Population dynamics, production, assimilation and respiration of two fresh water mussels: *Unio mancus*, Zhadin and *Anodonta cygnea* Lam.

Oscar RAVERA and Anna R. SPROCATI

CNR Istituto Italiano Idrobiologia, Largo Tonolli 50, 28922 Verbania Pallanza (Italy)

ABSTRACT

Long-term research aimed at following the variation in abundance of two freshwater mussels (Unio mancus and Anodonta cygnea) living in the same environment (Lagadone Stream, Northern Italy) was carried out. The causes influencing these variations were evaluated (natality, mortality and migration). To this aim the multiple capture and recapture method was adopted and the data were processed by the Jolly's stochastic method. In addition, the distribution of the size classes, the growth-rate and oxygen consumption were evaluated. The most important conclusions are: a) the population size of both the species has non-relevant variation over time, but a partial renewal of the population occurs due to immigration and recruitment, which compensate, at least partially, the losses by emigration and mortality and b) more than 90% of the energy intaken by the mussel through the food is dissipated with the respiration.

Key words: fresh water bivalves, Jolly's stochastic model, trophic ecology

1. INTRODUCTION

Population ecology of commercial marine bivalves is the subject of many studies; conversely, information on the fresh water bivalves is very scarce because the exploitation of these molluscs has never been important, except in limited areas and at certain periods. For example, in Northern America, pre-Columbian populations used freshwater mussels mainly for food. In the Tennessee Valley the shell of ten species are used in the button industry and exported to Japan for cultured pearl industry. In Rumania, the shells of freshwater bivalves, nominally those of the genus *Unio*, are exploited for button industry and their soft tissues are used as fodder in poultry farming (Tudorancea 1972).

According to Negus (1966), her studies on *Unio* and *Anodonta* were the first on the growth rate and production of freshwater bivalves. Magnin & Stanczykowska (1971) compared the results of their research on the production of fresh water bivalves from Canadian lakes with those by European authors because of the lack of American studies on this subject.

Most information started from the 1960's, when these molluscs were used as indicators of radioactive and stable pollutants (Halvorsen & Skulberg 1961; Ravera &

Vido 1961; Gaglione & Ravera 1964; Bedford *et al.* 1968; Manly & George 1977; Millington & Walker 1983; Storey & Edward 1989).

There is considerable information concerning the population density, standing crop and distribution of age classes in relation with the mollusc size. Information is scarce on oxygen consumption (e.g., Salanki & Lukacsovics 1967; Paterson 1983; Sheldom & Walker 1989), filtration-rate (e.g., Krzyzanek 1994) and net production (e.g., Negus 1966; Magnin & Stanczykowska 1971) and very scarce on the assimilation-rate, that is the net production plus oxygen consumption (e.g., Tudorancea 1972; Tudorancea & Florescu 1968, 1969, 1970).

If the commercial value of the freshwater bivalves is negligible, their role in the trophic ecology of certain environments is relevant. For example, the Unionidae represent, in term of biomass, more than 90% of the benthic fauna of the River Thames (Mann 1964) and about 95% of that of Lake Borrevann, Norway (Økland 1963).

Long-term research on the dynamics of two populations of bivalves (*Unio mancus*, Zhadin 1965, var. *elongatulus* (Pfeiffer) and *Anodonta cygnea*, Lam. 1799) applying a stochastic model (Jolly 1965) seemed interesting to evaluate, in addition to population size variations, also the causes influencing them (mortality, natality, migration). To this aim the multiple capture-recapture technique was applied. This method, largely used for fish, has previously seldom been adopted for aquatic invertebrates and never for population dynamics studies of fresh water mussels.

In addition, for both the species the size class distribution, production and respiration were evaluated.

2. STUDY SITE

Lagadone Stream is the outlet of Lake Piano (46°2' lat. N; 8°17' long. E), which inflows into Lake Lugano near Porlezza (Northern Italy). This stream has a width from 2 to 4 metres and a depth from 0.10 to 1 metre, and flows in a clay bed of the last Glacial age. Sediments are muddy-silty and very rich in organic material. The mean annual flow is 0.92 m^3 s^{-1} and the water temperature ranges from 5 °C (February) to 24 °C (August). The vegetation growing on the stream bank (*Populus, Robinia, Alnus, Corylus, Crataegus, Cytisus, Berberis, Clematis*) produces two effects: a) in Autumn, through the falling of leaves it supplies an important amount of organic material to the stream and b) during the Summer the canopy reduces the light intensity and, consequently, also the photosynthetic-rate of the aquatic producers (epipelitic algae).

3. METHODS

Sampling occurred on the following dates: 10th August 1975, 7th December 1975; 22nd Febraury 1976; 23rd May 1976, 29th July 1976 and 21st November 1977. The size of each sample, collected by hand at random in an area of 83 m^2 in Lagadone Stream ranged between 173 and 602 individuals of both *Unio* and *Anodonta*. The individuals captured for the first time were marked by an individual label on one valve by a dentist's drill. At each collection, the lenght of the shell of all the specimens (marked and unmarked) was measured with a maximum error of ±1 mm. The

mussels, after having been measured, were released in the area from which they had been collected. The growth-rate in lenght for 175 *Unio* and 282 *Anodonta* for different size classes was thus measured. The growth-rate of the soft tissues, expressed by wet weight, was calculated from the relation between the shell lenght and the weight of the soft tissues. In order to do this, 175 *Unio* and 282 *Anodonta* of different sizes were measured and their soft tissues weighed. The values were expressed in calories, according to the relation reported by Tudorancea & Florescu (1968) for Unionidae: 1 g (dry weight 105°C) = 4488.1 cal. From the ratio between wet and dry weight of the soft tissues of *Unio* (5.38) and *Anodonta* (7.58) it was calculated that 1 g w.w. is equivalent to 834.22 cal for *Unio* and 592.10 for *Anodonta*. Oxygen consumption was measured at four temperatures (6°, 12°, 20° and 25°C) for 77 *Unio* and 60 *Anodonta* of different size. The oxygen uptake by each individual was measured twice, with an adaptation period of 48 hours between the two successive measurements. During the experiment carried out, for a time ranging from 1 to 3 hours, according to the individual size and temperature, the specimens were kept in dark bottles filled with 1 litre of filtered stream water. At the beginning and at the end of the experiment, the oxygen concentration in the water was measured using the Winkler method. The amount of O_2-uptake was expressed in calories according to Ivlev's relation (1934): 1 mg O_2 = 3.38 calories. Population size, emigration, immigration and re-immigration rates were estimated by the Jolly's stochastic model (1963) improved by the same author in 1965. This model, used for insect populations (Jolly 1963; Ericson 1977) but never for molluscs; was adopted because of its extremely simple estimation of the population size variations and their causes (emigration plus mortality, immigration plus natality). In addition, by this model the standard deviations of N_i, $\emptyset_i$ and B_i parameters may be calculated (see Appendix).

4. RESULTS

4.1. *Population dynamics*

In table 1 the total number of individuals collected and those recaptured at least once have been listed. Because the sample of *Unio* collected in February was lost by accident, the values for this population relate to 5 collections, whereas those for *Anodonta* relate to 6. In tables 2 and 3 the variation over time of the population size and its causes are reported.

The percentages of the individuals marked at a sampling and collected at successive ones are reported in table 4.

Anodonta cygnea. Because in the first sampling (August) no marked individual could obviously be collected, the population size in this month cannot be calculated, but its order of magnitude may be estimated on the following considerations. Given the high survival probability ($\emptyset_i$ = 1.0, table 3), it may be assumed that from August to December both the death and emigration rates were negligible. The number of marked individuals calculated in the population in December (206) is identical to that of marked and released individuals in the August sampling. In addition, it is evident that 206 marked individuals represent only a part on the total population. As

a result, the population size in both the samplings (August and December) may be the same, that is 515 individuals.

Tab. 1. Total, marked and unmarked individuals collected at successive samplings. U=Unio; A=Anodonta; S=lost sample.

Date	Total number		Captured unmarked		Captured marked	
	U	A	U	A	U	A
10 August	208	206	208	206	0	0
7 December	48	125	35	75	13	50
22 February	S	210	S	75	S	135
23 May	223	281	159	98	64	183
29 July	122	147	100	46	22	101
21 November	319	283	261	218	58	65

Tab. 2. Values n_{ij} and α_{ij} calculated for *Anodonta* and *Unio*.
Values of n_{ij} - For example, for *Anodonta* the number 21 means that 21 individuals, among the 281 ($n_i=s_i$) collected at time 4 have been marked at time 2. The values of R_i is the total of each column; for example, $R_2= 94 = 67 + 21 + 5 + 1$.
Values of α_{ij} - The number at the top of each column is given by the addition of the individuals marked before a given sampling and collected in this sampling. For example, for *Anodonta* the number 183 is the sum of 37 (individuals marked at time 1) + 21 (individuals marked at time 2) + 125 (individuals marked at time 3). Omitting the top entry, each number is the addition of the individuals marked at sampling preceeding the time $\underline{i}$, not collected at time $\underline{i}$ and collected at successive sampling. For example, for *Anodonta*, 58 = 37 + 21. Z_{i+1} is the addition of the numbers listed in a column, without the top entry. For example, 77 = 58 + 12 + 7; that is the individuals marked at times 1 and 2 and collected at times 4, 5 and 6.

Anodonta

		Values of n_{ij}						Values of α_{ij}				
n_i	s_i	1	2	3	4	5		1	2	3	4	5
206	206							50				
125	125	50						68	135			
210	210	68	67					37	58	183		
281	281	37	21	125				7	12	28	101	
147	147	7	5	16	73			6	7	10	33	65
283		6	1	3	23	32						
$R_i =$			94	144	96	32	$Z_{i+1} =$	118	77	38	33	

Unio

		Values of n_{ij}						Values of α_{ij}				
n_i	s_i	1	2	3	4	5		1	2	3	4	5
208	208							13				
48	48	13										
223	223	47	17					47	64			
122	122	4	2		16			4	6		22	
319	319	15	2		17	24		15	17		34	58
$R_i =$			21		33	24	$Z_{i+1} =$	66	23		34	

From December to February the population decreased from 515 individuals to 384, because 131 individuals released the population for mortality plus emigration. This value is too high in relation to the number of lost molluscs from the population (62) calculated multiplying the population size (515) by the death probability (1-$\emptyset_2$= 0.22). The negative value of B_2 (-69) represents the minimum number of lost individuals. If the standard deviation of B_2 is taken into account ($\pm$53.37), the value of B_2 may attain the maximum value of 122, very similar to the difference between the population size in December and February.

Tab. 3. Values of the demographic parameters and their standard deviation (see note in the text) V = variance. The numbers 1-6 indicate the date of the successive samplings.

	i	α_i	M_i	N_i	$\emptyset_i$	B_i	$\{V(N_i)\}^{1/2}$	$\{V(\emptyset_i)\}^{1/2}$	$\{V(B_i)\}^{1/2}$	$\{V(N_i/N_i)\}^{1/2}$	$\{V(\emptyset_i/\emptyset_i)\}^{1/2}$
ANODONTA	1	-	-	-	1.00	-	-	-	-	-	-
	2	0.40	206	515	0.88	-69	55.88	0.050	53.37	55.88	0.050
	3	0.64	247	384	0.91	102	20.22	0.061	27.34	18.88	0.006
	4	0.65	294	451	0.65	75	30.34	0.098	35.45	29.99	0.096
	5	.069	253	368	-	-	51.99	-	-	51.17	-
	6	0.23	-	-	-	-	-	-	-	-	-
UNIO	1	-	-	-	0.79	-	-	-	-	-	-
	2	0.27	164	606	1.10	96	173.47	0.249	166.47	173.11	0.249
	3										
	4	0.29	219	763	0.52	684	151.64	0.132	191.40	151.36	0.130
	5	0.18	195	1081	-	-	302.22	-	-	301.87	-
	6	0.18	-	-	-	-	-	-	-	-	-

Tab. 4. Percentage of individuals marked at time I and collected at successive times II. For example, 11% on the *Anodonta* marked at time 1 was collected at time 3. The percentages also include the specimens collected more than one time.

Unio

II	2	3	4	5	6
I					
1	6.26		5.08	1.52	2.08
2			54.91	33.46	12.80
3					
4				2.92	1.85
5					6.58

Anodonta

II	2	3	4	5	6
I					
1	9.42	11.22	9.39	6.73	2.08
2		29.63	20.87	16.93	3.14
3			24.04	19.35	5.03
4				20.54	8.09
5					8.34

In May the population was composed of 451 individuals because from February to May 349 survived, 102 individuals joined the population and 35 were lost. From May to July the population size decreased to 368 individuals, as a result of 158 individuals lost, 75 immigrated and 293 survivors.

The population size at the last collection (November) cannot be calculated, because, in the absence of a successive sampling, the number of marked individuals is unknown. As a consequence, only an indicative estimation on the variation from July to November may be given. From July to November the α_i value decreased from 0.69 to 0.23, attaining the lowest percentage of recapture recorded for *Anodonta* (Tab. 3). The decrease of α_i value, that is the ratio between the number of marked and recaptured individuals and the total number of captured ones (marked + unmarked), may be the effect either of a population increase or of the selective loss of marked individuals from the population. Because of the marked individuals were always in good condition, a difference in mortality or emigration rate between marked and unmarked *Anodonta* seems to be less probable than a population increase from July to November.

Unio mancus. As for *Anodonta*, the population size of *Unio* for the August collection cannot be calculated. On the ratio between the population size calculated for December (606 individuals) and the $Ø_i$ value (0.79) an estimation may be obtained. If the immigration from August to December is excluded, the ratio (767) may be considered an acceptable estimation of the population size in August. If this is correct, the population from August to December lost 161 individuals.

From December to May the population increased from 606 individuals to 763. Because the $Ø_2$ value (1.1) calculated for December was higher than the unit (Tab. 3), it is probable that some individuals, emigrating between August and December, joined the population between December and May. These reimmigrates (61) added to the 96 individuals (B_2) that rejoined the population may explain the population increase during this time interval.

In July the population attained the value of 1081 individuals because 684 individuals joined the population, which lost 366 individuals. The survivors were 397, that is the 52% of the May population.

As for *Anodonta*, the population size of *Unio* at the last collection (November) cannot be calculated. Because the α_6 value is identical to that of α_5 (0.18), one may suppose that the population size did not change from July 1976 to November 1977. On the other hand, it is not possible to exclude some variations in population size during an interval of 15 months.

4.2. Distribution of the length classes over time

From figure 1 it is evident for both the species that there are few individuals of the smaller size classes and of the larger ones (that is the younger and the older), while those of the intermediate size are the most frequent. It is probable that this size distribution is the combined effect of the higher death-rate of both the older and the younger individuals and of the more rapid size-growth of the latter, in relation to that of the individuals of intermediate age (Botnariuc & Tudorancea 1967). In addition,

one of the most important causes of death for both the species is predation by rats (*Rattus norvegicus*), which prefer the larger, and thus the older, individuals. The distribution of size-classes of both species is quite constant during the year, a typical pattern of species with a long life-span. This distribution is not significantly modified by the movement of the individuals from the studied area to those adjacent and vice-versa, because this movement is a "wandering" and not an actual migration of individuals belonging to certain size-classes.

Anodonta cygnea. After February the frequency of the smaller individuals increased, and in December and February the larger sized ones were more frequent than in May and July. In July no individual larger than 104 mm was present. It is probable that these larger individuals were eliminated by an increase of the mortality with age. Indeed, according to the age-length relationship reported by Negus (1966) for *Anodonta anatina* and by Økland (1963) for *A. piscinalis* the individuals larger than 104 mm are more than 11 years old, considered an advanced age for the Unionidae (e.g., Brander 1956). After February the increased frequency of the smaller individuals was probably due to recruitment.

Unio mancus. The percentage of collected individuals on the total population is far lower than that of *Anodonta* (Fig. 1). In contrast with *Anodonta,* in *Unio* variations over time of the frequency of the smaller as well as of larger individuals were not evident.

4.3. Growth rate and production

The relationship between shell length and wet weight of the soft tissues is expressed by the equation: $y=ae^{bx}$ for *Unio* and $y=ax^b$ for *Anodonta* (Fig. 2). The correlation coefficient between the measured values and the theoretical ones is highly significant for both species; for *Unio* r=0.99 (wet weight) r=0.98 (dry weigth), for *Anodonta* r=0.99 (w.w.) r=0.91 (d.w.).

From the results attained by Jolly's method, the population density for successive sampling was calculated. From the relationship between shell-length and soft tissues weight and knowing the distribution of the individuals in the length classes (Fig. 1) the biomass of each size class was estimated. The data of density and biomass for each sampling is reported in table 5.

From the shell-length measurements on captured and recaptured 175 *Unio* and 282 *Anodonta,* the length increment for each length class was calculated. The correlation coefficient between the measured values and the theoretical ones is highly significant for both species (r=0.83 for *Unio* and 0.70 for *Anodonta*) (Fig. 3). The relation between length and its increment is expressed by the equation: $y=ax^b$, with b value negative, that is the increment decreases with the increase in the shell length. At the same length the increment of *Anodonta* was always greater than that of *Unio* (Fig. 3). On the annual increment in shell length and the relationship between length and weight, the mean annual increment of the soft tissues weight for different size classes was calculated.
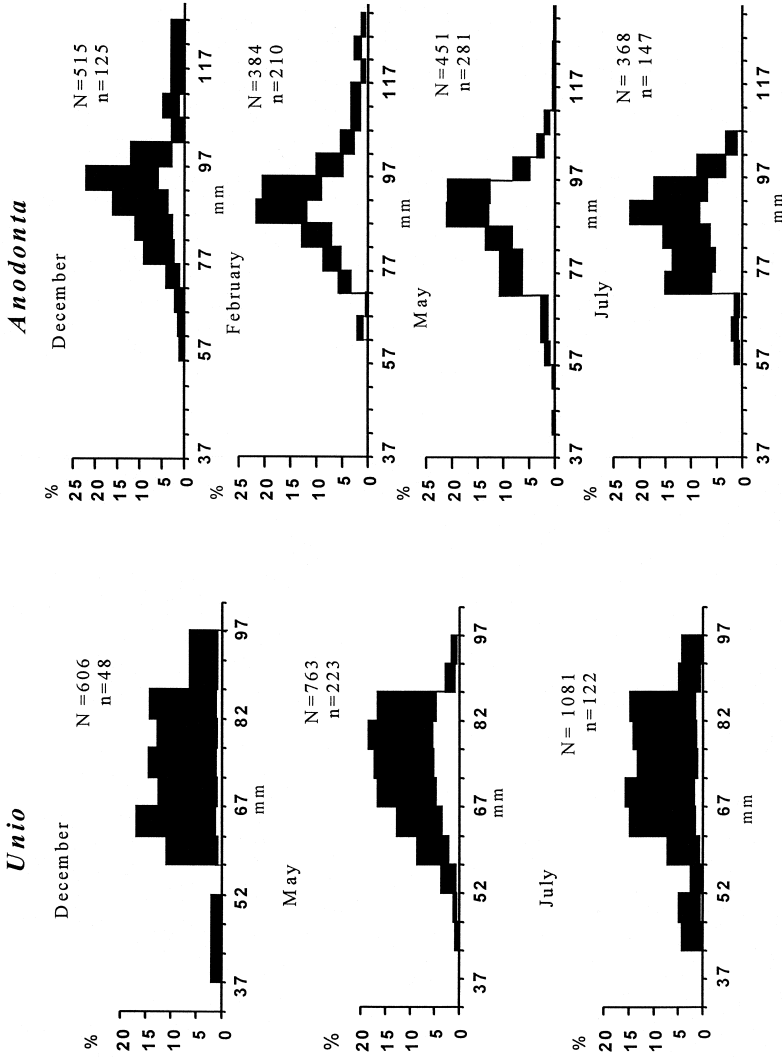
Fig. 1. Percentage frequency of the length classes. The black histogram is related to the whole population, the white to the sample. N = total number of individuals in the population. n = total number of individuals in the sample. The number reported on the abscissa indicates the central value of the length class.
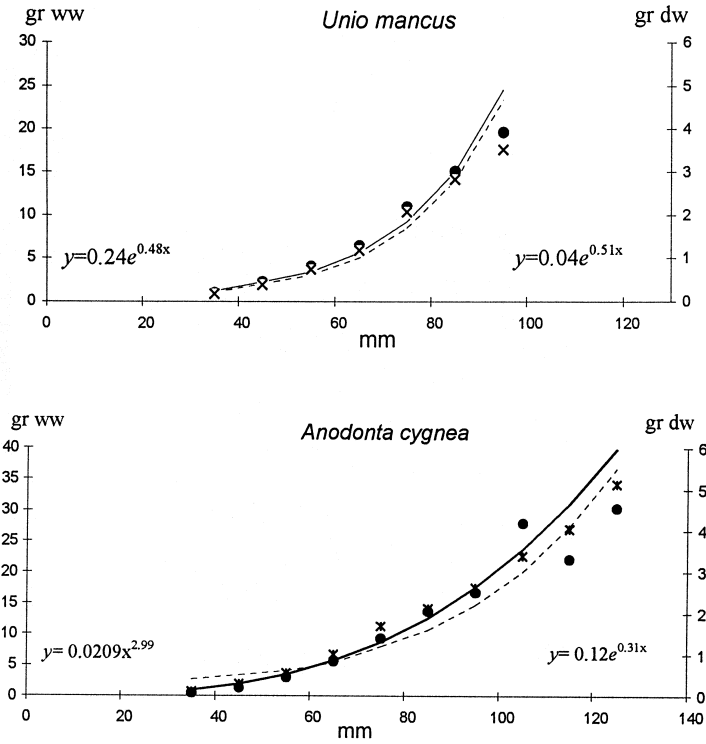
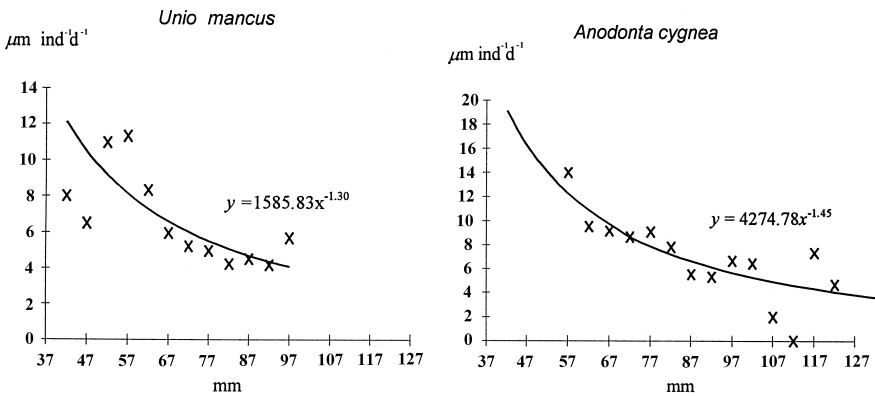Fig. 2. Relationship between shell length (mm) and weight of the soft tissues (grams).

Fig. 3. Relationship between shell length (mm) and its increment (μm ind^{-1} d^{-1}). Each value is the average of more dates (see the text).

The net production was calculated by the addition of the products between the number of individuals belonging to each length class and the increment in wet weight calculated for the corresponding class.

The influence of temperature and the mussel size on oxygen consumption is schematised in figure 4. The correlation coefficients between the measured values and the theoretical ones are always greater than 0.90 and are highly significant. The oxygen uptake was calculated by the addition of the products between the biomass (wet weight) of the individuals belonging to each length class and the amount of oxygen uptake by one gram (wet weight) of soft tissues calculated for the corresponding class and at the temperature at the sampling time.

$\mu g\ O_2\ g^{-1} ww\ h^{-1}$

Unio mancus

(1) $y = 32.42\ e^{0.08x}$
(2) $y = 15.96\ e^{0.09x}$
(3) $y = 17.19\ e^{0.08x}$

Temperature °C

$\mu g\ O_2\ g^{-1} ww\ h^{-1}$

Anodonta cygnea

(1) $y = 71.97\ e^{0.03x}$
(2) $y = 15.36\ e^{0.09x}$
(3) $y = 1.77\ x^{1.32}$
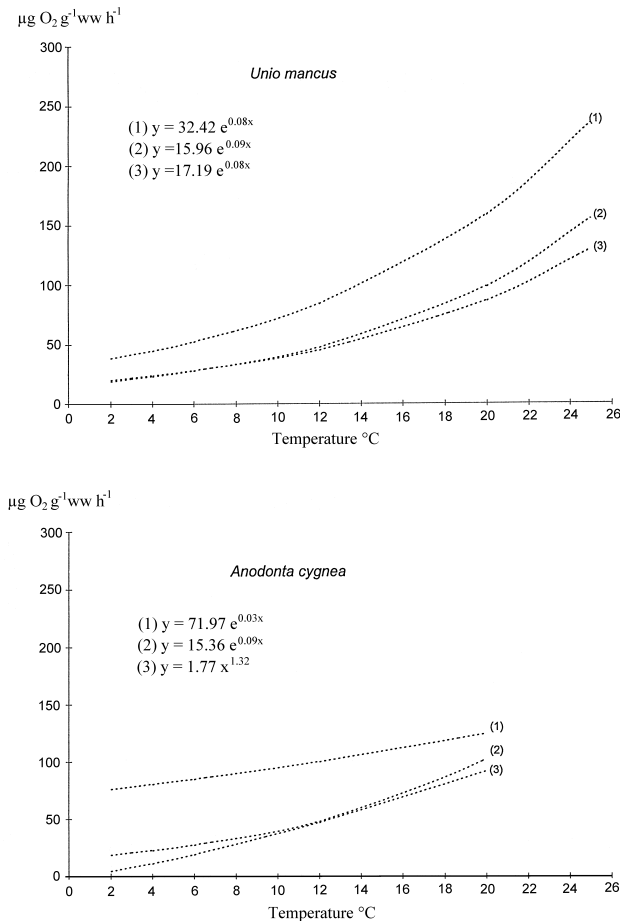
Temperature °C

Fig. 4. Relationship between oxygen consumption by the soft tissues ($\mu g\ O_2\ g^{-1}\ ww\ h^{-1}$) and water temperature for three size classes. For *Unio* the classes are: 1) mm 30 - mm 71 (g 0.1 - g 8.0); 2) mm 72 - mm 87 (g 8.1 - g 16.0); 3) > mm 87 (> g 16.0). For *Anodonta*: 1) mm 30 - mm 71 (g 0.1 - g 8.0); 2) mm 72 - mm 92 (g 8.1 - g 16.0); 3) > mm 92 (> g16.1).

The gross production (that is, assimilation) is obtained by the addition of the net production and the oxygen uptake. In table 5 the values of gross and net production and oxygen uptake calculated for both the species and different sampling times are reported.

Tab. 5. Population density, biomass, net and gross production and oxygen uptake. Gross production (in brackets) expressed in calories, net production and biomass in mg wet weight and calories.

	Month	Density	Biomass		Net and gross production		O$_2$-uptake	
		No ind m^{-2}	g ww m^{-2}	kcal m^{-2}	mg ww m^{-2} d^{-1}	cal m^{-2} d^{-1}	mg O$_2$ m^{-2} d^{-1}	cal m^{-2} d^{-1}
UNIO	December	7.30	81.68	68.12	23.34	19.47 (207.47)	55.62	188.00
	May	9.19	98.80	82.23	28.79	24.01 (835.58)	240.11	811.57
	July	13.02	113.78	94.89	39.80	33.19 (1590.96)	460.88	1557
ANODONTA	December	6.20	99.42	58.86	20.30	12.02 (175.17)	48.27	163.15
	February	4.65	74.13	43.88	14.83	8.78 (102.84)	27.83	94.06
	May	5.43	73.30	49.39	17.30	10.24 (573.62)	166.68	563.38
	July	4.43	54.88	32.49	13.95	8.26 (625.04)	182.48	616.78

5. DISCUSSION AND CONCLUSIONS

The most commonly used method to determing the age of Unionidae consists in counting the number of annual rings on the shell, which show the Winter growth interruption (e.g., Crowley 1957; Haukioja & Hakala 1978). Using the age determination of an adequate number of mussels and the measurements of their shell the population age structure and the growth-rate of each age class may be assessed. Because of the supernumerary rings caused by injury to the mantle, alteration of the annual thermal cycle or other stresses, the identification of the actual annual rings is not easy. This is particularly difficult for adults (that is the individuals older than 3 years), because their more recent rings are concentrated in a small space on the shell border; for these specimens the error is about 1-2 years (e.g., Økland 1963; Magnin & Stanczykowska 1971). The percentage of individuals with supernumerary rings is generally rather high; for example Negus (1966) recaptured a sample of marked individuals in which the 50% had "false rings".

According to Hendelberg (1961) the age may be correctly determined by using the annual rings of the ligament. Indeed, by this method the actual annual rings may be more easily distinguished from the supernumerary ones, but the age of the shell with a corroded umbonal region cannot be determined (e.g., Nardi 1972; Bauer 1983). Other more complex methods, based on the accumulation in the shell of radioisotopes (Nelson *et al.* 1966), bauxite (Garcia & Plante 1992), or on electron microscopy (Garcia 1992) cannot easily be used for routine studies.

It is noteworthy that for the same age the size variability is very large; indeed, individuals of the same size may belong to 3, 4 and even 5 different ages (Botnariuc & Tudorancea 1967; Tudorancea & Florescu 1969).

We preferred to use the size of the mussel than its age for the following reasons: 1) the counting of the annual rings produces better results in bivalves from areas with a cold Winter and a mild Summer than in our region which has a relatively mild Winter and a warm Summer; 2) from the measurement of the shell length of the many recaptured specimens (n=691) the increment in length, in relation to the time between two successive samplings, may be accurately measured and 3) for demographic purposes, subdividing the population into age classes is undoubtedly important, but from the ecosystem economy point of view the distribution into size classes, directly related to the weight, seems to be no less important. Anyway, the net and gross production values calculated on the age class distribution must produce very similar results to those obtained by using the size criterion.

One of the most important advantages of the capture and recapture method used for this study consists in producing no alteration in population demography by collecting even a large number of specimens in relation to the population size (Tab. 1). The marking does not seem to have influenced the survival probability of the mussels. Indeed, during the whole research period only 4% of empty shells of the marked molluscs were collected.

On the data processed according to Jolly's stochastic model (Tab. 3) the population dynamics of both the species was schematized in figure 5. From this figure it is evident that, although the population size has no relevant variation over time, a partial renewal of the population occurred, due to immigration and recruitment which partially compensated the losses by emigration and mortality. In our study, the migration should be more correctly called "wandering", because the molluscs move into and out of the studied area. From December to July the mean individual weight (soft tissues) decrease from 11.19 g ww to 8.74 for *Unio* and from 16.03 g to 12.39 for *Anodonta* is the probable effect of the population renewal (Tab. 5).

The distribution of the lenght classes is quite constant over time (Fig. 1). This relative stability is the combined result of the long life span of these molluscs, the continuous renewal of food, and the scarce natural and anthropogenic stresses influencing their environments. According to Bauer (1983), after having survived to the glochidium stage and the critical stage that occurs when the young mussel leaves the host fish, the mussels are not very sensitive to environment stresses. Økland (1963) estimated that the maximum age for European Unionidae is 15 years, but most of the individuals are less than 10 years old. This is probably the reason why the middle and large individuals are more frequent in mussel populations than the small ones and their span is rather long (Bauer 1983; Negus 1966; Nardi 1972). Most of the specimens collected form Lagadone River ranged from 57 mm to 87 mm for *Unio mancus* and from 72 mm to 102 mm for *Anodonta cygnea*. A *Unio mancus* population from Lake Maggiore (Northern Italy) had a similar length class frequency (Ravera 1964).

The most frequent causes of mortality seem to be eutrophication (Bauer 1983), predation by crayfish (Krzyzamek 1994) and by fish, limited to the small mussels, (Tudorancea 1972) and parasites (Krzyzamek 1994). In certain habitats with a rapid

decrease of the water level, a part of the population dies because the mussels are not able to migrate towards the water to avoid drying up (Økland 1963; Tudorancea 1972).
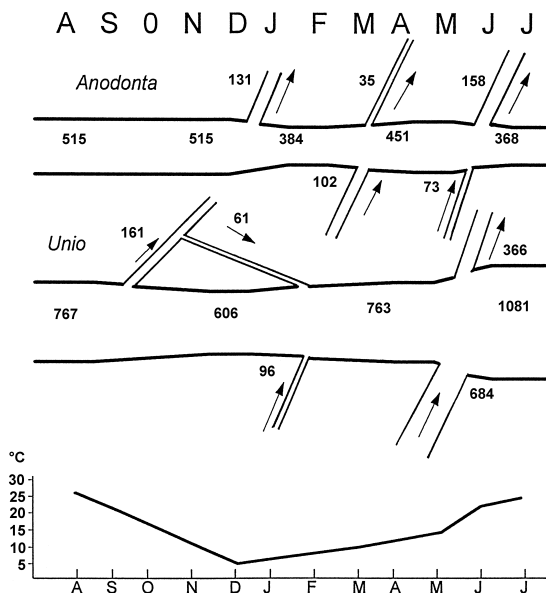

Fig. 5. Population dynamics of *Anodonta* and *Unio* (data from Tab. 3). The numbers inside the frame represent the populations-size, those outside the frame indicate the individuals joining the population or leaving it according to the direction of the arrow. For example, 606 means that the population of *Unio* in December was 606 individuals and 102 means that between February and May 102 individuals joined to *Anodonta* population.

For the large individual size of the Unionidae, if compared with those of the other benthic freshwater species, there is no significant competition with other species and the predation pressure is generally limited. In addition to the age the sole factor of control on both our populations seems to be predation by the rats inhabiting the stream bank (Gandolfi & Parisi 1973). The food supply to the Unionidae from Lagadone Stream consists mainly in organic particles transported by the slow outflow from Piano Lake, which is rich in plankton.

Population density of Unionidae varies with the environmental characteristics and its variation range is about one order of magnitude. Järnefeld (1921) calculated for *Anodonta anatina* living on sandy and gravelling bottom a mean value of 10 individuals m^{-2} and a value of 4 ind m^{-2} for the same species living on clayish sediment. According to Økland (1963) an abundance of 1.8 Unionidae m^{-2} is common in oligotrophic waters and 8.2 m^{-2} in eutrophic waters. The same author reported for *Anodonta piscinalis* from the eutrophic Lake Borrevann an abundance ranging from 10 ind m^{-2} to 19 ind m^{-2} according to the habitat characteristics. Negus (1966) found

that population density varied with the depth from 10.99 ind m^{-2} (from 0 to -1 metre) to 6.85 ind m^{-2} at depths greater than 3 m. Lower values have been reported by Tudorancea & Florescu (1968) for *Unio tumidus* ranging from 0.74 ind m^{-2} in October 1966 to 3.32 ind. m^{-2} in September 1977. Our data showed that the seasonal variations in abundance of both the species were not very different from the densities reported for populations settled in various habitats. This shows the importance of recording the population density for at least one annual cycle.

In Lagadone Stream *Unio* was always more abundant (from 7.30 ind m^{-2} to 13.03) than *Anodonta* (from 4.43 ind m^{-2} to 6.20). The biomass values calculated on the wet weight of the soft tissues for *Unio* varied from 8.17 kg ha^{-1} to 11.39 and for *Anodonta* from 5.49 to 9.94. The highest value of the total biomass (*Unio* and *Anodonta*) occurred in December (18.10 kg ha^{-1}) and the lowest in July (16.87 kg ha^{-1}). These values are very low if compared to those of other authors. Indeed, the values for all the Unionidae from the Lac de Deux Montagnes and Lac Saint Louis (Montreal, Canada) were 857.5 kg ha^{-1} and 70.8 kg ha^{-1} respectively (Magnin & Stanczykozska 1971). Negus (1966) reported a bivalve biomass of 1207.3 kg ha^{-1} for the Thames River.

The oxygen-uptake increases with the water temperature and decreases with the size of the mussel if it is related to the weight unit. This pattern was more evident at temperatures over 12°C and in specimens weighing less than 8 g. As a consequence, the higher frequency of small individuals in the *Unio* population than in the *Anodonta* population may be one of the causes of the higher oxygen uptake calculated for the *Unio* population. For the same weight class the O$_2$-uptake difference was rather small, between 6°C and 12°C (Fig. 4). From the data listed in table 5 the daily O$_2$-uptake on one gram wet weight of soft tissues may be calculated; this value varied from 0.68 mg O$_2$ g^{-1} ww day to 4.05 for *Unio* and from 0.37 mg to 3.32 for *Anodonta* in relation to the size structure of the population and to the water temperature. Since the temperature has a strong influence on the respiration, the seasonal variations of the oxygen uptake were greater than those for biomass and production.

The few studies on the energetics of the freshwater mussels are generally limited to the net production, except those by Tudorancea & Florescu (1968, 1969) which calculated production, respiration and assimilation rates on *Unio tumidus* and *Anodonta piscinalis*, species similar to those of our study.

By comparing our data with those of these authors, the following conclusions may be drawn (Tab. 6): a) the values of biomass, production, respiration and assimilation calculated for *U. tumidus* are similar to those found for *A. piscinalis*, whereas the values for *Unio mancus* are very high, if they are compared with those found for *Anodonta cygnea*; and b) the values of biomass, production, respiration and assimilation estimated for the Unionidae from Lagadone Stream are far higher than those calculated by Tudorancea & Florescu.

Despite the above-mentioned differences, all four species dissipate most of the energy intaken through the food as heat by respiration. This is evident in the high value of the ratio between respiration and assimilation rates, that ranges from 90.25% for *A. piscinalis* to 98.68% for *A. cygnea*. It is probable that these molluscs need so great a supply of energy for their filtration activity. Indeed, according to

Stanczykowska *et al.* (1976) the filtration rate of Unionidae ranges from 1.46 l ind^{-1} d^{-1} to 11.76 l, with an average of 7.20 l ind^{-1} d^{-1}.

Tab. 6. Comparison between two species of gen. *Unio* and two species of genus *Anodonta*. For *Unio mancus* and *Anodonta cygnea* the maximum and the minimum values calculated during the period of the research are reported. (1) values from Lagadone Stream (2) Tudorancea & Florescu 1968. (3) Tudorancea & Florescu 1969.

	Unio		*Anodonta*	
	mancus[1]	*tumidus*[2]	*cygnea*[1]	*piscinalis*[3]
biomass (kcal m^{-2})	68.12 – 9.49	6.60	32.49 – 58.86	7.79
net production (kcal m^{-2} y^{-1})	7.11 – 34.63	1.68	3.01 – 4.39	2.45
O$_2$ – uptake (kcal m^{-2} y^{-1})	68.62 – 568.67	23.37	34.33 – 225.12	22.67
assimilation (kcal m^{-2} y^{-1})	75.73 – 603.30	25.06	37.53 – 228.13	25.12
net production $\times$ 100 / assimilation	5.74 – 9.39	6.71	1.32 – 8.53	9.75
O$_2$ – uptake $\times$ 100 / assimilation	90.61 – 94.26	93.29	91.74 – 98.68	90.25
net production / biomass	0.10 – 0.36	0.25	0.07 – 0.09	0.31

In conclusion, the Unionidae, which are slow producers of potential food for higher trophic levels, accumulate a significant amount of energy available, after their death, to other organisms, in their soft tissues. Through their high respiration-rate, fresh water mussels mineralize a great amount of organic matter and through filtration decrease the concentration of suspended particles. In addition, several solutes (e.g., heavy metals) are accumulated through epithelium in their soft tissues. Because of these characteristics, the freshwater mussels play an important role in the environments where their population density is high.

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APPENDIX

Notation and assumptions

- l = number of samples
- $\alpha_i = M_i/N_i = m_i/n_i$

- $M_i = \dfrac{s_i Z_i}{R_i} + m_i$ = total number of marked individuals in the population at time $\underline{i}$

- $N_i = M_i / m_i / n_i$ total number of individuals when the $\underline{i}$ sample is collected

- $\emptyset_i = M_{i+1} / M_i - m_i + s_i$ probability that an individual alive at the release of the $\underline{i}$ sample will survive till the time of collection of the $\underline{i} + 1$ sample

- $B_i = N_{i+1} - \emptyset_i (N_i - n_i + s_i)$ number of new individuals joining the population in the interval between the i and $\underline{i} + 1$ samples and alive at time $\underline{i} + 1$.

  m_i = number of marked individuals in the $\underline{i}$ sample
  n_i = number of individuals captured in the $\underline{i}$ sample
  s_i = number of individuals released from the $\underline{i}$ sample after marking

- $Z_i = \displaystyle\sum_{K=i}^{1} a_k, i-1$ = number of individuals marked before time $\underline{i}$ which are not collected in the $\underline{i}$ K = i sample but are collected subsequently

- $R_i = \displaystyle\sum_{K=i+1}^{1} n_{ki}$ = number of the s_i individuals released from the $\underline{i}$ sample that are collected K = i + 1 subsequently

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- Multiplying $\emptyset_i$ value by N_{i-1} the number of survival individuals from time $\underline{i}$ - 1 to time $\underline{i}$ may be estimated.
- Multiplying $(1 - \emptyset)$ value by N_{i-1} the number of individuals releasing the population from time i - 1 to time $\underline{i}$ may be estimated.

In Jolly's model "emigrated" means the dead individuals as well as the real emigrates; i.e. the individuals which left the population. The "immigrates" are the individuals which joined the population from the outside plus the newborns. The immigrates also include emigrates which have rejoined the population in a successive time.