	13	218	31	513	357	32	0	6	64	120	2168	868	58	390
August	6	132	12	282	269	20	0	2	84	64	3202	646	82	754
September	6	189	54	694	386	40	2	2	88	72	3870	556	82	662
October	4	193	27	481	535	61	2	0	192	56	2544	662	70	600
November	4	229	90	1170	613	59	4	0	70	56	2900	620	84	750
December	1	170	35	479	700	60	1	0	74	30	2970	262	24	428
2002														
January	3	159	72	564	915	117	0	0	206	106	3050	484	70	616
February	6	61	26	432	293	50	0	2	78	42	2584	346	122	648
March	4	58	30	325	432	41	0	0	74	36	2562	334	76	436
April	10	40	26	310	237	62	0	0	106	10	2334	442	64	516
May	27	60	25	843	334	23	1	2	144	48	2808	528	82	414
June	38	31	29	355	262	21	1	0	170	68	2136	908	82	442
July	42	67	44	894	605	56	1	2	210	92	4746	262	124	504
August	35	96	96	825	1055	149	3	0	188	46	4318	156	66	360
September	57	82	64	1014	832	51	6	0	210	44	5210	100	94	524
October	0	26	71	1267	805	83	9	0	152	26	3890	124	92	312
November														
December	20	26	34	482	608	60	1	0	150	36	3544	120	92	312
2003														
January	88	37	36	724	698	98	0	0	138	24	2518	70	60	242
February	33	53	31	678	741	88	0	0	78	6	1810	50	38	126
March	32	33	27	420	332	60	0	0	38	18	1862	82	34	126