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Consumption of macrophytes by invertebrates in Tancada lagoon (NE Spain)

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SUMMARY: *Gammarus aequicauda* and *Sphaeroma hookeri* are the most abundant macroinvertebrates on *Ruppia cirrhosa* (1275 and 1290 individuals.m^{-2}), and *Potamogeton pectinatus* (140 and 680 individuals.m^{-2}) in Tancada lagoon, a Mediterranean coastal lagoon in the Ebro Delta (NE Spain). Consumption and assimilation efficiencies were calculated from bell jar experiments. *Gammarus* grazing effects are higher than *Sphaeroma* on both *Ruppia cirrhosa* and *Potamogeton pectinatus*. Green *Ruppia* leaves lost 0.3 mg per mg *Gammarus* per day, while *Potamogeton* leaves lost 0.2 mg per mg *Gammarus* per day. Decomposing *Ruppia* leaves lost 0.35-0.54 mg per mg *Gammarus* per day. Losses of weight by both *Ruppia* and *Potamogeton* due to *Sphaeroma* feeding were less than half those by *Gammarus*. Assimilation efficiencies are higher for *Gammarus* (44-78 % feeding on *Ruppia* 2 % feeding on *Potamogeton*) than for *Sphaeroma* (26-48 % feeding on *Ruppia*). These assimilation efficiencies were higher than those reported by other authors working at higher latitudes perhaps because of the higher temperature under which the experiments were carried out.

Key words: Consumption, macroinvertebrates, macrophytes.

RESUMEN: CONSUMO DE MACROFITOS POR INVERTEBRADOS EN LA LAGUNA DE LA TANCADA (NE DE ESPAÑA).— *Gammarus aequicauda* y *Sphaeroma hookeri* constituyen las poblaciones de macroinvertebrados más abundantes asociadas a *Ruppia cirrhosa* (1275 y 1290 individuos.m^{-2}) y *Potamogeton pectinatus* (140 y 680 individuos.m^{-2}) en la Tancada, laguna costera mediterránea situada en el delta del Ebro (NE España). Se estudió experimentalmente el consumo y la asimilación en laboratorio. El efecto del «grazing» por *Gammarus* es superior al ocasionado por *Sphaeroma* tanto en *R. cirrhosa* como en *P. pectinatus*. La pérdida de biomasa de hojas verdes de *Ruppia* fue de 0.3 mg por mg de *Gammarus* por día, mientras que en *Potamogeton* fue de 0.2 mg por mg de *Gammarus* por día. Esta tasa es superior cuando se utilizan hojas de *Ruppia* en descomposición (0.35-0.54 mg por mg de *Gammarus* por día). Las pérdidas de peso, tanto en *Ruppia* como en *Potamogeton*, debidas al consumo por *Sphaeroma* son inferiores a la mitad de las observadas en *Gammarus*. La eficiencia de asimilación es mayor en *Gammarus* (44-78 % con *Ruppia*, 2 % con *Potamogeton*) que en *Sphaeroma* (26-48 % con *Ruppia*). Estos valores son superiores a los presentados por otros autores en latitudes superiores, debido, posiblemente, a las temperaturas superiores a las que nuestras experiencias se llevaron a cabo.

Palabras clave: consumo, macroinvertebrados, macrofitos.

INTRODUCTION

Macroinvertebrates feeding on submerged macrophytes process organic matter to different trophic levels, directly through consumption and by increasing the decomposition rates of the organic matter. Consumption of senescent and dead plant material by invertebrate populations has been reported to stimulate microbial decomposition and mineralization (ODUM & DE LA CRUZ, 1967, MANN, 1972). A study of feeding preferences and rates can give indications of the likely water management effects on macroinvertebrate populations and related ecological processes.

In many brackish environments on Mediterranean coasts, *Potamogeton pectinatus* L. and *Ruppia*

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cirrhosa (Petagna) Grande (or other *Ruppia* species) meadows overlap spatially and/or temporally (VERHOEVEN, 1979). Regulation of water flows, both from the continent and from the sea, can determine changes in the environmental characteristics leading to the dominance of one of these macrophytes (MENÉNDEZ & COMÍN, 1989). This could also have effects on the macroinvertebrates living on submerged macrophytes, particularly on *Gammarus aequicauda* (Martynov) and *Sphaeroma hookeri* (Lejuez), which are the most abundant macrofaunal species in this type of environment (VERHOEVEN, 1980).

Laboratory feeding experiments using *Gammarus aequicauda* and *Sphaeroma hookeri* on *Ruppia cirrhosa* and *Potamogeton pectinatus* were conducted to investigate their respective consumption rates and assimilation efficiencies. Some notes are also presented on *Hydrobia* feeding on *Ruppia*. The abundances of the species of macrofauna living on *R. cirrhosa* and *P. pectinatus* in Tancada lagoon (Delta of the Ebro River, NE Spain), are also given. This lagoon develop extensive beds of these submerged macrophytes (MENÉNDEZ & COMÍN, 1989).

MATERIAL AND METHODS

Monthly samples of macroinvertebrates and macrophytes were collected from June 1986 to September 1986 and March 1987 to May 1987, with a core sampler (16 cm diameter) which sampled the water column between 30 and 50 cm high, macrophytes, and the first 5 cm of sediment. The samples were filtered through a 1 mm mesh size net. Dry weights of plants and macroinvertebrates were determined after drying to constant weight at 60 °C (about 48 h). Three replicates were collected each time.

Specimens of *Gammarus aequicauda*, *Sphaeroma hookeri* and *Hydrobia* sp. were collected in the macrophyte meadows of Tancada lagoon for laboratory experiments. The animals were transported to the laboratory in aerated plastic tanks and stored without food at 5 °C for three days in order to decrease metabolic rates and mortality (HARRISON, 1977; VERHOEVEN, 1980). Before the experiments started, the animals were gradually acclimated to the experimental temperature. Experimental tanks were filled with 5 l of lagoon water filtered through 0.5 µm filters. Between 15 and 30 adult specimens of *Gammarus*, 30-60 adult specimens of *Sphaeroma* and 60 adult specimens of *Hydrobia* were used in each experiment together with 5 or 10 g fresh weight of food. The initial amount of food per animal was the same in all the tanks containing the same animal species. For each experiment a control without animals was established. The plant materials used were green *Ruppia* leaves, green *Potamogeton* leaves, *Ruppia* leaves at the early phase of decomposition and epiphytes from the lagoon. The tanks were kept at constant temperature (23 ± 1 °C) and light (112 µE m^{-2} s^{-1}, 12 hours a day) conditions. Water lost by evaporation was replaced with distilled water every day. All experiments were carried out in duplicate. At the beginning of each experiment fresh/dry weight ratios of animals and macrophytes were calculated from a sample of the natural population.

After 24-29 days the animals were removed and the remaining detritus was washed though a sieve of 500 µm onto 0.5 µm filter. The fraction > 500 µm was accounted as plant material and the fraction < 500 µm as detritus (HARRISON, 1977).

The consumption index (CI) was calculated following WALDBAUER (1968) equation.

$$CI = \frac{\text{mg dry weight food ingested}}{\bar{x}\text{ dry weight animals}\cdot\text{time}}$$

For each calculation the average between initial and final dry weight of the animals was used.

RESULTS

Abundance of macroinvertebrates associated with macrophytes

The abundance of macroinvertebrate species in Tancada lagoon changed over a wide range during the period March to September (Fig. 1). This is the best period of the year for animal populations to increase because temperatures and food availability are favorable for animal reproduction and growth (MENÉNDEZ & COMÍN, 1989).

Gammarus aequicauda and *Sphaeroma hookeri* are the most abundant species. They are both more abundant living on *Ruppia* than on *Potamogeton* with maxima in spring (Fig. 2). The herbivore *Idotea chelipes* (Pallas) also develops its population on macrophyte meadows in spring and early summer. *Corophium volutator* (Pallas), *Hydrobia* sp. and *Chirono-*

[1]Change in dry weight of available food minus dry weight of the plant lost in the control tank.

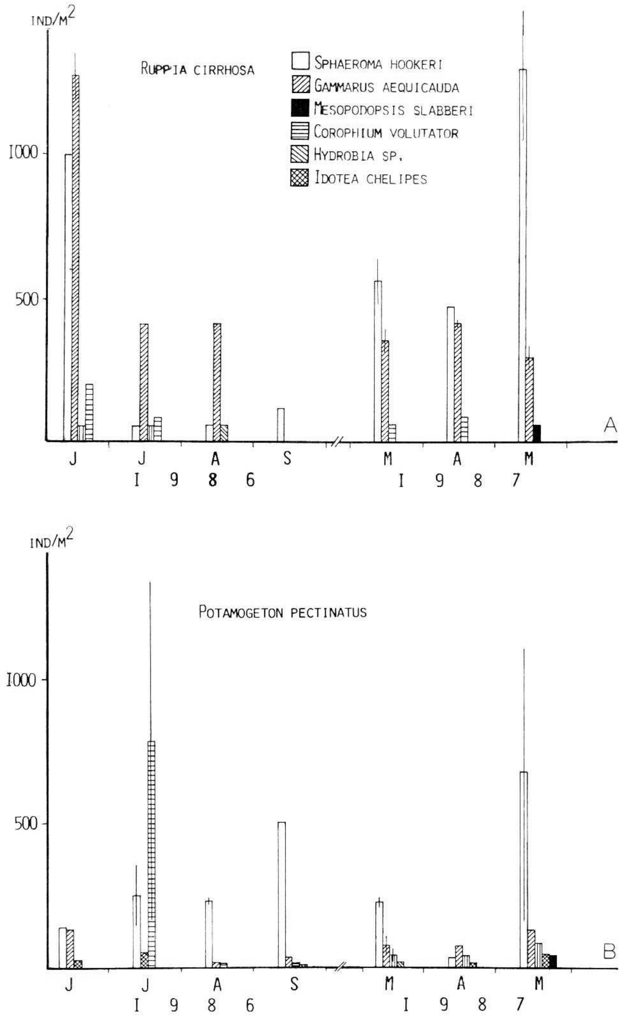

FIG. 1. — Number of individuals of the major invertebrate species per square meter in Tancada lagoon A: In *Ruppia cirrhosa* meadows. B: In *Potamogeton pectinatus* meadows. (The vertical bars indicates the standard deviations. If it is not shown it was less than 5 % of the average).

mus salinarius (Kieffer) were also found in the samples, either in the sediment or on the macrophytes, as well as *Mesopodopsis slabberi* (Van Beneden), although in relatively low numbers or for only a short time.

Laboratory experiments

In all experimentals with animals, more *Ruppia* and *Potamogeton* were lost and more detritus produced than in the controls (Table 1). So, in all the experiments the animals fed on the plants. In the control tanks, decrease of macrophyte weight and increase of detritus also occurred. The decrease of the weight of the plant material in this situation must have been due to microfauna grazing and microbial decay. The increase of detritus must have also been due to microfauna activities.

Changes in animal dry weight, were either positive or negative (Table 1) because of growth and reproduction and, mortality respectively. Increases in animal dry weights were recorded only for animals feeding on *Ruppia*.

In the experiments where leaves of *Ruppia* in the early phase of decomposition were used the calculated amounts of detritus produced by the animals (10 in Table 1), were significantly higher than the respective amounts of food consumed ($p < 0.1$). This is likely to occur because bacterial and fungal growth can also occur on detritus and faecal material as observed previously by KAUSHIK & HYNES (1971). In these cases it is not possible to calculate the amounts of food assimilated.

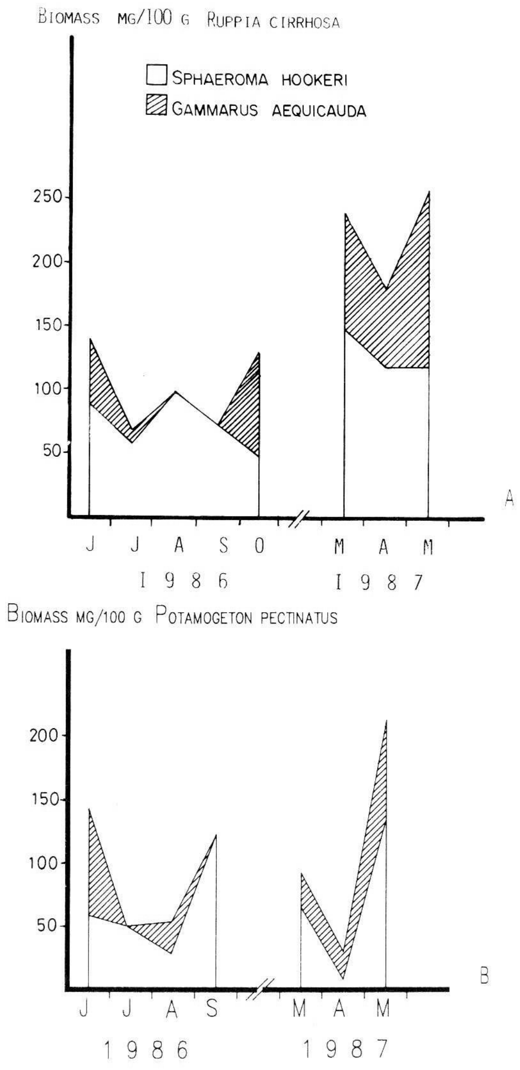

FIG. 2. — Biomass (dry weight) of the more abundant invertebrates related to macrophyte biomass. A: In *Ruppia cirrhosa*. B: In *Potamogeton pectinatus*.

TABLE I.— Variables measured at the beginning and end of the laboratory experiments. The animals and the plants offered as food are indicated. (*Ruppia* (dec): *Ruppia* at the early phase of decomposition. A: Adults, J: Juveniles)

	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*
Gammarus-Ruppia	17	59.28	4A + 33J	39.73	−19.55	5000	670	35.9	634.1	238.9	428.7	190.3
Gammarus-Ruppia	17	42.79	10A + 38J	43.05	0.26	5000	670	85.3	584.7	82.52	379.3	297.28
Gammarus-Ruppia (dec)	27	71	6A + 171J	123.3	52.32	10008	1476.7	0	1476.7	986.5	819.6	0
Gammarus-Ruppia (dec)	34	51	13A + 162J	75	24	10002	1475.8	0	1475.8	836.5	818.7	0
Gammarus-Ruppia (dec)	34	54	9A + 180J	81.68	27.68	10017	1478	0	1246	783.5	589	0
Gammarus-Potamogeton	17	41.5	11A + 38J	36.2	−5.3	5000	920	492	428	219.5	224.2	4.7
Gammarus-Potamogeton	17	53.8	4A + 15J	16.36	−37.44	5000	920	514.3	405.7	—	201.9	—
Gammarus-Epiphytes	40	54	2J	1	−53	4090	1776.6	952	784.6	163	128	0
Gammarus-Epiphytes	40	56	4A + 6J	12	−44	4234	1839.2	1043	796.1	93	139.7	46.7
Sphaeroma-Ruppia	30	110.38	10A + 38J	107.8	−2.5	5000	670	64.6	605.4	298	400	102
Sphaeroma-Ruppia	30	91.89	21A + 35J	162.2	−29	5000	670	95.7	574.3	190	368.9	178.9
Sphaeroma-Ruppia (dec)	61	85.2	28A + 23J	80.7	−4.5	10307	1501.7	394.5	1107.2	231	539.8	308.7
Sphaeroma-Ruppia (dec)	62	82.1	43A + 24J	104.7	22.6	10258	1494.5	414.7	1079.7	412.2	512.7	100.5
Sphaeroma-Ruppia (dec)	61	89.5	44A + 95J	120	30.5	10193	1485.1	316	1169	488.8	602	113.2
Sphaeroma-Potamogeton	30	90.1	18A + 44J	68.2	−21.9	5000	920	717.6	202.4	15.8	0	0
Sphaeroma-Potamogeton	30	98	18A + 22J	66.2	−31.8	5000	920	818.2	101.8	94.1	0	0
Sphaeroma-Epiphytes	30	134.4	14A + 27J	71.6	−62.8	5000	410	354.8	55.2	331.2	0	0
Sphaeroma-Epiphytes	30	117.8	19A + 73J	98.6	−19.2	5000	410	297.7	112.3	158.6	0	0
Hydrobia-Ruppia (dec)	60	177.5	60	117.8	−59.7	10277	1497.3	832.6	664.6	88.8	97.6	8.4
Hydrobia-Ruppia (dec)	60	135.5	60	101	−32.5	10293	1499.6	897	602.5	57.8	34.8	0
Hydrobia-Ruppia (dec)	60	174.4	60	111.5	−62.9	10227	1490	931	559	57.8	0	0
Control-*Ruppia*						5000	670	465.1	204.9			
Control-*Ruppia* (dec)-*Gammarus*						10000	1475	817.9	657.1			
Control-*Ruppia* (dec)-*Sphaeroma*						10000	1466.5	899.3	567.2			
Control-*Potamogeton*						5000	920	716.1	203.8			
Control-Epiphytes-*Gammarus*						10000	1776	1119	656.5			
Control-Epiphytes-*Sphaeroma*						5000	410	99.4	310.6			

1. Initial number of animals (all adults).
2. Initial dry weight of the animals, mg.
3. Final number of animals (J = juveniles, A = adults).
4. Final dry weight of the animals, mg.
5. Change in dry weight of the animals, mg.
6. Fresh weight of the available food, mg.
7. Dry weight of the available food, mg.
8. Dry weight of the remaining food, mg.
9. Change in dry weight of the available food (initial dry weight-final dry weight), mg.
10. Detritus produced by the animals (detritus accumulated in the experiment tanks minus detritus accumulated in the control tank), mg.
11. Food consumed by the animals (change in dry weight of the available food minus dry weight of the plant lost in the control tank), mg.
12. Food assimilated (food consumed by the animals-detritus produced by the animals), mg.

Feeding on epiphytes was very low. Consumption of decomposing *Hydrobia* on *Ruppia* was also very low (Table I).

In spite of the higher abundances of *Sphaeroma* (both in number of individuals and weight) lower amounts of macrophytes were lost in the experiments in comparison with those of *Gammarus* (2 in Table 2). Consumption of macrophytes by *Gammarus* is higher than by *Sphaeroma* ($p < 0.01$) (3 in Table 2).

Gammarus feeding on green *Ruppia* and *Potamogeton* assimilated more food than *Sphaeroma*. The assimilation efficiency was about 60 % of the food consumed in the case of *Gammarus* with *Ruppia* (44 % and 78 %) and 2 % for *Potamogeton*, and lower in the case of *Sphaeroma*, about 40 % for *Ruppia* (26 % and 48 %) and 40 % for *Potamogeton*.

DISCUSSION

The community of grazing invertebrates in Tancada lagoon is dominated, both in number of individuals and biomass, by *Gammarus aequicauda* and *Sphaeroma hookeri*, with a few other species much less abundant. The pattern of seasonal variation presented here for the macrophyte beds is not the same for all the lagoon area. During late autumn grazers accumulate on macrophyte detritus driven to the lagoon shores by wind and water motion (Menéndez *et al.*, in press). Low temperatures in winter are responsible for low densities of macroinvertebrates. Verhoeven (1980) also described a similar pattern of seasonal changes of macroinvertebrate densities in *Ruppia* dominated communities in the Camargue (France) and The Netherlands.

TABLE 2. — Variables on the feeding activity of the animals calculated from data in Table 1.

	1	*2*	*3*	*4*	*5*
GAMMARUS-*RUPPIA*	0.16	0.44	0.3	0.18	44.33
GAMMARUS-RUPPIA	0.06	0.47	0.3	0.17	78.27
GAMMARUS-RUPPIA (DEC)	0.42	0.63	0.35	—	—
GAMMARUS-RUPPIA (DEC)	0.55	0.97	0.54	—	—
GAMMARUS-RUPPIA (DEC)	0.24	0.38	0.36	—	—
GAMMARUS-POTAMOGETON	0.19	0.38	0.20	0.004	2
GAMMARUS-POTAMOGETON	0	0.40	0.20	—	—
GAMMARUS-EPIPHYTES	0.24	1.18	0.19	—	—
GAMMARUS-EPIPHYTES	0.11	0.97	0.17	0.05	33.53
SPHAEROMA-RUPPIA	0.09	0.19	0.12	0.03	26.66
SPHAEROMA-RUPPIA	0.05	0.15	0.1	0.05	48
SPHAEROMA-RUPPIA (DEC)	0.09	0.46	0.22	0.13	59.09
SPHAEROMA-RUPPIA (DEC)	0.15	0.4	0.19	0.04	19.47
SPHAEROMA-RUPPIA (DEC)	0.16	0.38	0.2	0.04	18.5
SPHAEROMA-POTAMOGETON	0.006	0.08	*	*	*
SPHAEROMA-POTAMOGETON	0.04	0.04	*	*	*
SPHAEROMA-EPIPHYTES	0.11	0.018	*	*	*
SPHAEROMA-EPIPHYTES	0.05	0.0	*	*	*
HYDROBIA-RUPPIA (DEC)	0.02	0.15	0.022	0.002	9.09
HYDROBIA-RUPPIA (DEC)	0.017	0.17	0.01	—	—
HYDROBIA-RUPPIA (DEC)	0.014	0.13	*	*	*

1. Detritus produced by dry weight of the animals and time, mg detritus/mg animals/day.
2. Food lost by dry weight of the animals and time, mg food lost/mg animals/day.
3. Consumption index (CI): food consumed by dry weight of the animals and time, mg food consumed/mg animals/day.
4. Food assimilated by dry weight of the animals and time, mg food assimilated/mg animals/day.
5. Assimilation eficiency, AE = (C − E)/C × 100, % consumed food assimilated by the animals.

* Not calculated because there was no consumption, see column 11 in table 1.

– Not calculated because detritus produced was higher than food ingested, see column 12 in Table 1.

The experimental design and the gravimetric method used for consumption calculations overestimate the amounts of macrophytes consumed by *Gammarus* and *Sphaeroma* and the detritus produced because both calculations take into account the loss by decomposition which is accelerated by grazing. In addition the effects of cannibalism and coprophagy on consumption rates were not investigated.

Applying the consumption rates calculated here (Table 2), the amounts of macrophytes consumed by animal populations in Tancada lagoon, would only be the following percentages of the dry weight biomass at the time of maximum animal biomass/plant biomass ratio. In May for *Gammarus* (143 $mg.m^{-2}$) on *Ruppia* (100 $g.m^{-2}$) 0.043 %, in June for *Gammarus* (86 $mg.m^{-2}$) on *Potomogeton* (100 $g.m^{-2}$) 0.017 %, and in March for *Sphaeroma* (410 $mg.m^{-2}$) on *Ruppia* (268 $g.m^{-2}$) 0.015 %. We conclude that grazing by macroinvertebrates does not play an important direct role in the consumption of green biomass of macrophytes, but is important in accelerating the decomposition of vegetable material accumulated at the end of the growing season in Tancada lagoon.

Feeding activities contribute greatly to macrophyte fragmentation and, consequently, to increase the surface to volume ratio of particles, enhancing microbial colonization and macrophyte decomposition (VALIELA, 1984). Then the calculation food assimilated from the difference between food consumed and excretion by animals may be underestimated because excretion estimations may include high density populations of microorganisms which grow on the faecal pellets.

The assimilation efficiencies calculated here are higher than those calculated by VERHOEVEN (1980) for the same two species feeding on *Ruppia* in the

TABLE 3. — Comparison of assimilation efficiency in different species of Amphipods and Isopods with data from the literature.

	Assimilation efficiency, %	*Reference*
Hyalella azteca		
Epiphytes on *Chara*	47-92	HARGRAVE, 1970
Diatoms	75	
Green algae	45-55	
Bacteria	60-83	
Blue green algae	5-15	
Sediment + microflora	6-15	
Elm leaves	5	
Orchestia botae	30-50	SUSCHENYA, 1970
Idotea chelipes		
Ruppia cirrhosa	39-40.4	VERHOEVEN, 1980
Gammarus pseudolimnaeus		
Fungal mycelium	42.6-75.6	BARLOCHER & KENDRICK 1975
Autumn shed leaves		
Ulmus americana	18.6 ± 4.2	
Acer saccharum	17.2 ± 3.8	
Gammarus zaddachi		
Ruppia cirrhosa	22.1-28.1	VERHOEVEN, 1980
Gammarus salinus		
Ruppia cirrhosa	20.2	VERHOEVEN, 1980
Gammarus aequicauda		
Ruppia cirrhosa	25.1-28.3	VERHOEVEN, 1980
Gammarus aequicauda		
Ruppia cirrhosa	44-78	This study
Gammarus aequicauda		
Potamogeton pectinatus	2	This study
Sphaeroma hookeri		
Ruppia cirrhosa	16.6-28.3	VERHOEVEN, 1980
Sphaeroma hookeri var. *mediterranea*		
Ruppia cirrhosa	0-6.9	VERHOEVEN, 1980
Sphaeroma hookeri		
Ruppia cirrhosa	26-48	This study
Sphaeroma hookeri		
Potamogeton pectinatus	0	This study

laboratory (15 °C, 28 days, 2500 lux 12 h/day) (Table 3).

This may be a consequence of the higher temperature under which our experiment took place which can accelerate metabolic and decomposition rates. *Hydrobia* feed mainly on detritus, bacteria and small algae (FENCHEL *et al.* 1975). NIENHUIS & VAN IERLAND (1978) also observed that it consumes small portions of epidermal cells of macrophytes. We also observed in our experiments that *Hydrobia* spends most of the time feeding on pellets of *Gammarus* and *Sphaeroma* and not on vegetative portions of macrophytes. Plant detritus and animal pellets can be quickly colonized by fungi (MOTTA, 1978) bacteria (MANN, 1972) and other organisms. Which may then be eaten by grazers and deposit feeders.

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