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DENSITY FLUCTUATIONS IN POPULATIONS (1982 - 1986) AND BIOLOGICAL OBSERVATIONS OF *POTAMOPYRGUS JENKINSI* IN TWO TROPHICALLY DIFFERING LAKES

JAAP DORGELO

KEYWORDS : *Potamopyrgus jenkinsi*; gastropod; population dynamics; eutrophication; floating; burrowing; macrophytes; temperature; tolerance; carination.

ABSTRACT

The hydrobiid snail *Potamopyrgus jenkinsi* (E.A. Smith), characterized by parthenogenesis and ovovivipary, was quantitatively sampled monthly between June, 1982, and December, 1986, on sandy bottoms in the shallow zones of the meso-oligotrophic Lake Maarsseveen I and the eutrophic Lake Maarsseveen II. The snail demonstrated a very clumped distribution in both lakes. The mean numbers of juveniles and adults taken together fluctuated strongly. Organisms in Lake I showed relatively high densities (up to 25,000 per m^2) in 1982, followed by a sudden drop to values approaching zero in December, 1982, with a subsequent rapid increase in densities, fluctuating between 2,000 and 200 per m^2. In Lake II, densities of snails fluctuated between 13,000 and 300 per m^2 with decreases in the spring of 1985 and 1986. The various types of decreases in the lakes are extensively discussed, but no explanation is presently available. The reduction in Lake I was of catastrophic proportions, but the speed of recovery of the population was remarkable.

Floating was observed only in Lake I, and only during the occurrence of the highest densities on the sediment. Burrowing behaviour was very common, but strongly suppressed under an uninterrupted dark regime. A shift of temperature from 15 to 22 °C had the same effect. A number of submerged macrophyte species from Lake I proved to attract *P.jenkinsi* in the absence of sandy substrate, though these plants were only covered by the snail during the period of the highest densities in 1982. Temperatures of 20 °C or lower were well tolerated, unlike temperatures of 25 and 30 °C. Growth was distinct at 10, 15 and 20 °C. Keeled individuals were encountered in much higher numbers in Lake I than in Lake II.

INTRODUCTION

Eutrophication, the allochthonous supply of inorganic nutrients enhancing primary production (RODHE, 1958) leads to a wide range of biological, chemical and physical changes in aquatic ecosystems (see DORGELO, 1987). Relatively little attention has been given to functional responses of macro-invertebrates to eutrophication. The results presented here are part of a study on the ecophysiology and population dynamics of populations of selected freshwater molluscs, the gastropod *Potamopyrgus jenkinsi* and the mussel *Dreissena polymorpha*, in lakes of different trophic state. They deal with the fluctuations in the mean numbers of *P.jenkinsi* in the meso-oligotrophic Lake Maarsseveen I and the eutrophic Lake Maarsseveen II during 1982 - 1986. The structural aspects of these dynamics will be published elsewhere.

Additionally, data on the biology of this species are given. Floating of *P.jenkinsi* in nature had so far not been mentioned in the literature. Its burrowing behaviour as well as its behaviour in the vicinity of aquatic macrophytes was observed in the laboratory. The temperature tolerance of winter animals was established, and, finally, some observations on the occurrence of keeled individuals are given.

P.jenkinsi (E.A. Smith) has been introduced into Europe (BONDESEN and KAISER, 1949; FROMMING, 1956), probably from New Zealand or Australia (WINTERBOURN, 1970). It was reported in Europe for the first time in the 19th century. This species has spread widely since, enhanced by active upstream movements, water fowl, and even by fish as it has been demonstrated to survive a six hours passage through the gut of a trout (HAYNES *et al.*, 1985). This passive transport and active migration go together with euryoecious characteristics, since this species is found in fresh, brackish (REMANE, 1970; FENCHEL, 1975), stagnant, running, oligotrophic, eutrophic, acid, alkaline, calcareous and granite waters, and in caves (LUCAS, 1960). It was encountered for the first time in The Netherlands in 1913 (see BOETTGER, 1951). As a detritivorous/herbivorous organism (CALOW and CALOW, 1975; HAYNES and TAYLOR, 1984) it has a broad base for its nutritional requirements. Furthermore, it is parthenogenetic (BOYCOTT, 1919), a rarity in snails (BONDESEN and KAISER, 1949), and ovoviviparous. Males, as described by PATIL (1958), do occur, but seem to be very rare in The Netherlands (WALLACE, 1985). This snail is free of parasitic trematodes (ROBSON, 1923; KEULEN, 1981). Predation on *P.jenkinsi* has been reported for trout (WHITEHEAD, 1935), bream and roach (C. Davids, pers. comm.), and for diving waterfowl (*Aythya ferina*; *A.fuligula*), wintering in the IJssel Lake (B. bij de Vaate, pers. comm.).

MATERIAL AND METHODS

Specimens of *P.jenkinsi* were collected from sandy bottoms in the meso-oligotrophic Lake Maarsseveen I and the eutrophic Lake Maarsseveen II (see for lake characteristics DORGELO and GORTER, 1984) during the period from June, 1982, until December, 1986. Mean numbers per m^2 were calculated from samples taken at various depths. Earlier sampling demonstrated that the snails were not encountered on the muddy substrates found at greater depths (see also WHITEHEAD, 1935). Moreover, the majority of the snails were caught between 0 - 5 m depth in Lake I and between 0 - 1.5 m depth in Lake II in all seasons (Dorgelo, unpublished data). Therefore, from January, 1984, when sampling was strictly standardized for population structure analysis, 20 samples were taken monthly between depths of 0.5 and 5.0 m in Lake I, and 10 at a depth of 0.5 m in Lake II.

The sampling was performed by means of a Petersen grab, and, later, hydraulic lift samplers; both types of apparatus have the same sampling efficiency for *P.jenkinsi* (DORGELO and HENGST, 1986). The sampling station in Lake I was located on the north-westerly shore in 1982 and 1983, and, since this site became increasingly overgrown with *Potamogeton lucens*, at the opposite side of the lake during 1984 - 1986. The station in Lake II was on the north-westerly shore. Periodic controls showed similar densities at other sites with sandy substrates in both lakes.

Floating animals were collected with a hand-operated sampling net.

The burrowing behaviour of these organisms was analyzed in the laboratory using 33 x 20 x 18 cm plastic aquaria filled with lake water above 2 cm of sandy lake substrate under natural light conditions, or in the dark.

Data on the influence of submerged macrophytes as attractive, repellent or indifferent substrates for *P.jenkinsi* were analyzed as described by DORGELO and HEYKOOP (1985) for *Daphnia longispina*, using fresh and artificial plants in a 100 x 10 x 10 cm glass aquarium. The live plant was placed in one corner of the aquarium, the artificial plant in the opposite corner, and 50 snails were released in the center of the aquarium. Since *P.jenkinsi* has a strongly positive phototaxis, and since it was not sure that the experiments would take place under homogeneously distributed natural light conditions, a similarly sized aquarium without plants ran in parallel as control. Sand from the lake was not added to the aquaria in order to prevent preference of the sediment as an interference.

Temperature tolerance experiments were conducted with animals collected in January, 1985, from the ice-covered lakes (water temperature : 1.5 °C). Various size classes, separated by sieving the conical shells through split-shaped perforations, were abruptly exposed to 5, 10, 15, 20, 25, and 30 °C (after acclimation to 15 °C over a 24 hour period) in plastic aquaria as described above.

RESULTS

Density fluctuations.

In the meso-oligotrophic Lake I, densities were highest in 1982 (about 25,000 individuals per m^2). The population showed a dramatic drop to zero between November, 1982, and March, 1983, and increased rapidly again to achieve a level fluctuating between 200 and 2,000 individuals per m^2. After the middle of 1984, these levels were between 300 and 1,500 individuals per m^2 (Fig. 1). The high SD values, also present at higher sample numbers during 1984 - 1986, reflect the dispersed distribution of the snails. The highest SD values were found at the relatively high densities in 1982 (up to 8,928). The highest value observed after 1982 was 2,683, whereas on 76 % of the sampling days after 1982 the values were lower than 1,000.

The dramatic decrease in numbers in December, 1982, included all size classes equally at various depths. The reduction was also observed at other localities in the lake (see also WIEDIJK, 1983). At the end of the following year (1983) a further decrease was encountered.

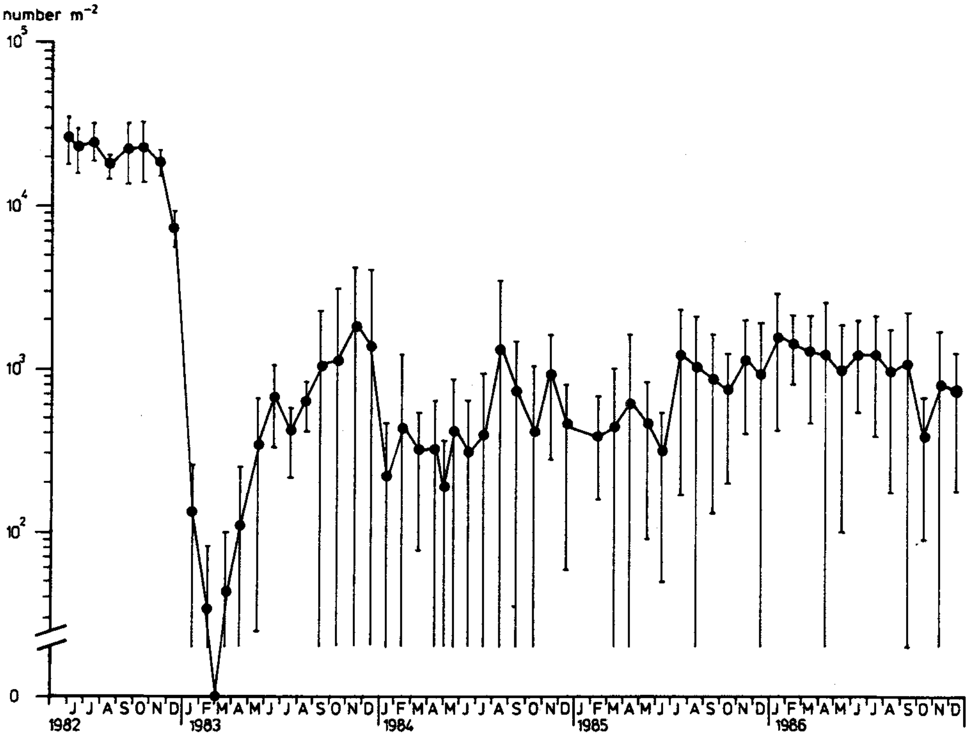

Fig. 1. Mean numbers per m^2 (± SD) of *P.jenkinsi* collected in Lake Maarsseveen I from June, 1982, through December, 1986. Number of samples 4 - 5 (1982 - 1983) and 20 (1984 - 1986).

Date		0.5		1.5		3.0		4.5		6.0 m	
1983.09.27	<1.00	126	1789	82	1164	4	57	7	99	21	298
	1.0-1.5	26	369	41	582	1	14	3	43	11	156
	1.5-2.0	13	185	16	227	1	14	0	0	0	0
	>2.0	0	0	0	0	0	0	0	0	0	0
1983.10.25	<1.00	3	43	213	3025	8	114	13	185	2	28
	1.0-1.5	4	57	81	1150	4	57	7	99	1	14
	1.5-2.0	0	0	19	270	2	28	7	99	1	14
	>2.0	0	0	1	14	1	14	0	0	0	0
1983.11.22	<1.00	165	2343	219	3110	7	99	9	128	14	199
	1.0-1.5	65	923	61	866	5	71	16	227	12	170
	1.5-2.0	24	341	22	312	1	14	4	57	1	14
	>2.0	2	28	0	0	0	0	0	0	0	0
1983.12.19	<1.00	42	596	439	6234	0	0	0	0	0	0
	1.0-1.5	20	284	120	1704	0	0	0	0	0	0
	1.5-2.0	7	99	34	483	0	0	0	0	0	0
	>2.0	0	0	1	14	0	0	0	0	0	0
1984.01.11	<1.00	6	85	10	142						
	1.0-1.5	5	71	5	71						
	1.5-2.0	3	43	2	28						
	>2.0	0	0	1	14						

Table 1. Densities of various size classes of *P.jenkinsi* over depth between 1983.09.27 and 1984.01.11 (one sample per depth). Size classes are given as shell width in mm.

Analysis of this period by depth and size class (Table 1) demonstrates the substantial contribution to the decrease in the number of young individuals, occurring in shallow water. The high SD values (exceeding the mean values) were in this case caused by great differences in density at various depths.

In the eutrophic Lake II (Fig. 2), densities fluctuated between about 1,000 and 10,000 individuals per m^2 until the end of 1984. Then, in the spring of 1985 as well as 1986, the numbers dropped considerably from densities of about 13,000 and 8,000, respectively, to densities of about 400 and 300 individuals per m^2, respectively. At other locations similar low levels were also observed. The SD values were not frequently as high as in Lake I. The clumped distribution, however, was also striking, although by this time sampling was performed over a much smaller depth range (see 'methods').

Floating.

Floating snails were observed in 1982 during the period of relatively high densities on the sandy sediment in Lake I, but only at places without wave action, and mainly along reed belts. Sampling was conducted along the south-easterly shore on 1982.07.01 and 1982.09.07, and along the north-easterly shore on 1982.07.21. Table 2 presents the numbers and percentages of snails collected, both on the surface and on the sediment at a depth of 0.5 m. All size classes present on the sediment were found floating, on 1982.07.01 even in approximately similar

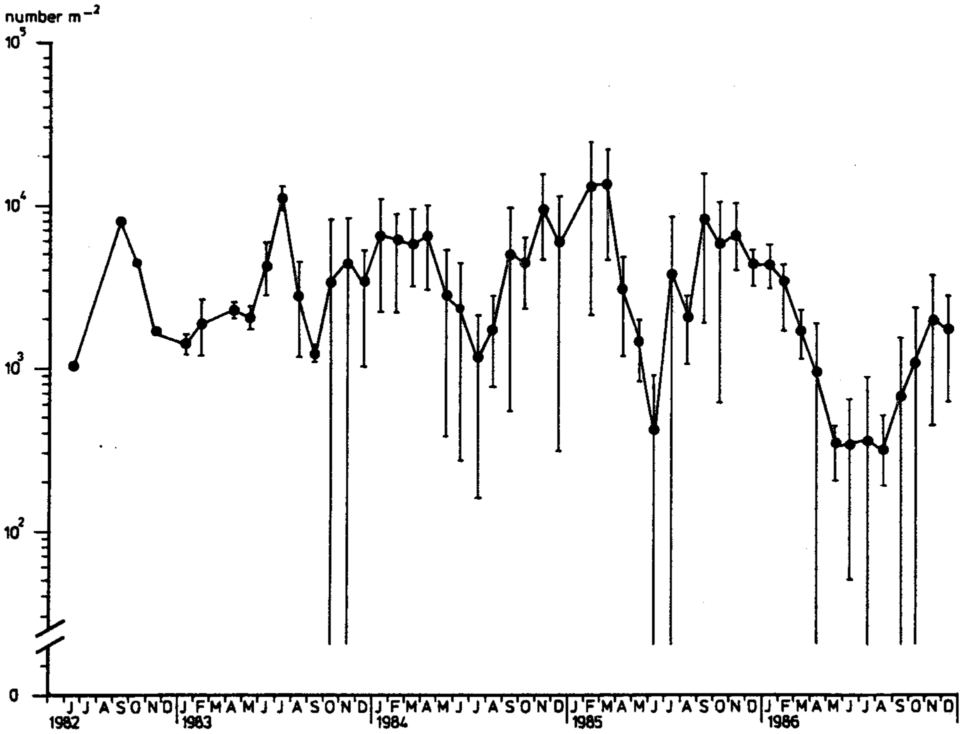

Fig. 2. Mean numbers per m^2 (± SD) of *P.jenkinsi* collected in Lake Maarsseveen II from June, 1982, through December, 1986. Number of samples 1 (1982), 4-5 (1983) and 10 (1984-1986).

percentages. Floating densities, however, were markedly lower than those on the sediment.

In 1983, only very low numbers of floating snails were observed. This was also true for Lake II, in both 1982 and 1983.

	Size class											
	<1				1.0-1.5				1.5-2.0			
	Surface		Sediment		Surface		Sediment		Surface		Sediment	
Date	Number	%	Number	%	Number	%	Number	%	Number	%	Number	%
1982.07.01	242	33	384	32	391	54	697	58	94	13	126	10
1982.07.21	72	34	339	45	129	61	340	45	11	5	78	10
1982.09.07	136	72	659	68	51	27	256	26	1	1	54	6

Table 2. Numbers and percentages of *P.jenkinsi* collected at the water surface and on the sediment at 0.5 m depth. Size classes according to shell width in mm. Individuals >2.0 mm were not encountered.

Burrowing.

P.jenkinsi crawls upon or digs into the upper layer of the sediment. When examining undisturbed sandy bottoms in shallow water of Lake I only a few snails could be seen. After turning over the top layer of the sediment with a sampling net, however, many individuals became visible.

The burrowing behaviour was studied under experimental conditions. Fig. 3 demonstrates that nearly all the snails, regardless of the lake of origin, remained covered or near so in the sand after the first week, when observed daily at 6.00 p.m. When a temperature shift from 15 to 22 °C was imposed (Fig. 3) the animals were increasingly observed upon the surface of the sand. A minority was seen on the walls of the aquarium, whereas a few were observed to be floating during the period of the experiment. Since the light/dark regime may influence burrowing behaviour, another experiment was done, using a natural light/dark and a dark regime (Fig. 4). In both the aquaria with 50 and 100 snails, the numbers of snails remaining buried in the sand were highest under the light/dark regime. At both densities (corresponding to 1,680 and 840 individuals per m^2), the percentage of burrowing animals was similar.

Relationship to macrophytes.

In 1982, when relatively high densities of *P.jenkinsi* were present, many snails were seen on submerged macrophyte species and on the underwater parts of reed in Lake I (submerged macrophytes are absent in Lake II). *Potamogeton pactinatus* was populated to such an extent that it resembled strings of beads. From 1982 onwards, snails were rarely observed on submerged macrophytes. Scuba divers studying these plants in the north-easterly part of the lake from February to July, 1983, failed to observe *P.jenkinsi* (Mario de Kluijver,

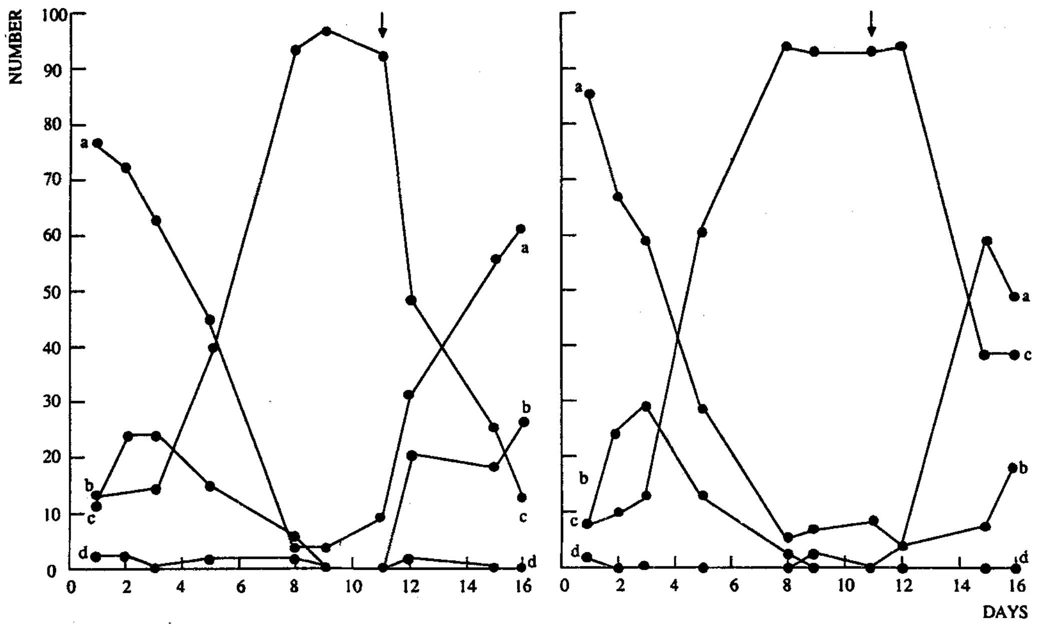

Fig. 3. Numbers of *P.jenkinsi* (shell width 0.5 - 2.0 mm) found on the sand (a), on the walls of the aquaria (b), in the sand (c), and floating (d). Left : Lake I animals; right : Lake II animals. Arrow : temperature shift imposed from 15 to 22 °C. Period : 1982.09.20 through 1982.10.05, Observation time : 6.00 p.m. N = 100 animals.

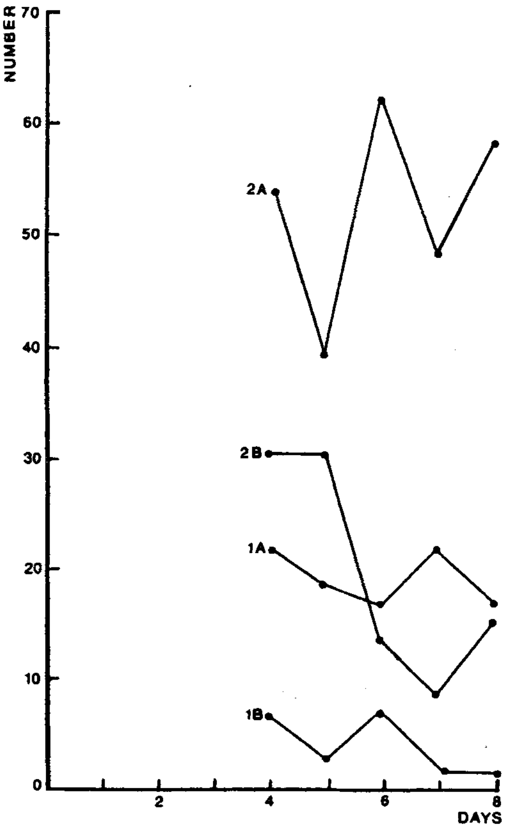

Fig. 4. Numbers of *P.jenkinsi* from Lake I (shell width 0.5 - 2.0 mm) found in the sand under a natural light regime (a) and in a dark regime (b). Periode: 1982.11.11 through 1982.11.19. Observation time: 6.00 p.m. N= 50 animals (1) or 100 animals (2).

pers. comm.). BREGMAN (1984) also reported very few *P.jenkinsi* on reed stalks in 1983, but precise observation by individual plant species was lacking.

Therefore, in 1984, *P.jenkinsi* and macrophytes, both taken from Lake I, were brought together under experimental conditions. All macrophytes employed were occupied by the majority of the snails after 24 hours, whereas the numbers in the control aquarium without plants were fairly equally distributed in both halves (see for explanation Table 3). The numbers on *Elodea nuttalli* were lowest.

Temperature tolerance.

Table 4 shows the temperature tolerance of two size classes from both lakes. The tolerance to 30 °C was low, to 25 °C intermediate, and to lower temperatures high. Duplications of tolerance experiments can reveal variation to such an extent that detailed interpretations are risky (DORGELO, 1974). Hence, the differences between the size classes and the lakes are considered of minor importance.

At the end of this experiment distinct growth in the 0.60 mm class was observed at 20, 15 and 10 °C, but was not seen at 30, 25 and 5 °C.

Carination.

Observations of the occurrence of keeled individuals in 1983 in both lakes are presented in Table 5. The percentages fluctuated per sample, but the mean percentages were highest in Lake I. They were for the 1.0 - 1.5 mm shell width class and for all size classes wider than 1.0 mm taken together 19.0 and 25.8 %, respectively, in Lake I, and 10.8 and 12.9 %,

	A				B			
Macrophyte species	1		2		3		4	
Chara sp.	80	80	4	8	56	46	44	54
Elodea nuttalli	70	72	6	8	58	56	42	44
Potamogeton lucens	92	84	6	6	50	48	50	52
Potamogeton perfoliatus	74	88	8	8	46	52	54	48
Ranunculus circiralis	92	92	4	4	42	48	58	52

Table 3. Distribution of *P.jenkinsi* in Lake I in % after 24 hours of exposure in the test (A) and the control aquaria (B). The experiments were done in duplicate in September, 1984. N = 50; 1.0 - 1.5 mm shell widths.
1. % of animals on the live macrophyte; 2. idem, on the artificial plant; 3. idem, in the half of the aquarium at the macrophyte side; 4. idem, in the half of the aquarium at the artificial plant side. N.B. The percentages of 1 and 2 together are less than 100 due to animals found between the live and artificial plant.

	Lake I				Lake II			
	a		b		a		b	
Temperature	0.60	1.75	0.60	1.75	0.60	1.75	0.60	1.75
30 °C	5.7	5.2			2.8	5.1		
25	73.7	79.7			66.8	71.8		
20			28	19			28	20
15			30	30			29	24
10			30	30			27	26
5			29	30			30	26

Table 4. Temperature tolerance of *P.jenkinsi* from Lake Maarsseveen I and Lake Maarsseveen II. Shell width classes of 0.60 and 1.75 mm. N = 30 at t = 0. a. median survival times (LT_{50}) in days; b. numbers of live animals after 105 days.

respectively, in Lake II. It was remarkable that there was a delay in the appearance of the first keeled specimens in Lake I during the period of recovery of the population after its collapse at the end of 1982.

DISCUSSION

Fluctuating densities.

a. Earlier data of the Maarsseveen Lakes.

Quantitative data of the densities of *P.jenkinsi* observed on the sediments before 1982 are very scarce. In 1977 VAN BEMMEL and KOOMAN (1977) found far fewer individuals in Lake II (490 per m^2) than in Lake I (19,700 per m^2). It should be noted, however, that these data are based upon only one grab sample per sampling date. MOL *et al.* (1982) reported,

Lake I	1.0 - 1.5 mm		Total		Lake II	1.0 - 1.5 mm		Total	
Date	Collected	Keeled (%)	Collected	Keeled (%)	Date	Collected	Keeled (%)	Collected	Keeled (%)
1983.01.12	8	0	12	0	1983.01.12			176	21 (11.9)
.02.08	5	0	6	0	.02.08			225	20 (8.9)
.03.01	0	–	0	–	.03.15			1162	136 (11.7)
.03.29	5	0	7	0	.03.29	435	26 (6.0)	781	92 (11.8)
.04.26	3	0	3	0	.04.12			230	32 (13.9)
.05.25	38	0	51	0	.04.26	295	17 (5.8)	516	43 (8.3)
.06.21	153	0	193	0	.05.10			169	19 (11.2)
.07.25	25	0	73	0	.05.25	258	11 (4.3)	424	22 (5.2)
.08.10	244	20 (8.2)	290	33 (11.4)	.06.07			538	33 (6.1)
.08.23	58	10 (17.2)	207	44 (21.3)	.07.05			310	18 (5.8)
.09.04	30	8 (26.7)	53	15 (28.3)	.08.10			226	12 (5.3)
.09.20	63	17 (27.0)	138	47 (34.1)	.08.23	795	112 (14.1)	908	125 (13.8)
.10.04	117	34 (29.1)	161	53 (32.9)	.08.31	507	63 (12.4)	257	33 (12.8)
.10.18	99	9 (9.1)	146	15 (10.3)	.09.07	119	20 (16.8)	159	29 (18.2)
.11.02	69	11 (15.9)	109	24 (22.0)	.09.20	205	33 (16.1)	237	38 (16.0)
.11.22			214	80 (37.4)	.10.05	572	63 (11.0)	627	68 (10.8)
.12.19			182	62 (34.1)	.10.11			222	49 (22.1)
					.10.25	869	92 (10.6)	1169	146 (12.5)
					.11.08			321	105 (32.7)
					.12.06			303	57 (18.8)

Table 5. Numbers of live *P.jenkinsi* and the numbers of keeled individuals in the 1.0 - 1.5 mm shell width class, and of all individuals > 1.0 collected (the keel of smaller individuals is difficult to distinguish with certainty).

based on 5-7 samples per sampling date, about 600 per m^2 in Lake I at a depth of 3 m from April through October, 1978, followed by 2,814 per m^2 in December. GEERLINGS *et al.* (1980) reported 2,500 per m^2 in Lake I in 1979, without specifying the sampling procedure. DE WIJS (1980) reported high densities for Lake I in 1979, but sampling was not quantitative. KRUIZINGA (1982) reported densities for Lake I of 21,000 individuals per m^2 in 1981. In conclusion, it is entirely possible that the relatively high densities observed in Lake I in 1982 (up to 25,000 per m^2) have existed for a longer period.

b. Extremes and decreases.

A comparison of Lake I with Lake II demonstrates that the mean numbers in Lake I have greater extremes (ranging from 25,000 to 200-2,000 per m^2) than those in Lake II (normally 1,000-10,000 with decreases from 13,000 to 400 in 1985, and from 8,000 to 300 individuals per m^2 in 1986). Furthermore, the decline in Lake I resulted in continuing, lower densities whereas the two reductions during the spring of 1985 and 1986 in Lake II were followed by increasing densities. Such a decrease in spring followed by a subsequent increase has also been observed in a brackish region of the North Baltic Sea (LAPPALAINEN, 1979).

There are also records of strongly declining numbers in populations of *P.jenkinsi* in other ecosystems. ROBSON (1925, *vide* BONDESEN and KAISER, 1949) reported the sudden appearance of this species in new localities, but also observed the complete death of the population subsequently. OTTO (1927) found only empty shells in the Kagerplassen. Such remnants of a population in Lake Vechten (south of the Maarsseveen Lakes) were observed during three visits in 1984, whereas 4,500 per m^2 were present in September, 1983, at the same location. Drastically declining numbers from one year to another were also reported by HEYWOOD and EDWARDS (1962) and VAREILLE-MOREL (1981).

The nearly complete disappearance of *P.jenkinsi* in Lake I in December, 1982, was accompanied by a concurrent rapid death of animals in the laboratory in the first week of December. They were collected in November for a culture, using 50 individuals of 0.5-2.0 mm shell width per aquarium, *viz.* 1,680 per m^2, filled with lake water over a layer of 2 cm lake sediment. The animals from Lake II, kept under the same conditions in water and sediment from Lake II, remained vital for months. Expressed in the numbers of embryos in the brood pouch in November, 1982 (WIEDIJK, 1983), which were about the same as those found in November of the following years (Dorgelo, unpublished data), the animals from Lake I seemed to be in a good condition. The origin of the catastrophic decline is unknown.

The two marked declines observed in the Lake II during the spring of 1985 and 1986 were not accompanied by mortality among the animals kept in the laboratory.

In 1986, the surroundings of the sampling station in Lake II were searched for *P.jenkinsi.* Migration as a function of density-dependent movement, can, apart from reproduction and mortality, alter density patterns (see TAYLOR and TAYLOR, 1977). However, the densities found at greater depth as well as in the neighbouring reed belts were lower than those at the regular sampling station. Furthermore, increased predation by the common bream is not probable since these fish show relatively low values for food-related burrowing in spring behaviour (TEN WINKEL and DAVIDS, 1985).

The differing patterns of decrease in the numbers of snails in Lake I and II may have been evoked by the varying characteristics of these lakes. But which ? The lakes lie close together, are of approximately the same age (they exist since the sixties), and were created in the same type of landscape. Calcium is energetically very important for shell building in molluscs (RUSSELL-HUNTER *et al.*, 1970). DUSSART (1977) found *P.jenkinsi* more abundant in harder waters, and WILLIAMS (1970) showed differences in fecundity of snails kept in waters of different hardness. However, the calcium content of the Maarsseveen Lakes is the same, *viz.* about 60 mg.l^{-1} (Provincial Water Board of Utrecht, pers. comm.). The sandy sediment sampled in both lakes showed differences in size fraction ratios, but FROMMING (1956) demonstrated *P.jenkinsi* to grow equally fast on different types of substrate, when the other conditions were kept constant. PULLES (1986) measured the Cd, Cu and Zn concentrations of the sediment and the water in both lakes in April, 1986 (see also VAN DONK, 1987). The sediment concentrations were highest in Lake II, whereas those of the water were much lower and rather similar in both lakes. But, there are no indications of sudden increases of deposition of trace metals during the drops in population densities observed in the lakes.

Another aspect, finally, might be considered. Given the dynamics of the abundance of *P.jenkinsi* some authors emphasized its reproduction, or its status as an artificial introduction in European water. Parthenogenesis, together with the potential to reproduce throughout the entire year, contributes to abundance and rapid spread (FRETTER and GRAHAM, 1962). Moreover, species, recently introduced into a new habitat, may disappear as rapidly as they came (*ibidem*). However, *P.jenkinsi* did not disappear from the Maarsseveen Lakes. BONDESEN and KAISER (1949) called *P.jenkinsi* a species in evolution, being highly variable as to ecology, shell structure and reproduction; FRETTER and GRAHAM (1962) described this species as 'genetically unstable'. However, these statements were not founded by proof. The fact is that *P.jenkinsi* is found in many types of habitats, which demonstrates euryoecious properties. Furthermore, the absence of genotypical variation due to parthenogenesis may indeed lead to only temporary population growth, but the death of a population may normally be ascribed to an unsuitable environment.

c. Densities in other ecosystems.

Densities of *P.jenkinsi* on the sediment within the ranges found in the Maarsseveen Lakes have been reported by other authors. ADAM (1942) mentioned about 30,000 per m^2 in a Belgian brook, LUMBYE and LUMBYE (1965) about 23,000 per m^2 in an English marl pit, and STREIT and SCHRODER (1978) about 600 per m^2 in Lake Constance. Higher densities were reported by HEYWOOD and EDWARDS (1962), *viz.* 29,000 - 88,125 per m^2 in an English chalk stream. LUCAS (1959) found about 800,000 per m^2 in a slow-running Belgian brook but he included the dense vegetation above the sediment in his calculation. FRETTER and GRAHAM (1962) mentioned 'enormous numbers blackening the weed and mud over which it crawls'.

d. Trophic state of the ecosystem.

VAREILLE-MOREL (1981) reported higher numbers from eutrophic water undergoing organic pollution. The dynamics observed in the Maarsseveen Lakes, however, urge caution when short-term sampling is applied. Moreover, the strongly clumped distribution of *P.jenkinsi* (see also HEYWOOD and EDWARDS, 1962, and DUSSART, 1977) argues for many replicates in sampling. The mean densities in the eutrophic Lake II were only during 1983 - 1987 (mostly) higher than in the meso-oligotrophic Lake I.

The aggregated type of dispersal, which seems to be the rule rather than the exception in natural populations, may arise from patchiness of the habitat in space and time, caused by heterogeneities in either sediment and food or both, and/or from the behaviour of the organism (see CALOW, 1974, and SOUTHWOOD, 1977). Behaviour seems most likely for *P.jenkinsi,* since aggregations have been recorded at various depths with horizontal separation on a homogeneous sandy sediment covered with detritus in the Maarsseveen Lakes. The snail is an actively moving organism (DE WIJS (1980) reported a crawl speed of 3.2 $m.h^{-1}$) and may be considered to be able to form and disband groups rather quickly.

Thus, it appears that the numbers of *P.jenkinsi* do not increase with eutrophication. The individual growth, however, appeared to be significantly faster in the eutrophic Lake II when compared with that in the meso-oligotrophic Lake I (DORGELO, 1987).

Floating.

LINKE (1939) noticed the ability of the intertidal *Hydrobia ulvae* to float on the surface of the water. LEVINTON (1979) demonstrated the same for other *Hydrobia* species. LITTLE and NIX (1976) saw *P.jenkinsi* floating under laboratory conditions, but remarked that 'this species is not known to float in its natural habitat'. My results demonstrated this behaviour in the lake, although this activity is restricted to smooth water surfaces. This confirms the findings of BARNES (1981) who observed in the laboratory that many *H.ulvae* sank when the water surface was rippled.

Floating behaviour has been linked with the possibility for passive dispersal to other habitats under unfavourable conditions (NEWELL, 1962; MUUS, 1967; ANDERSON, 1971; LEVINTON, 1979). BARNES (1981), however, concluded that interpretations in terms of strategies for dispersal are seriously in error for *Hydrobia*. LEVINTON (1978) observed an increase in floating in *Hydrobia* with increasing population density under laboratory conditions. I observed the same for *P.jenkinsi* when the animals were placed in trays without sediment. In Lake I the numbers of floating snails were only of importance when the numbers on the sediment were most dense (1982). It appears that a density-dependent mechanism is probable.

ANDERSON (1971) found for *H.ulvae* that climbing of vertical objects preceded floating. This is in agreement with my finding which demonstrated that most snails were collected along the reed belts.

Burrowing.

P.jenkinsi is a very mobile snail. Besides actively crawling it demonstrates a quick response by allowing itself fall after slight disturbances, *e.g.* trembling, when attached to vertical objects (see also FROMMING, 1956, and MICHAUT, 1968). Another component of its behaviour is burrowing into the sediment. When kept under a dark regime the numbers of snails staying in the sand decreased. MICHAUT (1968) observed *P.jenkinsi* actively crawling on the walls of the aquarium or floating during the night, as opposed to sluggishness during daytime. KAVALIERS (1981) reported the freshwater gastropod *Helisoma trivolis* also to show a circadian rhythm with activity throughout the night.

After the increase in temperature the majority of the snails were observed upon the surface of the sand. This may be ascribed to increasing mobility and/or a decrease of the oxygen content in the top layer of the sediment.

Relationship to macrophytes.

None of the plant species tested repelled *P.jenkinsi*, yet this organism was scarcely in evidence on macrophytes after 1982, when lower densities were found on the sediment. DE WIJS (1980) reported the presence of *P.jenkinsi* on reed stalks in Lake I in 1979. GEERLINGS *et al.* (1980) and MOL *et al.* (1982) reported relatively high numbers of *P.jenkinsi* on various submerged macrophytes in Lake I. These findings concern the period in which high densities may have occurred in Lake I. Other authors mentioned lower (DVORAK and BEST, 1982) or high numbers of *P.jenkinsi* occurring on plants (LUCAS, 1959; MACAN, 1970). However, their data do not allow the conclusion that the plants were only occupied when the densities on the sediment became high. VAN BENTHEM-JUTTING (1959) found *P.jenkinsi* mostly on the bottom, also in the presence of several macrophyte species. For a detritivorous organism, the sediment may be the preferred place for food supply. Settling on *Elodea nuttalli* was lowest, which agrees with an observation of E.P.H. Best (pers. comm.); she made an inventory of the macrophytes of Lake I from 1976 - 1979 (BEST, 1981) and saw, during Scuba diving, far more *P.jenkinsi* on *Chara* than on *Elodea*.

WHITEHEAD (1935), studying a chalk stream, found very low numbers of *P.jenkinsi* or none at all in stony regions, on mud, and on *Callitriche* sp., *Potamogeton perfoliatus*, *Ranunculus* spp., and *Sium erectum*. Many snails were seen, however, on *Hippurus vulgaris*. Species-specific effects of macrophytes were demonstrated by STERRY *et al.* (1983), analyzing the behavioural responses of the freshwater pulmonate snail *Biomphalaria glabrata* to fresh homogenates of various aquatic macrophytes. Some species lacked attractants or arrestants, other species contained weak arrestants or induced strong repellant effects. Only two species induced significant attractant and arrestant effects. All observations were compared to those obtained with lettuce controls. Decaying *Lemna paucicostata* homogenate proved to be a significant stronger attractant and arrestant than fresh homogenate, linking the snail with its food source. HAYNES and TAYLOR (1984) analyzed the food finding and preference of *P.jenkinsi* and concluded that it detects chemicals in the water by chemoreception. It was attracted by well decayed *Elodea canadensis* and *Apium nodiflorum*, fresh *A.nodiflorum*, green algae and squashed *Gammarus pulex*, and it was repelled by extracts of fresh *Nasturtium officinale*, squashed *P.jenkinsi*, and water in which the leech *Glossiphonia complanata* had been living.

This species-specific effect of plants on the distribution of benthos may have a more general importance, since JOHNSON and MULLA (1983) found higher densities of chironomid midges (*Tanytarsus* spp.) in a portion of a lake kept free of *Myriophyllum spicatum* than in a portion containing dense stands of this macrophyte. This suggests that the presence of this plant creates an unsuitable habitat, perhaps acting as a physical barrier or elaborating biologically active chemicals.

Temperature tolerance.

Low temperatures were not lethal for *P.jenkinsi* according to the tolerance experiment. This agrees with the experience of DE WIJS (1980) who encountered many *P.jenkinsi* in Lake I in 1979 after a severe winter with ice-covered lakes from December through March. Similar observations were made in this study after the winters of 1984/85 and 1985/86 with periods of ice. Temperatures of 25 °C or higher were badly tolerated. In the lakes, however, the temperature in the littoral zone did not exceed 25 °C according to DORGELO and DE GRAAF BIERBRAUWER (1981) and TEN WINKEL (1987).

Carination.

BOETTGER (1948), BONDESEN and KAISER (1949) and FROMMING (1956) extensively reviewed the occurrence of the keel in populations of *P.jenkinsi* in different habitats. As a rule both the smooth and the keeled form have been encountered in natural populations. ROBSON (1926) bred keeled snails but obtained only smooth offspring. This result indicated that the formation of the keel was induced by the environment. BOYCOTT (1929) and BOETTGER (1948), breeding keeled snails, obtained a low percentage of keeled forms, but the conditions under which carination occurred were inconclusive. BOYCOTT (1929) suggested that 'bad conditions' favoured the formation of the keel. BONDESEN and KAISER (1949) generally observed lower percentages of keeled snails in waters of lower salinities (see also FROMMING, 1956, and FRETTER and GRAHAM, 1962) but concluded that there was 'no real relation between structure and salt content'. WARWICK (1969) stated that 'the keel develops in the presence of an adequate quantity of humic materials in the water or food', but this statement was not founded by proof.

In conclusion, there has been much speculation and the results obtained so far do not permit a satisfactory explanation. My results demonstrated that the mean percentage of keeled individuals was much higher in the meso-oligotrophic Lake I than in the eutrophic Lake II.

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Address of the author :
Department of Aquatic Ecology, University of Amsterdam, Kruislaan 320, 1098 SM Amsterdam, The Netherlands.