Reproductive Biology and Life History Strategy of *Bithynia tentaculata* (Linnaeus, 1758) and *Bithynia leachii* (Sheppard, 1823)

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Abstract: I studied the life histories of 6 populations of the iteroparous prosobranch snail *B. tentaculata* and 1 sympatric population of *B. leachii* for 3 years. Males and females out of 4 populations were kept in cages in the field during their entire lifespan. Data were collected on the principal life history traits. Reproductive traits studied were egg size and - number, spawn size and - number, oviposition site choice, hatching success of eggs and sex ratio of offspring, and the temporal aspects of reproduction. Differences were apparent for all examined traits and at 3 different levels: between species, between populations and also within populations. Additionally, I found several trade-offs between conflicting reproductive demands that differed in their outcome between species and populations.

Species level: Compared to *B. leachii*, *B. tentaculata* shows some differences in the overall growth pattern, is larger at maturity, attains a larger body size and shows only a slight sexual dimorphism, if any. The females lay fewer but larger spawns containing large eggs. They have a potential longer life span, but are more susceptible to parasitation by trematode larva. In direct comparison of the sympatric populations, *B. leachii* laid more eggs per reproducing female that had also a higher hatchability.

Population level: The populations of *B. tentaculata* showed several differences that seem to be local adaptations, differing with regard to mean shell height, shell height at maturity, sexual dimorphism and overall growth patterns. They also differed in size and number of eggs and spawns produced, egg hatchability and their reproductive pattern over time. In general, river snails were smaller than snails from standing waters and showed a trade-off with regard to egg number and egg size (producing many but smaller eggs and many but smaller spawns) that resembled the trade-off observed for *B. leachii*.

Individual females also showed different life history strategies within populations. Mostly I observed different reproductive patterns in space and time. Some females had a long reproductive period laying many small spawns, others laid few large spawns within short time and had therefore a long postbreeding period.

Key Words: *Bithynia*, life history, reproduction

Abstract: Ich habe 6 *B. tentaculata* Populationen und eine sympatrische *B. leachii* Population über einen Zeitraum von 3 Jahren beobachtet. Männchen und Weibchen aus 4 Populationen wurden bis zu ihrem Tod individuell in Käfigen am Entnahmestandort gehältert. Ich habe Daten zu den wichtigsten Aspekten des Lebenszyklus der Tiere gesammelt wie zur Reproduktionsbiologie, u.a. Lebenserwartung, Größe bei Geschlechtsreife, Eigröße und Eizahl, Laichschnurgröße und Laichschnurzahl, Wahl des Eiablageplatzes, Schlupferfolg, Geschlechterverhältnis des Nachwuches und zeitlicher Verlauf der Reproduktionsperiode. Signifikante Unterschiede traten sowohl zwischen den Arten, zwischen den Populationen als auch innerhalb der Populationen auf.

Verglichen mit *B. leachii* hat *B. tentaculata* einen etwas anderen Wachstumsverlauf, ist bei der Geschlechtsreife als auch als Adulttier größer und zeigt einen schwach ausgeprägten Geschlechts-dimorphismus. Die Weibchen legen wenige, dafür große Laichschnüre mit großen Eiern. Sie haben eine potentiell höhere Lebenserwartung, sind aber auch häufiger parasitiert. Im Vergleich der beiden sympatrischen Populationen legte *B. leachii* im Verlauf einer längeren Reproduktionsperiode mehr Eier als die größere *B. tentaculata*.

Auch die 6 *B. tentaculata* Populationen zeigten erhebliche Unterschiede. Sie unterschieden sich in der Durchschnittsgröße, der Größe bei Geschlechtsreife, dem Wachstumsverlauf und dem Vorhandensein eines Sexualdimorphismus. Eizahl und -größe, Laichschnurzahl - und größe, Schlupfraten und zeitlicher Verlauf der Reproduktion waren verschieden. Schnecken aus Fließgewässern waren kleiner und zeigten einen Trade-off, der an *B. leachii* erinnerte, indem sie ihre reproduktive Investition in zahlreichere, aber kleinere Eier in zahlreichen, aber kleinen Laichschnüren aufteilten.

Innerhalb der Populationen zeigten einzelne Weibchen abweichende Reproduktionsverläufe. Zumeist unterschied sich das raumzeitliche Muster der Reproduktion. Es gab Weibchen mit einer langen Laichperiode, in deren Verlauf zahlreiche Laichschnüre mit wenigen Eiern produziert wurden und Weibchen mit kurzer Reproduktionsperiode, in deren Verlauf wenige Laichschnüre mit vielen Eiern gelegt wurden. Dies hatte auch Auswirkungen auf die Dauer der postreproduktiven Phase vor der Überwinterung.

Schlagworte: *Bithynia*, Lebenszyklus, Fortpflanzung

I. INTRODUCTION

Scientists today agree that there exist several millions of different species, most of them as yet undescribed. They all differ to at least some extent in appearance, physiology, behaviour and life history. How this diversity did arise (and is maintained) is a challenging question for evolutionary thinking.

Life history theory is a comparatively new line of research that is deeply rooted in ecology and evolution. Living things in their bewildering array of extremely diverse life histories have something in common: They stand in a line of ancestors that reproduced successfully. Most organisms start their life as a zygote. Generally spoken, a lot of opportunities are open from this starting point to reach a condition where reproduction is possible. Which size and age should the organism reach before it reproduces? When mature, organisms can reproduce once, several times or continuously throughout their lifes.

Organisms differ in their allocation of resources to growth, maintenance and reproduction. They also differ how the allocation pattern to the conflicting demands changes during their lifetime. They can divide their limited resources to produce few, large offspring of high quality or numerous, small offspring that are more mortality-prone. In the end, the general problems faced are the same for oaks, elephants, snails or seals; but the answers differ.

The principal life history traits are (following Stearns, 1992):

-Size at birth
-Growth pattern
-Age at maturity
-Size at maturity
-Number, size, and sex ratio of offspring
-Age- and size-specific reproductive investments
-Age- and size-specific mortality schedules
-Length of life

Trade-offs between conflicting demands link these traits. Some important trade-offs are:

-Reproduction versus growth
-Current versus future reproduction
-Current reproduction versus survival
-Number versus size of offspring

The possible outcome of trade-offs as the phenotypic plasticity an organism can show in its life history traits are constrained by lineage specific effects (its evolutionary past).

Life history theory sets out to analyse all those aspects of the life history of organisms. The set of traits that characterizes a particular life cycle is called a life history strategy. The field is in itself controversial. This is not in the least astonishing because the exploration of life histories lies at the heart of evolutionary thinking. Therefore it is a battle ground for very diverse concepts ranging from strictly mechanistic adaptationists views over epigenetics to Neo-Lamarckian ideas.

Long-term studies on the life-histories of individual invertebrates under natural conditions are sparse, but empirical data are needed to test the predictions of general life history theory. Especially data on intraspecific and individual variation in populations in the field are missing for invertebrates. A lot of empirical and theoretical work on general life history theory, life history variability and evolution of life histories has been carried out on molluscs and especially on freshwater snails in recent years (e.g. Aldridge 1982; Brown 1983, 1991; Calow 1978, 1981, 1983; Hart and Begon 1982; Lam 1994; Lam and Calow 1989a,b; Ribi and Gebhardt 1986; Tompa et al. 1984).

In studies based on population means or mass culture of animals the individual variation within the population is either not assessed or underestimated. In order to gain a more detailed insight into the underlying patterns that are shaping life cycles and population dynamics, I followed up the life histories of individuals in this study. Even if this study consists therefore out of many solely descriptive observations, this is not seen as a disadvantage. In my opinion a profound knowledge of the species' autecology is indespensible for further research. Autecology provides the firm ground for a meaningful analysis of complex systems like biocoenoses or ecosystems where numerous species interact.

The genus *Bithynia* is represented by two species in Central Europe. *Bithynia tentaculata* is an iteroparous snail common in European and West Asian inland waters that has successfully invaded North America since the last century (Frömming 1956; Harman 1968). It is a sexually reproducing dioecious prosobranch that lives up to 4 years (Fig. 1).
B. tentaculata was chosen because of its common occurrence and its broad habitat use (rivers, streams, lakes, permanent and temporary water bodies of diverse quality) and because more studies concentrated on short-lived and semelparous pulmonates than on prosobranchs so far (Brown 1983; review in Costil and Daguzan 1995a).

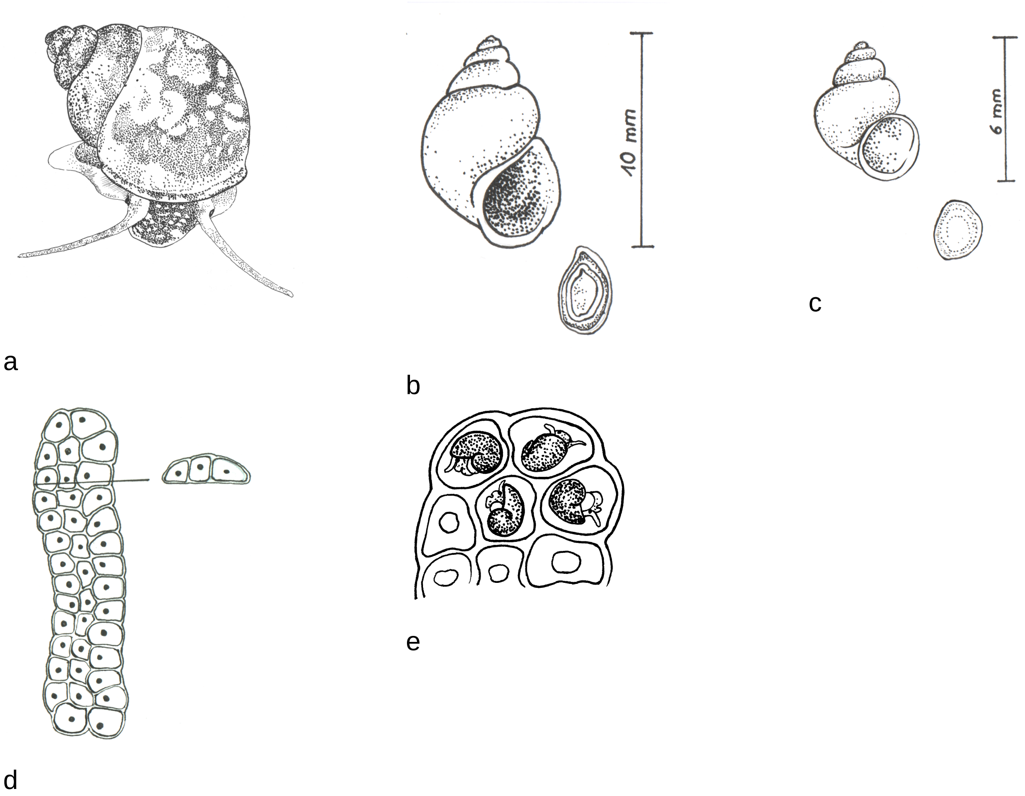


Fig.1a): Crawling adult snail of *B. tentaculata*; b): Shell and operculum of *B. tentaculata*; c): Shell and operculum of *B. leachii*; d): *B. tentaculata* spawn and cross-section of spawn (redrawn after Hss 1971); e): Spawn with hatching juveniles

B. leachii is somewhat smaller and less common than *B. tentaculata* and is, in contrast to *B. tentaculata*, restricted to water bodies with fairly good water quality (Fig. 1). Its life-cycle is less well known and there exist only a few more or less anecdotal observations in the older literature. *B. leachii* is only found in still waters and, most interestingly, seems to occur always sympatric with *B. tentaculata* (Boycott 1936; Frömming 1956; Grabow 1994; Heitkamp 1982; Macan 1977; Nottbohm 1984; Wesenberg-Lund 1939). In general terms, *B. tentaculata* is eurytopic compared to a stenotopic *B. leachii*.

The autecology of *B. tentaculata* has been investigated in detail in Great Britain, the St. Lawrence River, Quebec/Canada and in Oneida Lake, upstate New York/USA (Lilly 1953; Tashiro 1982; Tashiro and Colman 1982; Vincent et al. 1981; Vincent and Harvey 1985; Young 1975). Vincent and Gaucher (1983) already discussed interpopulation and spatio–temporal variations of the life cycle, but they worked with grouped snails for only one reproductive season. The reproductive biology, development of spawn and hatching rates under the influence of different temperatures were studied in 1995 in the laboratory and under field conditions (Richter and Wächtler 1999).

My study has the following aims:

A) To investigate the virtually unknown autecology of *B. leachii*

B) To improve our knowledge of the autecology of *B. tentaculata*

C) To understand why *B. tentaculata* is eurytopic and successful compared to a stenotopic and rare *B. leachii*

D) To test the hypothesis that different environmental conditions should lead to discernible differences in the life history traits between populations of the same species even in close spatial proximity

E) To investigate if there is evidence that different female life histories exist simultaneously even within a population

F) To delineate biotic and abiotic factors shaping the life histories of the species

G) To assess the impact of trematode parasites on snail reproduction

II. MATERIAL AND METHODS

1. STUDY AREA AND SAMPLING METHOD

During this study, I examined six populations of *B. tentaculata* and one coexisting population of *B. leachii*. All populations lived in Lower Saxonia, Northern Germany (Fig. 2). Three populations were in very close spatial proximity to each other near the southern shore of the Dümmer, a shallow lake of post-glacial origin (Fig. 2c). These populations were chosen because they live under conditions that differ strongly in regard to limnological and biological factors but otherwise are subject to the same climatic conditions.

The first of these populations lived in the river Hunte, which is a medium sized lowland river running to the river Weser. The second lived in an artificial canal built to divert highly eutrophic waters coming from intensively cultured marshland from the Dümmer (it crosses beneath the Hunte) and the third in a ditch running parallel to the canal at the edge of a meadow. Marshland without any trees or shrubs is surrounding the habitats.

At the sample site the Hunte is approx. 20 m wide and 1 m deep. It is slowly streaming with some floating vegetation (*Ceratophyllum demersum, Potamogeton natans*), the steep banks are dominated by *Glyceria maxima*. Snails were sampled by sweeping a pond net through the vegetation, mainly the stems of *G. maxima* which were preferred by *B. tentaculata.* Snails were restricted to areas with vegetation, the river bed and bank sections free of vegetation were not populated by *B. tentaculata.*

The canal (referred to as the Canal further on) is about 7 m wide and about 1 m deep with a very thick layer of mud on the bottom. The water is slowly streaming. Submerse and floating vegetation (*Ceratophyllum demersum, Callitriche palustris, Nuphar lutea*) grows throughout the whole water body. The bank is dominated by *Carex gracilis* and some *Glyceria maxima*. Snails were sampled using a pond net or by direct examination of submerse vegetation. Sampling by net was difficult because of large amounts of detritus. Snails were limited to the upper waters because of frequent oxygen depletion in deeper water levels in late spring and summer.

The ditch (referred to as the Ditch further on) is about 150 m long without any drain. It is approximately 1,5 m wide and the water level is very variable, depending on weather and season. In dry summers the Ditch may dry up for several weeks. It is surrounded by dense-growing *Carex gracilis*. The bottom is covered by a thick layer of plant debris consisting

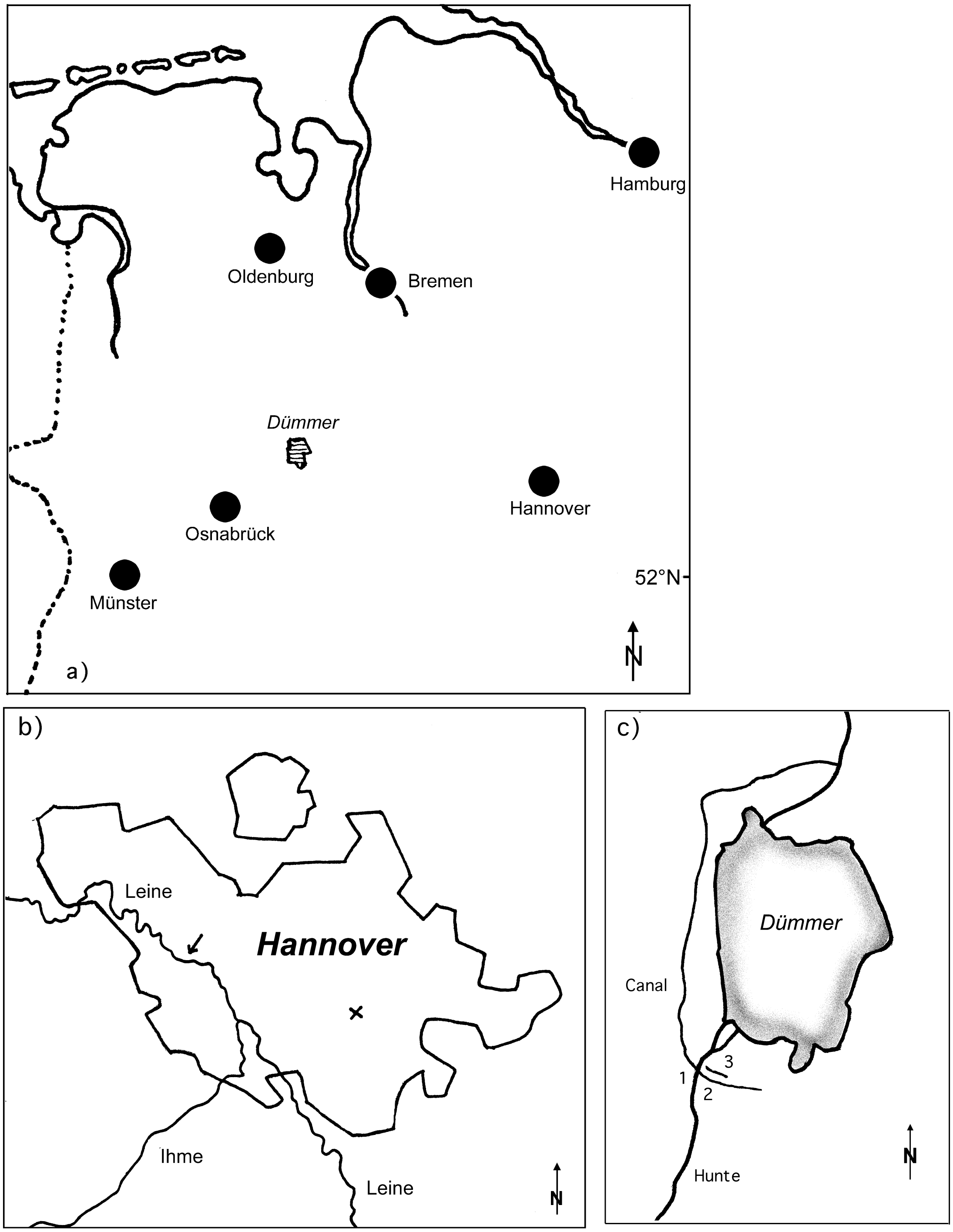


Fig. 2a): Map of Northern Germany; b): Map of Hannover, arrow indicates sampling site in the river Leine, cross indicates location of the Veterinary School where the Pond and the Small Pond are located; c): Map of the Dümmer, numbers mark sampling sites: 1 = Hunte, 2 = Canal, 3 = Ditch

mainly of *C. gracilis* stems and leaves. Due to high concentrations of humic components the colour of the water is brown. When active, *B. tentaculata* stayed near the water surface because of frequent oxygen depletion in deeper water. *Ceratophyllum demersum*, *Polygonum amphibium* and *Lemna minor* are the most common macrophytes. Snail sampling followed the routine as described above.

3 other populations of *B. tentaculata* studied were located in Hannover, the capital city of Lower Saxonia (Fig. 2b). They lived in a further lowland river, the Leine, a pond and a small pond both of an artificial origin (referred to as the Pond and the Small Pond further on). The population of *B. leachii* studied shared its habitat with *B. tentaculata* in the Pond. All habitats are persistent and eutrophic, elevation above sea level (approx. 55 m) is the same for all of them.

The Leine is a lowland river typical for densely populated areas with its river bed influenced by man for centuries. At the sampling site the river, approx. 50 m wide and several meters deep, splits into a running section and a canal for industrial purposes. It is met by a brook (the Fösse) that starts at the slag heaps of a salt mine near the outskirts of Hannover and runs further through the city to the Leine.
The *B. tentaculata* population studied lived in a layer of solid stones tipped into the river as a reinforcement of its bank. The water is always muddy and there are no macrophytes in it. Some nettles and a *Salix* sp. grow on the river bank. Water velocity fluctuates greatly throughout the year with maxima during winter or spring floods, but is normally low in summer and autumn. Water velocity is further reduced beneath the stones were layers of mud aggregate. Snails were sampled by lifting stones out of the water and examining their bottom surface to which *B. tentaculata* was restricted.

The Pond was built around 1930 and covers an area of approximately 2700 m^2 with an average depth of 1 m. It is located in the botanical garden of the Tierärztliche Hochschule (Veterinary School) Hannover. The shores are lined by full grown trees and dense vegetation. The sample site for both the populations of *B. tentaculata* and *B. leachii* was an area where gravel was tipped from the shore. The submerse vegetation consisted mainly of *Ceratophyllum demersum, Elodea canadiensis, Nuphar lutea* and green algae forming dense mats in summer. Sampling was by pond net and direct examination of vegetation and gravel. During summer, dense vegetation made sampling difficult.

The Small Pond is an artificial garden pond near the department of zoology which covers an area of approx. 40 m^2. It is about 0,5 m deep with a thick layer of mud and rotting plant debris on the bottom. It is made of black plastic foil and was built in the eighties. The vegetation is dominated by *Stratiotes aloides* and *Lemna minor*, which cover the entire water surface during summer and autumn. Dense mats consisting of *Elodea canadensis* and green algae form in summer in the upper water body. Due to frequent oxygen depletion, *B. tentaculata* is restricted to the upper 20-30 cm of the water during most part of summer and autumn. Snails were sampled by pond net, directly from the plastic foil and by examining the vegetation.

2. FIELD STUDY

2.1. Population dynamics, sex-ratio and parasitic load

The populations were sampled monthly from March/April, when snails become active after overwintering until September/October when snails migrate from shallow waters into greater depths where they rest inactive in the mud, beneath plant debris or under stones over the winter period. Exact timing of these events depends to a great extent on weather conditions and can vary for several weeks between years. Although some snails can be present later than October in shallow waters, sampling was stopped because older and/or bigger snails tend to migrate earlier than juveniles. Therefore late sampling would not reflect the true population structure.

On several occasions high water and flooding prevented sampling. Sample size varied greatly depending on season, population, weather, water level and abundance of vegetation, but normally between 50 and 100 snails were sampled each time. The 3 Dümmer populations were sampled in 1997 and 1998, the 4 populations in Hannover in 1997, 1998 and 1999.

After sampling, snails were transported to the laboratory at the Tierärztliche Hochschule, Hannover and were examined under a stereo microscope.

On some occasions (at least twice per habitat) all molluscs present were sampled, the species determined and the level of abundance recorded.

2.2. Population structure and sex-ratio

When snails are lying on their "back" and the operculum is in view of the observer, one can see the penis of the males behind the right tentacle when the snails are stretching out of their shells in an attempt to regain contact to the bottom surface with their foot. Depending on the population, a precursory structure developing into a penis in later life may be seen with males as small as 2 or 3 mm.

Snails were grouped as males, females or gender unknown and the shell height was measured to the nearest tenth of a millimetre using vernier callipers. With these data length–frequency graphs were calculated. At times when small snails of unknown gender dominated the samples, additional adults were sampled. This additional snails were used to determine the sex-ratio and parasitic load of the population under study, but were not used in length–frequency graphs.

2.3. Parasitic load

Infection with larval trematodes was examined by cracking the snails using tweezers and looking for sporocysts, rediae or cercariae in the snail tissues under a stereo microscope (magnification up to 40x). These stages are normally located in the digestive gland and/or the reproductive organs and lead to castration of snails. Progressive infections may involve the whole body of snails, tissues are then severely damaged and the snails can contain several thousand cercaria.

Obviously, very early (cryptic) infection stages could not be detected by this method. Since it was the aim of this study to detect the influence of parasitic castration on reproduction for different populations and to assess the probability for an individual snail to loose its reproductive capacity due to castration during its lifetime, this omission does not seem very serious. In fact, the level of cryptic infections in a population shows itself in the pattern of snails infected over time. On the same token, trematode larval stages were not classified because the observed effect under study (loss of reproductive ability) was the same regardless of trematode species.

In 1997, only preliminary studies on parasitation were carried out. In 1998 all 6 *B. tentaculata* populations and in 1999 the 3 populations in Hannover were checked regularly.

2.4. Individual life histories and reproduction

Females of *B. tentaculata* and *B. leachii* were kept caged in the field. Each female inhabited an individual cage of approximately 425 cm^3 made of plastic mesh. Each cage contained a device of acrylic glass for spawn deposition and as a foot-rest for filter-feeding. 30 female snails sampled in March/April some weeks before the onset of the reproductive period were used per population. Snails were sampled, sexed, caged and kept afterwards at the sampling sites.

1997 30 female *B. tentaculata* per population were kept in the Ditch, the Leine, the Pond and the Small Pond (Tab. 1). 1998 and 1999 30 male and female *B. tentaculata* per population were kept in the Leine, the Pond and the Small Pond. 1998 and 1999 28 male and female *B. leachii* were kept in the Pond. Because of their smaller size permitting escape out of the mesh cages made for *B. tentaculata*, *B. leachii* inhabited cages made out of acrylic tubes closed by fine-meshed cloth at both ends.

Tab. 1: Number of snails in field experiments

	B. tentaculata				***B. leachii***
Origin	Ditch	Leine	Pond	Small Pond	Pond
Females 1997	30	30	30	30	-
Females 1998/1999	-	30	30	30	28
Males 1998/1999	-	30	30	30	28

Cages were controlled at least once a week until the end of reproductive activity. Each time new spawns were counted, marked individually and their development was observed. The number of dead eggs and of hatching juveniles was counted. Due to the transparent egg membrane, the embryonic development inside the egg is easily observed (Fig. 1d). Hatching juveniles leave a characteristic hole in the egg membrane (Fig. 1e; Lilly 1953; Richter and Wächtler 1999). After the reproductive season controls were shifted to a biweekly pattern. The controls stopped with the onset of overwintering in October/November and started again in March/April the following years.

The shell height of the caged snails was measured every four weeks using vernier callipers, dead snails were removed weekly. If the body condition of dead snails permitted, they were examined for signs of parasitation. Snails were observed until they died. The last observation period ended with the onset of overwintering in 1999.

2.5. Size of eggs and juveniles

Eggs sampled on one (*B. tentaculata* and *B. leachii* from the Pond) or two (Small Pond and Leine) occasions in 1999 were measured under a stereo microscope. Since the eggs, which have a round shape when laid singly, are fairly rectangular when laid in rows, length and breadth were measured and multiplicated. This approximation of the area covered by the eggs was used in comparisons. It was the aim to compare mean egg size between populations and to test the hypothesis that egg size diminishes over time. Theoretical work suggests that females should make greater investments per individual egg in the early than in the late reproductive period (Begon and Parker 1986). In 1999, newly hatched juveniles of the populations in Hannover (except the Leine population) were measured under a stereo microscope to compare mean juvenile shell height.

2.6. Transplant experiment

In 1998, 5 pairs of *B. leachii* were transplanted within their cages into the Leine, where this species, at least in the area of the sampling site, does not occur. It was the aim of this experiment to show if reproduction of *B. leachii* was possible in running waters.

2.7. Temperature

Since temperature is the most important single abiotic factor, it was recorded weekly (reproductive period) to monthly (rest of the year) for the habitats under study using min–max thermometers. All other abiotic factors were not observed since there were no means for any permanent recordings of water chemistry and related parameters. Occasional measurements are regarded as being of limited ecological value by the author.

3. LABORATORY STUDIES

3.1. Individual life histories and reproduction

Snails of all habitats were maintained in laboratory culture. In 1997 females of the 6 *B. tentaculata* populations were kept individually in 500 ml beakers that were filled with tap water (Tab. 2). Water was changed bimonthly. Snails were sampled before the onset of the reproductive period. They were fed with dried green algae and Mikromin© by Tetra once or twice a week. Mikromin© is a product normally used for raising fish fry but has also some tradition in molluscan studies.

The temperature and light regime followed within limits conditions experienced in the field. Due to problems with temperature regulation (temperatures below 12° C could not be maintained), a proper overwintering could not be simulated. After air temperatures were above freezing point in late winter 1998, snails were maintained outdoors for 3 weeks instead and returned to the laboratory afterwards.

Beakers were controlled 2 or 3 times a week during the reproductive period. New spawns were marked individually and eggs counted. The spawns were observed until the juveniles hatched. Females were measured every 2 or 3 months with vernier callipers until they died. Females not reproducing were sexed a second time to prevent that males were mistaken as females.

After the first reproductive period, 1 or 2 males were added to every living female in autumn, and, in some cases, in spring 1998. During the second reproductive period in

1998, procedures followed the routine of 1997. Females and males were marked with nail varnish. Males were also measured every 2 or 3 months to detect differences in the growth pattern between sexes.

Tab. 2: Number of snails in laboratory culture

	Dümmer			**Hannover**		
	Hunte	Canal	Ditch	Leine	Pond	Small Pond
Females 1997	40	30	18	50	33	32
Males 1997/ 1998	30/15	0/23	29	28	28	27

3.2. Critical shell height for reproduction

Since observations in the field and the laboratory suggested that females below a critical shell height in early spring were not able to reproduce the entire year irrespective of any growth later on, females below this size were sampled in March/April 1998 and kept with males in 500 ml beakers. Snails were measured bimonthly and beakers were checked for spawns regularly. 10 pairs from the Leine with females < 6,7 mm and 9 from the Pond with females < 6,9 mm were used.

3.3. Sex-ratio of progeny

It was the aim of this experiment to find out if the sex-ratio of the snails's progeny is 1:1 or different.

10-20 adult females per population and species were kept in the laboratory in 1997. Snails were maintained in 1 litre aquaria to lessen food competition between females and their progeny. When the juvenile snails had reached a sufficient size, they were sexed under a stereo microscope and measured with vernier callipers.

Additionally, on 3 occasions in the summer of 1997, some 100 young snails sampled in the Pond too small for immediate sex and species determination were kept in 5 l aquaria until they reached a sexable size. Then they were sexed and the sex- and species ratio established. The same was done with juveniles from the Leine once in 1997.

3.4. Shell growth marks and age determination

To test the hypothesis that growth marks on the shells of *B. tentaculata*, which some scientists use for age determination, are formed during the process of overwintering, 46 juveniles from the Ditch too small for sex determination were sampled in October 1997 and kept at room temperature during the winter period. In February 1998, the snails were sexed and the number of growth rings counted.

3.5. Female choice of oviposition site

The aim of this experiment was to find out if female *B. tentaculata* show any substrat preferences for egg laying when a choice of several naturally occurring substrata is given.

Experimental set-up:

Four round areas with a diameter of 35 cm were separated by plastic mesh in an aquarium. The plastic protruded from the water so that the snails could not leave the areas. Snails could move uninhibited within each area. Each area was divided into 8 segments of identical size. 2 segments per area contained one out of four different substrata (Fig. 3). Tested substrata were wood, gravel, tree leaves and aquatic macrophytes (*Nuphar lutea* stems and leaves). All substrata were sampled in the Pond and checked for spawns before the experiment.

Females were sampled in June 1997. Each of the 4 areas contained females of a different population. 9 females from the Canal, 11 from the Ditch, 13 from the Pond and 15 from the Small Pond were used. The females were left in the areas for 2 weeks, then they were recovered and it was recorded on which substrata they were found. The substrata were checked for spawns afterwards and spawns and eggs were counted.

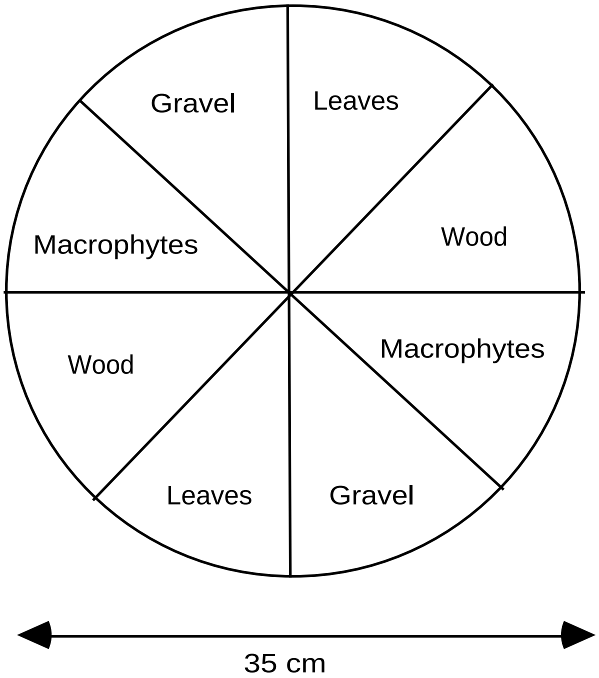


Fig. 3: Experimental set-up for the oviposition site choice of female *B. tentaculata*

3.6. Reproductive success of *Bithynia tentaculata* under the influence of *Lymnaea stagnalis*

B. tentaculata and *L. stagnalis* often coexist in their habitats. In this study, *L. stagnalis* was found in 3 out of 6 habitats. A detrimental influence through grazing by the much larger and mobile *L. stagnalis* on spawns and early juvenile stages of *B. tentaculata* was assumed. On the other hand, the smaller *B. tentaculata* is able to use habitat structures not accessible by the larger *L. stagnalis*. The negative influence of *L. stagnalis* should therefore be reduced by increasing structural diversity of the habitat.

Preliminary study

Ten aquaria containing 5 l of tap water were used in the laboratory in 1998. Each aquarium contained 6 females and 4 males of *B. tentaculata.* Two aquaria were used as controls and contained only *B. tentaculata* and a mud layer on the bottom, the other 8 contained 2 adult *L. stagnalis* each. Two of the aquaria had only a mud layer on the bottom, 2 additionally a gravel layer, 2 mud and macrophytes (*Elodea canadiensis, Ceratophyllum demersum* and *Stratiotes aloides*) and 2 mud, gravel and macrophytes. Dead *L. stagnalis* were replaced when necessary. Visible spawns on the glass were marked and observed. After the reproductive period aquaria were examined for juveniles.

Experimental set-up

In April 1999 8 plastic tubs with a capacity of 50 l were filled with tap water and some pond water. They all had a layer of mud on the bottom, 4 had an additional layer of gravel. Only gravel was used since the preliminary study showed no pronounced difference between gravel and macrophytes. Gravel has also the advantage that it can be easily examined for juvenile snails. The tubs were left for some weeks to allow colonisation by algae and bacteria. The tubs were located outside, evaporation was compensated for by rainfall.

10 males and 10 females of *B. tentaculata* were added per tub. 2 tubs contained only *B. tentaculata* and served as controls. 2 tubs contained *B. tentaculata* and 10 adult *L. stagnalis*, two tubs 5 *L. stagnalis* and a gravel layer, two tubs 10 *L. stagnalis* and a gravel layer. After 6 months the tubs were searched for juveniles and adults of both species and their number was recorded.

3.7. A simulation of severe dry periods

The Ditch at the Dümmer frequently dries up in hot summers with poor rainfall and therefore the population of *B. tentaculata* is obviously adapted to survive this unfavourable periods. It seemed interesting to test whether this is a special adaptation of this population or whether the species as a whole is capable to survive dry periods.

14 aquaria with a capacity of approximately 1,5 l were filled with pond water in June 1997. They had a layer of mud and gravel on the bottom. 2 of them were used for each of the 6 *B. tentaculata* populations and 2 contained *B. leachii* from the Pond. They contained 10-12 *B. tentaculata* and 28 *B. leachii*; altogether 66 female and 61 male *B. tentaculata* and 31 female and 25 male *B. leachii*. The water evaporated gradually until the aquaria fell dry in October. 4 weeks later water was added and the living snails were counted. To avoid any disturbances during the drying process, the number of surviving snails was not determined prior to desiccation.

3.8. Parasitation and reproduction

During this study I frequently observed that a certain percentage of adult females did not reproduce. Because there obviously seems to be no advantage in fitness terms related to not reproducing, I assumed that non-reproducing females were castrated by parasites. To test if parasitation is the only cause for reproductive failure, 33 adult females from the Hunte population were kept in 0,5 l beakers from May 1998 to late August 1998. Then the non-reproducing females were crushed and searched for parasitic stages.

4. STATISTICS

All statistics throughout this study were made with StatView 5.0 (1998), SAS Institute using a Macintosh Power PC. Due to the nature of the data which often did not allow the use of parametric statistics because of different variances between groups and/or data lacking normal distribution, non-parametric tests (Kruskal-Wallis One-Way ANOVA, Wilcoxon Rank Sum Test, Fisher's Exact Test) were applied several times.

Non-parametric tests were preferred over data transformation. Statistical significance is claimed when the P-value is at least < 0,05 or smaller. Smaller P-values are not marked differently for non-parametric tests in this study because of the comparatively small number of 30 or less per group.

After finding significant differences using a Kruskall-Wallis-Test, a posteriori comparisons were made using U-Tests.

A posteriori comparisons after a significant ANOVA normally used Bonferroni/Dunn Tests that controlled for number of comparisons. In some instances the less conservative Fisher's Post-Hoc Test was preferred.

For the comparison of egg number of first spawn to egg number of last spawn a paired T-Test was used. In cases when the exact number was not clear because 2 or more spawns had been laid between controls, the mean egg number of spawns was used in analysis. All T-Tests in this study are two-tailed.

To compare the shell height at maturity between populations, the heights of the 5 smallest reproducing snails per year were used in analysis.

The tendency for larger females to lay larger spawns at the onset of breeding than small females predicted by Begon and Parker (1986) was examined in a correlation analysis using the mean of the spawns laid in the first 3 weeks for females that reproduced at least for 5 weeks.

Throughout the text the term significant is always used in the sense of statistically significant in regard to the applied statistical methods. For better readability, the term significant may lack when there is direct reference to a significant P-value in the text.

Box Plots: In the results section, variables are often displayed as box plots. Each box plot is composed of 5 horizontal lines that display the 10th, 25th, 50th, 75th and 90th percentiles of a variable (this means, for example, that half of all data points are contained within the box between the second and the forth horizontal line. The 50th percentile is equal to the median of a distribution). All values above the 90th percentile and below the 10th percentile are plotted separately as small open circles to display outliers. Since my interest was on individuals showing divergent traits, box plots were often chosen to present data.

III. RESULTS

1. HABITAT CONDITIONS

1.1. Utilizable habitat size

Water velocity and oxygen

Because of the special requirements of any living organism, the physical size of a habitat and its utilizable size for a given organism are mostly not the same. A rough assessment of the 6 habitats leads to following classification:

A) The rivers:

High water velocity makes it impossible for *B. tentaculata* to adhere to the surface of vegetation or stones. As a result, sites with strong water currents like the river bed were not populated by snails. Snails living in the Hunte used solely the vegetation on both river banks, preferring areas near the water surface. The snails in the Leine were living more or less densely clustered on the underside of stones. This structures reduced water velocity effectively so that fine detritus and mud settled down. Oxygen supply seemed sufficient since even very muddy parts were populated in summer.

B) Habitats with oxygen depletion in summer:

Oxygen depletion and long periods with anaerobic conditions and H_2S formation occurred regularly in the Canal, the Ditch and the Small Pond each summer. This was due to the heavy load of plant debris and organic detritus in the habitats. As a consequence, *B. tentaculata* lived near the water surface during summer and avoided all parts deeper than 30-50 cm. Snails reentered bottom parts only when water temperatures decreased in autumn.

The failure to keep caged snails alive at the Dümmer was due to a long-lasting oxygen depletion in all but the upmost water levels in the Canal and the Ditch during the summer of 1997.

At the end of the reproductive period in July 1998 one containment with about 50 *B. tentaculata* dropped into the anaerobic zone at the bottom of the Small Pond. Since controls happened on a weekly basis, snails were exposed at maximum for seven days to hypoxic conditions. About 80% of the snails were dead at recovery of the containment and most others died the following week. All eggs that had remained at the season's end were also dead. This illustrates the pronounced effect of oxygen availability on the gill-breathing *Bithynia*.

C) Habitats without oxygen depletion:

The Pond was the only habitat with standing water that was populated in all depth during summer. *B. tentaculata* and *B. leachii* were found directly beneath the water surface and in depths of approximately 1,5 m. Except for deeper layers of rotting plant debris, the whole habitat was utilizable the year round even when snails preferred the parts near the water surface in summer.

1.2. Temperature

The temperature profiles of the three habitats in Hannover resembled each other very closely. The water temperature rised steadily from mid-March to June, being more or less stable in the range of 15°C to 22°C during summer until autumn. Temperatures started to decrease slowly then, reaching their minimum during winter (Fig. 4).

Neither the maxima (ANOVA, P = ,1875) nor the minima (ANOVA, P = ,1685) differed significantly between the habitats, but there was a trend towards the Pond being slightly warmer than the Small Pond. The highest temperatures were frequently measured in the Pond but never exceeded 24°C. The lowest temperatures were encountered in the Leine where the temperature dropped to 1°C in winter. In contrast, the temperature in the ponds seldom dropped below 4°C and periods of ice cover were short in both winters.

To search for differences in temperature fluctuations between habitats, the weekly differences between the minima and maxima for any given temperature measurement were used in an analysis of variance, but there was no difference found (ANOVA, P = ,8788). The temperature regime in the habitats therefore seems homogenous on a long-time scale.

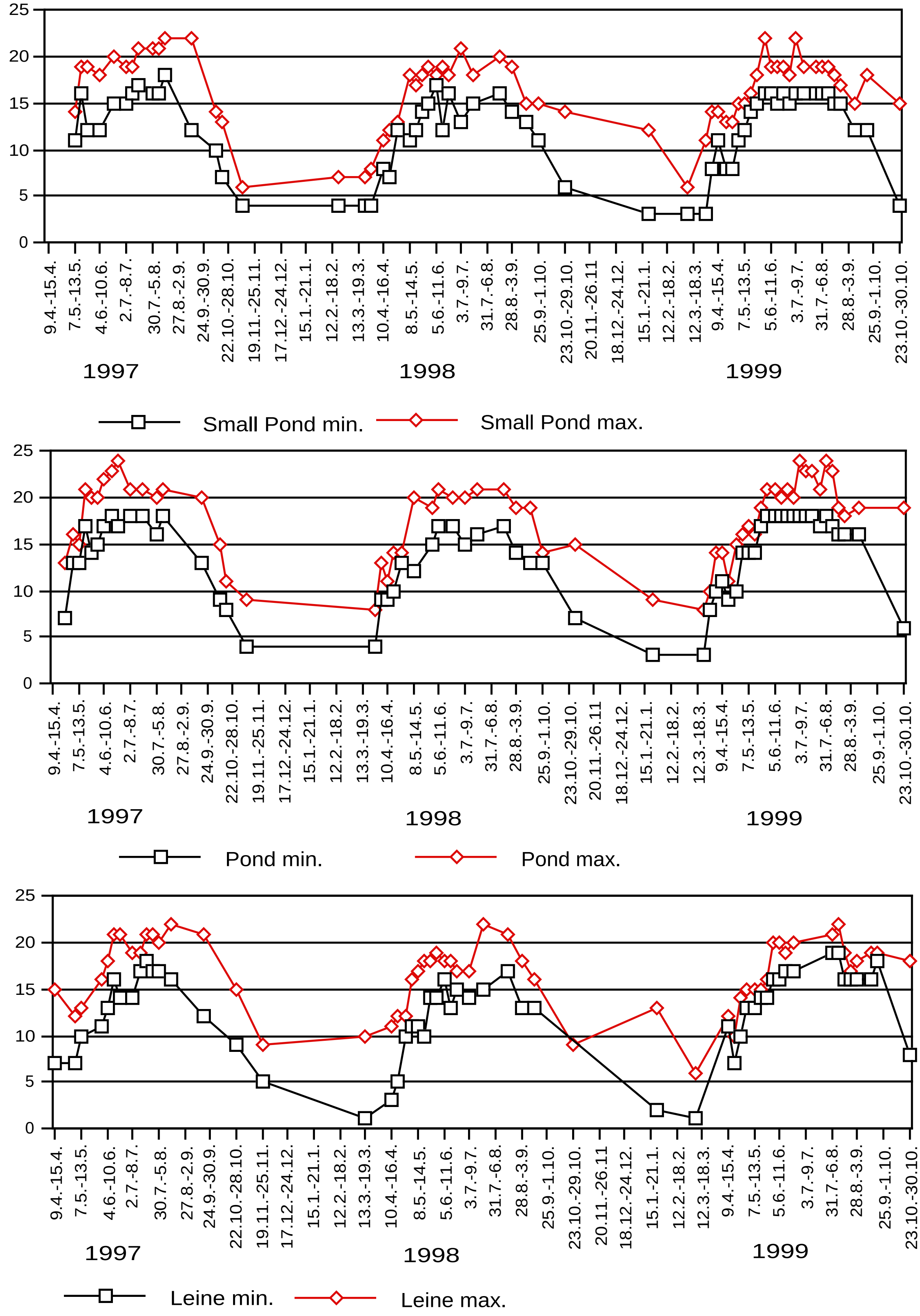


Fig. 4: Temperature regime of the three habitats in Hannover (y-axis in °C)

1.3. Predators

The presence or absence of predators deeply influences the living conditions for any organism and may alter the size of the utilizable habitat.

A) Shell invading predators: Leeches, water bugs and beetles were present in all habitats. *Chaetogaster* sp. was especially common in the Ditch.

B) Shell breaking predators: Crayfish (*Orconectes sp.*) were present in the Leine and in the Pond. Fish were absent in the Small Pond and in the Ditch with the exception of nine-spined stickleback in 1998 in the latter habitat. All other habitats had a diverse fish fauna which could not be classified any further.

Dabbling ducks were commonly present on the Leine and the Canal and to a lesser degree on the Pond and the Small Pond.

1.4. Co-occuring molluscan species

Overall 20 gastropod and 5 bivalve species were found (Tab. 3; the genus *Pisidium* is not included). The most diverse were the 3 habitats at the Dümmer whereas in Hannover only few molluscan species were present. Prosobranch diversity was generally low with 4 species out of 6 present in only 1 of the habitats. Only in one habitat, the Leine, lived more than 2 different prosobranch species. Pulmonate diversity was generally higher than that of prosobranchs with exception of the Leine where only *Radix ovata* was found. 11 pulmonate species occurred in the Canal, 10 in the Ditch and 9 in the Hunte.

Members of the Unionidae were found in three habitats with three species living in the Hunte and one species in the Canal and the Pond. *Sphaerium corneum* was quite common and found in 4 habitats whereas *Dreissena polymorpha* was only found in the Leine.

Several species were altogether rare and only few individuals were found. This is the case with *Viviparus contectus*, *Potamopyrgus antipodarum*, *Valvata cristata* , *Acroloxus lacustris*, *Galba truncatula*, *Radix auricularia*, *Gyraulus albus* and *Hippeutis complanatus*. *Anisus vortex* was very abundant in all its habitats. All other gastropod species showed intermediate patterns, rare in some habitats and common elsewhere.

Tab. 3: Species composition of the different habitats

	Hunte	**Canal**	**Ditch**	**Small Pond**	**Pond**	**Leine**
GASTROPODA						
Viviparus contectus		*				*
Potamopyrgus antipodarum						*
Bithynia tentaculata	*	*	*	*	*	*
Bithynia leachii					*	
Valvata piscinalis	*					
Valvata cristata						*
Acroloxus lacustris	*	*			*	*
Lymnaea stagnalis			*	*	*	
Stagnicola sp.	*	*		*	*	*
Galba truncatula			*			
Radix ovata	*		*		*	*
Radix auricularia	*	*				
Planorbis planorbis	*	*	*			
Planorbis carinatus	*	*	*			
Anisus vortex	*	*	*	*		
Bathyomphalus contortus	*	*	*			
Gyraulus albus		*	*			
Hippeutis complanatus		*	*			
Planorbarius corneus		*	*			
Physa fontinalis	*	*				
BIVALVIA						
Unio pictorum	*					
Anodonta cygnea	*	*				
Anodonta anatina	*				*	
Sphaerium corneum	*	*		*		*
Dreissena polymorpha						*

1.5. Abundance of the molluscan species in different habitats

Hunte

B. tentaculata was by far the most common species and dominant most time. In spring 1997 *Valvata piscinalis* was dominant and three times as abundant as *B. tentaculata* but numbers receded during summer. *Anisus vortex*, *Physa fontinalis* and *Sphaerium corneum* could be common sometimes, all other species were rare.

Canal

B. tentaculata and *A. vortex* were the most abundant species but their presence was strongly fluctuating. Common were *Planorbis planorbis* and *P. fontinalis*, all other species were rare.

Ditch

The Ditch was clearly dominated by pulmonate species. *P. planorbis, P. carinatus, A. vortex, Bathyomphalus contortus* and *Planorbarius corneus* were very common with a maximum in late summer/autumn. *B. tentaculata* was most common in spring and early summer when the pulmonates had not yet reached high numbers. The other pulmonates were rare.

Small Pond

With exception of *Stagnicola* sp. all molluscan species were common but their abundance was fluctuating with time of year. *B. tentaculata* was mostly present in large numbers but in late summer *A. vortex* was sometimes predominant. *Lymnaea stagnalis* was rare in early spring but numbers increased dramatically when juvenile hatching started in late spring/summer. *Sphaerium corneum* was always common but never predominant.

Pond

B. tentaculata was common in spring, rare after the die-off in summer and common again in late summer/autumn when juveniles were grown. *B. leachii* was rare the first 2 years and predominant over *B. tentaculata* in the second half of 1999. All other snail species were mostly rare. The number of species was low for a comparatively large habitat as the Pond.

Leine

B. tentaculata was the dominant snail species comprising more than 80% of all snails in all the years. Only *Radix ovata* was also common during 1998, all other prosobranchs were rare to non-existent. In the summer 1998 *Dreissena polymorpha* was the predominant mollusc species comprising more than 50% of all individuals but its numbers decreased rapidly during winter.

2. GROWTH PATTERN, POPULATION DYNAMICS AND SEX-RATIO OF FIELD POPULATIONS

2.1. Some remarks on field sample data

Following sample data are biased, simply because large snails are more easily found than smaller ones. Fortunately, this bias is in the same direction for all populations. Dense submerse vegetation presented the major obstacle for sampling, regardless of sampling technique, so sampling data from habitats without macrophytes like the Leine are more accurate than data from habitats with extensive vegetation like the Canal, the Ditch or the Pond. For latter habitats difficulties increased from spring to summer with increasing plant growth, in some instances making it impossible to search successfully for snails during summer months. This explains most of the lacking data points in graphs.

As a further consequence, newly hatched snails smaller than 2,5 mm could not be sampled appropriately and were therefore excluded from analysis. This leads to the effect that mean shell size in diagrams drops with a delay of approximately one month to the start of juvenile hatching in the field. In my opinion this poses no problems for comparisons because this shift is encountered in all habitats and for both species.

2.2. Growth pattern and population dynamics

2.2.1. Introductory remarks

First, there is a comparison of the population means for shell height for every habitat and species separately, combined with evidence from the length-frequency diagrams. The first part is followed by the same data viewed under the angle of different years for all observed populations simultaneously. The same procedure is employed on the temporal fluctuations of sex-ratio within and between populations.

Sample size for individual data points is not included in the figures showing mean shell height and sex-ratio, but can be seen in the length-frequency diagrams (which use the same data sets).

2.2.2. Habitats

Hunte

On the whole, the curves for both years are fairly congruent. Mean shell height in early spring was different in 1997 and 1998 (T-Test, $P < ,0001$), the population consisting of larger size classes in 1997 than the following year when there were a lot of snails well below adult size (Figs. 5a and 8).

In both years there was an increase in mean shell height during spring to early summer followed by a steep decline which marks the hatching of juveniles. Juvenile hatching started 4 weeks earlier in 1997 than in 1998. In contrast to 1998 there were already juveniles present in June 1997. In both years the population consisted mainly of young individuals by July. In 1998 there was almost a complete replacement of elder individuals during summer months.

There was moderate shell growth in both years from late summer onwards till the onset of overwintering. The slope of the curve was much steeper in spring than in autumn in both years. The mean shell height before and after overwintering as the length-frequency data of the population were in correspondence.

Canal

The population was already very large in early spring both years, consisting almost exclusively of adult animals and showing only very moderate growth until summer (Figs. 5b and 8). In 1997 there was a steep decline in July when juveniles hatched and adults vanished, followed by rapid growth of juvenile snails. The newborns already reached mean adult sizes before winter.

The mean shell height before and after overwintering corresponded directly as did the length-frequency distributions of the population. Intense vegetation made sampling impossible in the summer of 1998. In August there was a mixture of very small to large snails with no size class overproportionally present. Until October there was apparently no growth and the population mean was below the value for 1997, but this may be an artefact due to the small sample size (n =16).

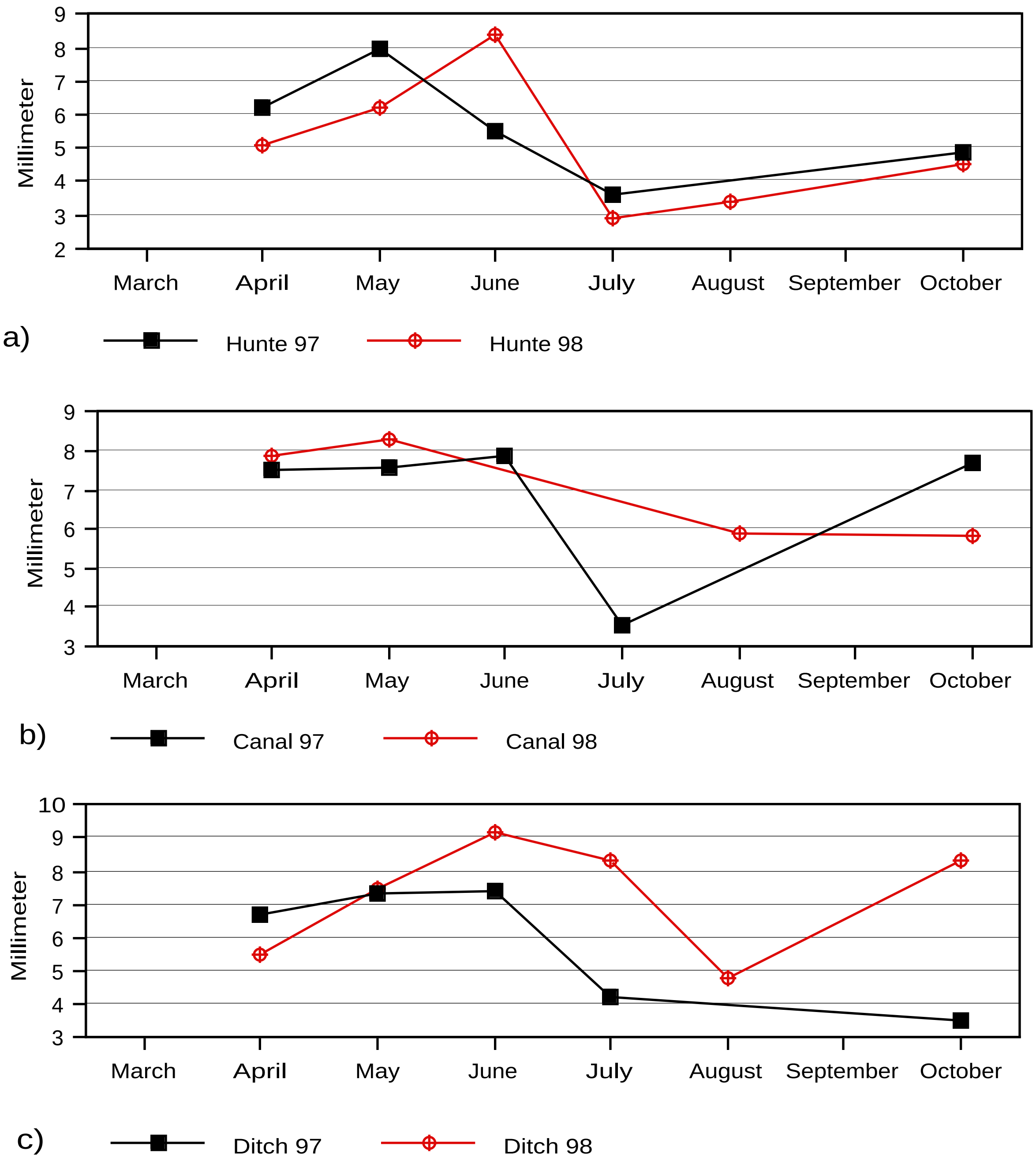


Fig. 5: Mean shell height graphs for Dümmer populations of *B. tentaculata*
(n = 1451/Hunte; n = 514/Canal; n = 780/Ditch)

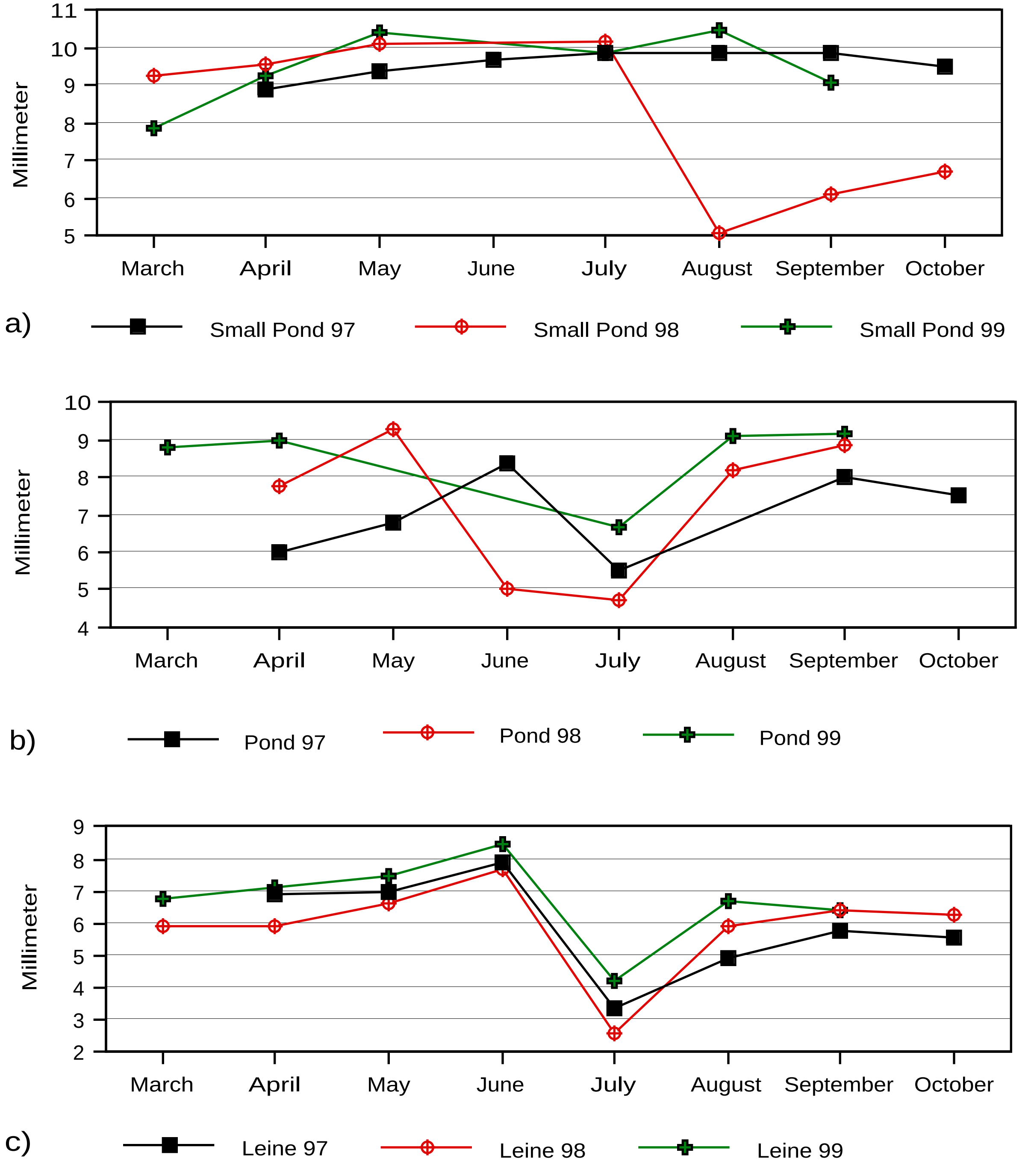


Fig. 6: Mean shell height graphs for *B. tentaculata* populations in Hannover (n = 2304/Small Pond; n = 1046/Pond; n = 2825/Leine)

Ditch

The graphs for both years are very different (Figs. 5c and 8). Mean shell height in April was different in both years (U-Test, Tied P = ,0001), the population consisting mainly of subadult snails in 1998.

In 1997 there was only moderate growth after overwintering with a great part of the population retaining a size below the critical shell size for reproduction. Juvenile hatching started in July. The population seemingly did not grow afterwards until overwintering. In October nearly the whole population was represented by very small individuals. Mean height before and after overwintering did not correspond.

In 1998 there was initially a rapid increase in shell size during spring with all individuals reaching adult sizes in summer. Juveniles first appeared in July again but main juvenile hatching occured a month later than the previous year. After the reproductive period the population grew very fast reaching a maximum in the adult size classes in autumn.

Small Pond

The population structure in the Small Pond showed some peculiarities as the population almost completely failed to reproduce in 1997 and 1999 (Figs. 6a and 9). In April 1997 mean shell height was already near 9 mm. There was a small, but constant increase until July when the population mean reached 10 mm. Almost all animals were in the size classes 9 to 11 mm by then. Mean shell height remained on this high level until autumn with a small decline in October. This was due to the appearance of very few juveniles in this month.

In March 1998 the mean shell height was already well above 9 mm. The population structure was in correspondence with that of the previous October, the whole population comprised of the size classes 9 to 11 mm with only very few smaller juveniles present. The mean shell height increased to 10 mm in May and stayed on this level until August. In August the population consisted of nearly 80% of newly hatched snails. Mean shell size dropped to 5 mm and increased about 1mm per month until October.

In March 1999 mean shell height was below March 1998 (U-Test, Tied P = ,0222) and well above the level of the previous October (T-Test, P = ,0003). This points in the direction that mortality is higher in smaller size classes during winter. The population grew very fast until May when 90% of all snails were 10 mm or larger, some reaching exceptionally large shell sizes of 13 mm and above. Juveniles were always present in samples from July onwards but they comprised only a small fraction of the population and size classes of 10 mm and above remained dominant until autumn.

Pond

The population means were different in all years in April (ANOVA, P < ,0001; Bonferroni/Dunn post hoc test, P < ,0001 for all three comparisons between years).
In 1997, the population started from a low level with no prevalent size class and grew until June when half the snails were in the 9 mm size class (Figs. 6b and 10). Juveniles appeared in July comprising 60% of the total population. At the same time a fungal disease started killing the adult snails (most likely a pathogenic member of the family of Saprolegniales (Oomycota), pers. com. by A. de Cock, Bureau for Schimmelculturen, the Netherlands). Mean shell height increased until September again and dropped a bit in October when a second autumnal rush of juveniles entered the population.

In April 1998 the mean shell height was already 8 mm and increased to above 9 mm in one month. In June and July the population was dominated by small size classes when juveniles hatched and the fungus killed large numbers of adult snails. Until August mean shell height increased for more than 3 mm in just one month and increased further in autumn. In September 75% of the population was in or above the 9 mm size class.

In March 1999 the population set out from this high level and in April 85% of all snails had a shell height of 9 mm or above. Due to a very early and severe fungal infection this year, the population declined drastically in early summer 1999. Nearly no snails were found until July when the newly hatched snails had reached searchable sizes. Growth again was rapid until August but came to a halt later on. It should be mentioned that the fungal infection started earlier every year, but never occurred again after July, thereby not affecting the new generations.

Leine

This population showed the most uniform course throughout the years (Figs. 6c and 9). After overwintering the mean shell height increased slowly to its maximum in June, then dropped to its minimum in July when juveniles hatched in large numbers. Hatching was followed by rapid growth in late summer that slowed down in autumn and came to a halt at the end of the season.

The population composition was different in spring 1998 when the mean shell height was well below that of the other years (March: U-test, Tied P = ,0010; April: Kruskall-Wallis–Test, Tied P < ,0001). There were differences in the population composition before and after overwintering. Population means were slightly above the October values in March 1998 and 1999. The differences were only significant between October 1998 and March 1999 when the mean shell height difference was 0,5 mm (T-Test, P = ,0385). This underlines the aforementioned trend that winter mortality is higher in the smaller size classes.

B. leachii

Data for *B. leachii* are sparse as a consequence of the rareness of this species that only became abundant in 1999. Compared to *B. tentaculata* the length-frequency distribution was more homogeneous because *B. leachii* curbs growth at a smaller size (Figs. 7 and 10). Most snails remained in the 5 mm size class or below, with the exception of spring 1999 when 40% were in the 6 mm and some females even in the 7 mm size class.

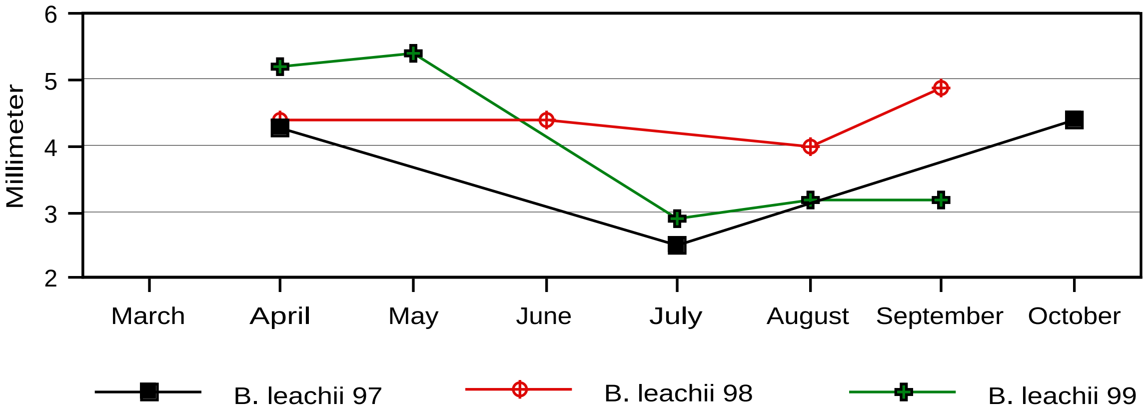
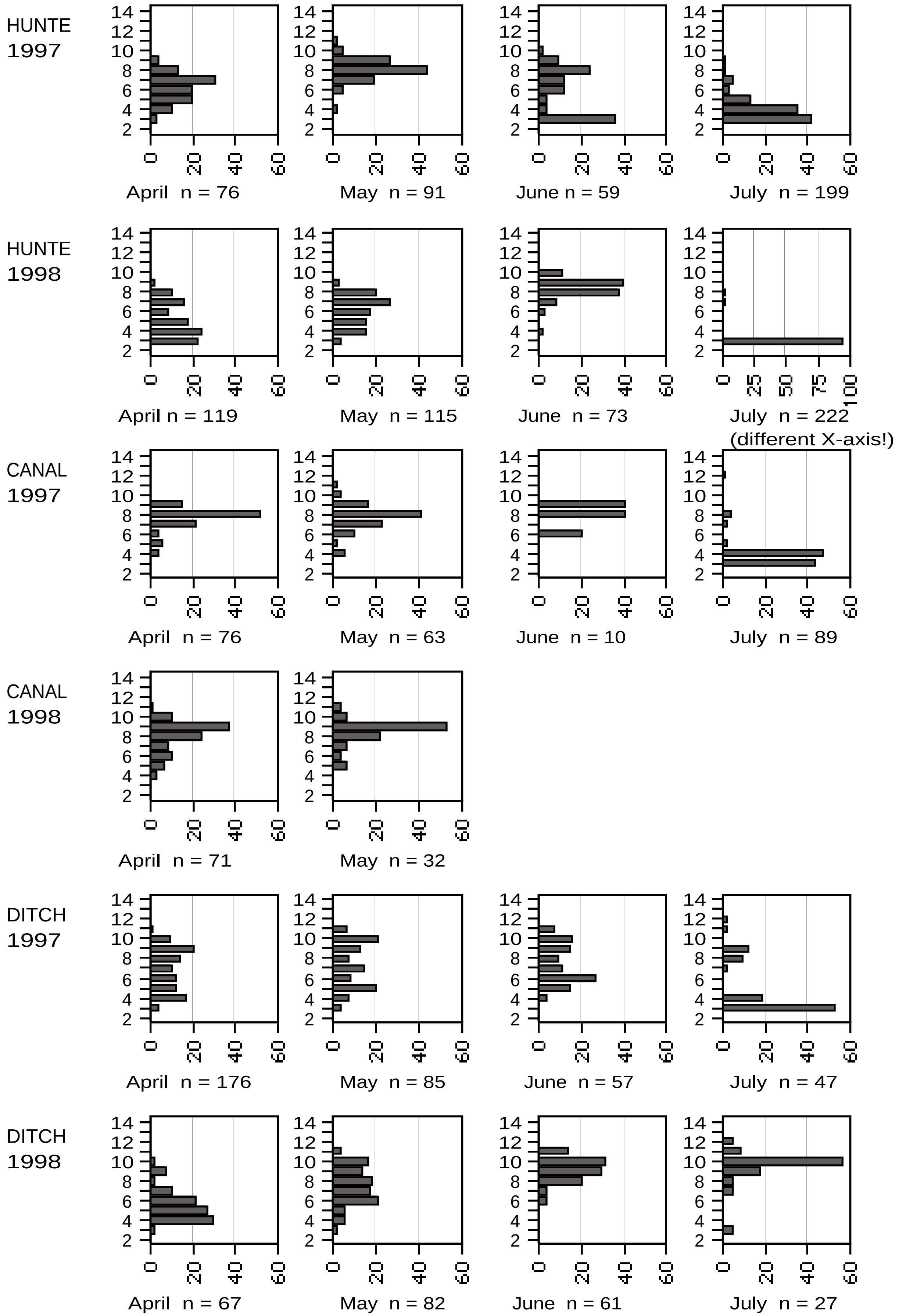


Fig. 7: Mean shell height graph for *B. leachii* (n = 317)

Only 1999 is discussed in detail when nearly 200 *B. leachii* were sampled. Being slightly above 5 mm, the mean shell height in April 1999 was nearly 1 mm above the previous years (Difference was significant, ANOVA P < ,0001; Bonferroni/Dunn P < ,0001 for comparisons between years). The population grew moderately in spring and juveniles dominated from July onwards. The mean shell size was 3 mm in July. The increase in shell size was only moderate during autumn in 1999.



April n = 76
May n = 91
June n = 59
July n = 199

April n = 119
May n = 115
June n = 73
July n = 222

April n = 76
May n = 63
June n = 10
July n = 89

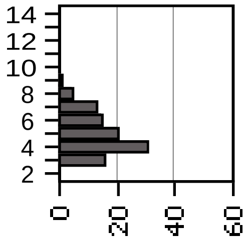
April n = 71
May n = 32

April n = 176
May n = 85
June n = 57
July n = 47

April n = 67
May n = 82
June n = 61
July n = 27

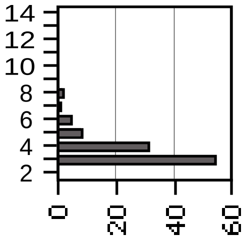
Fig. 8: Length-frequency graphs for the Dümmer populations of *B. tentaculata*

HUNTE
1997

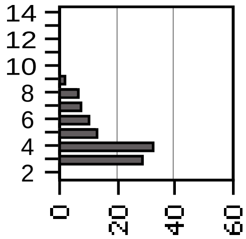


October n = 153

HUNTE
1998

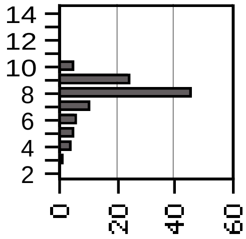


August n = 232



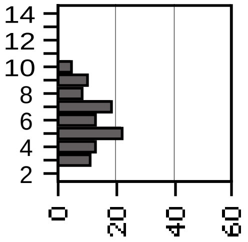
October n = 112

CANAL
1997

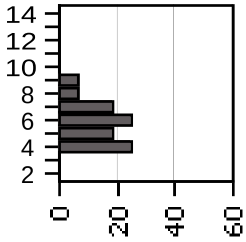


October n = 86

CANAL
1998

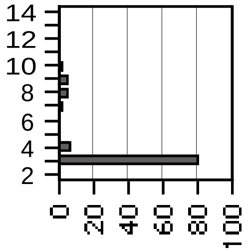


August n = 71



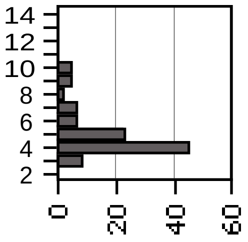
October n = 16

DITCH
1997

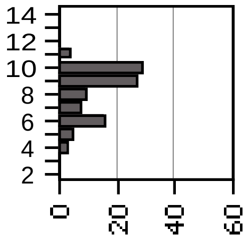


October n = 52 (different X-axis)

DITCH
1998



August n = 49



October n = 77

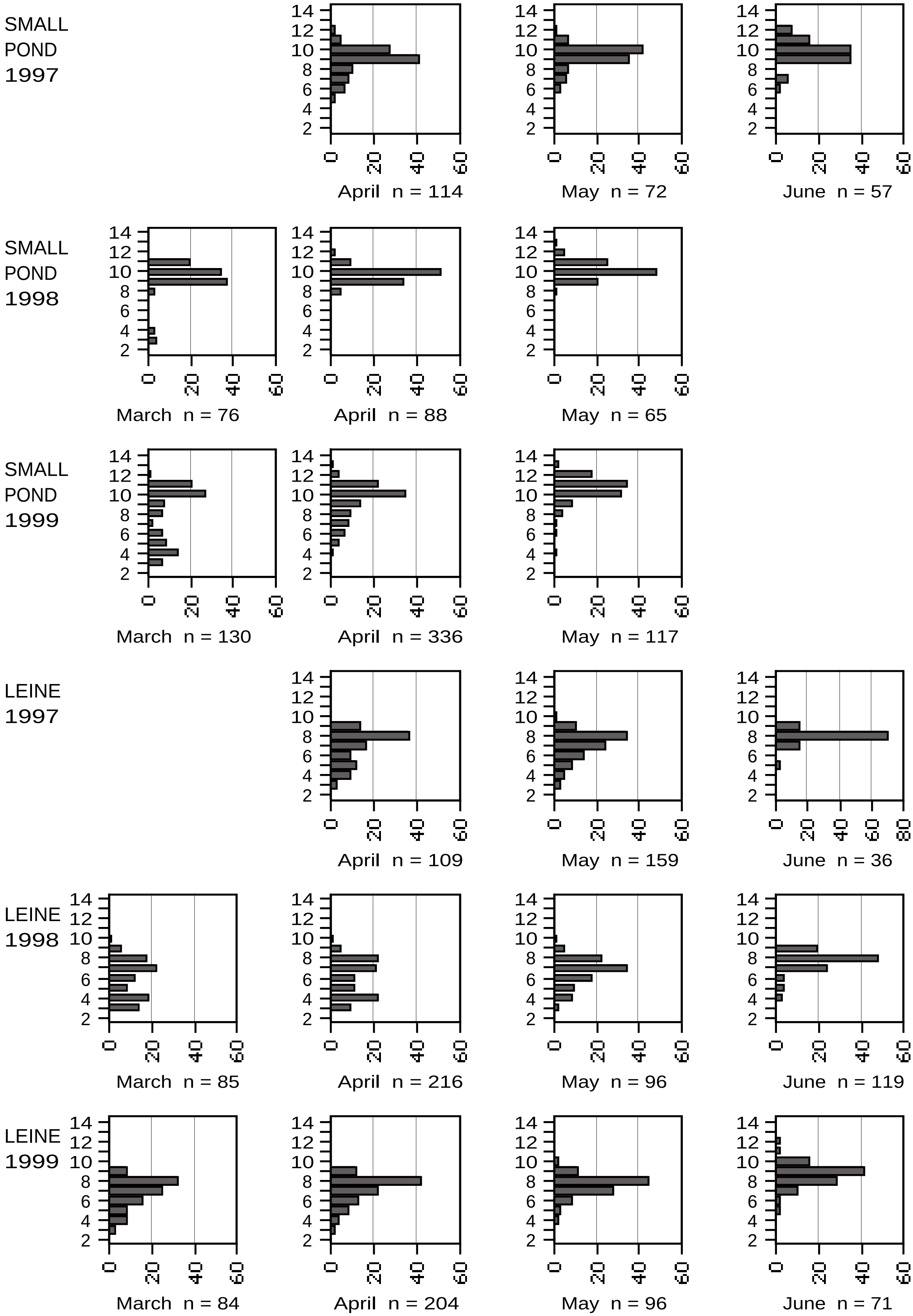
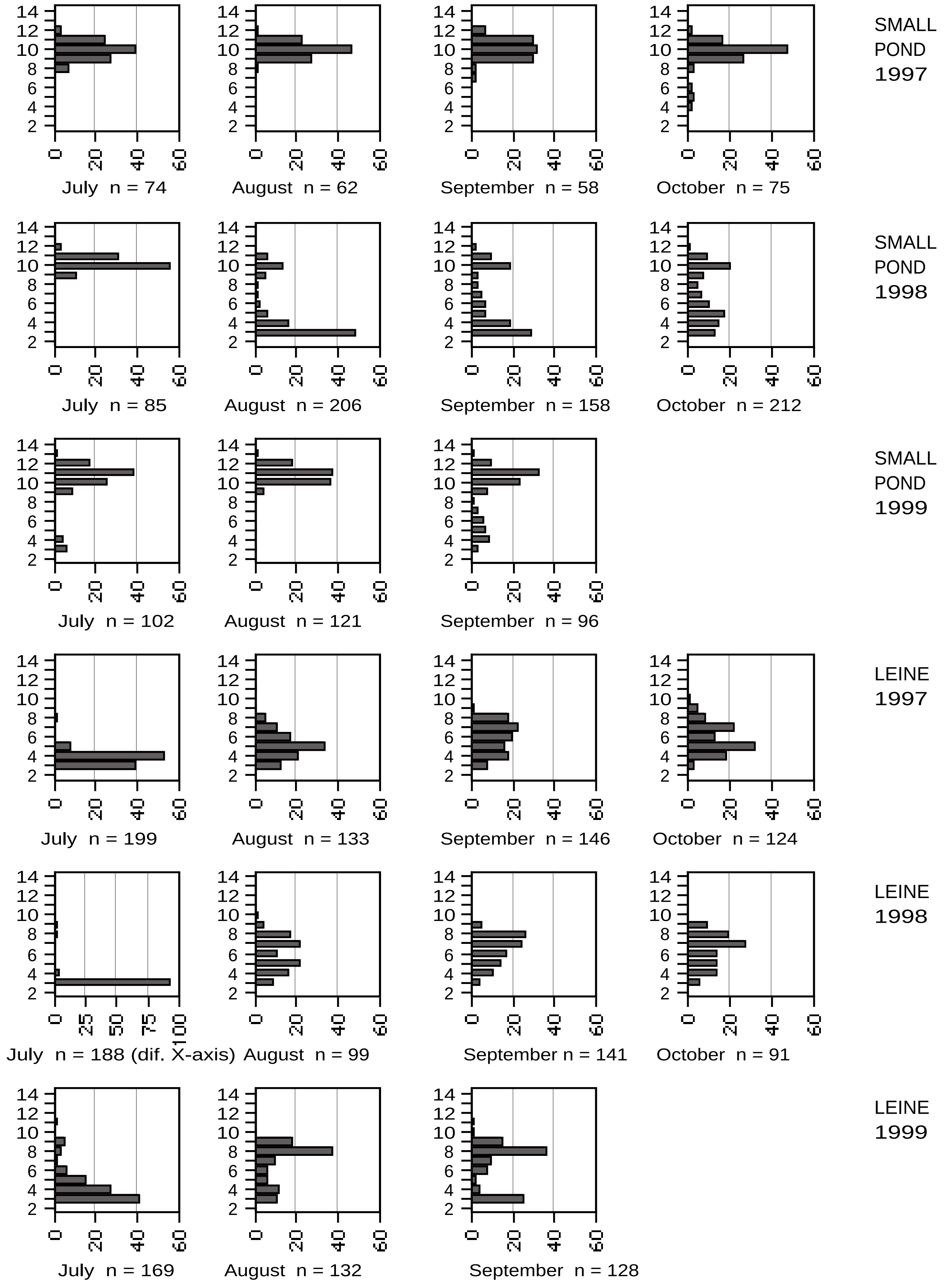


Fig. 9: Length-frequency graphs for the Small Pond and Leine populations of *B. tentaculata*



July n = 74
August n = 62
September n = 58
October n = 75

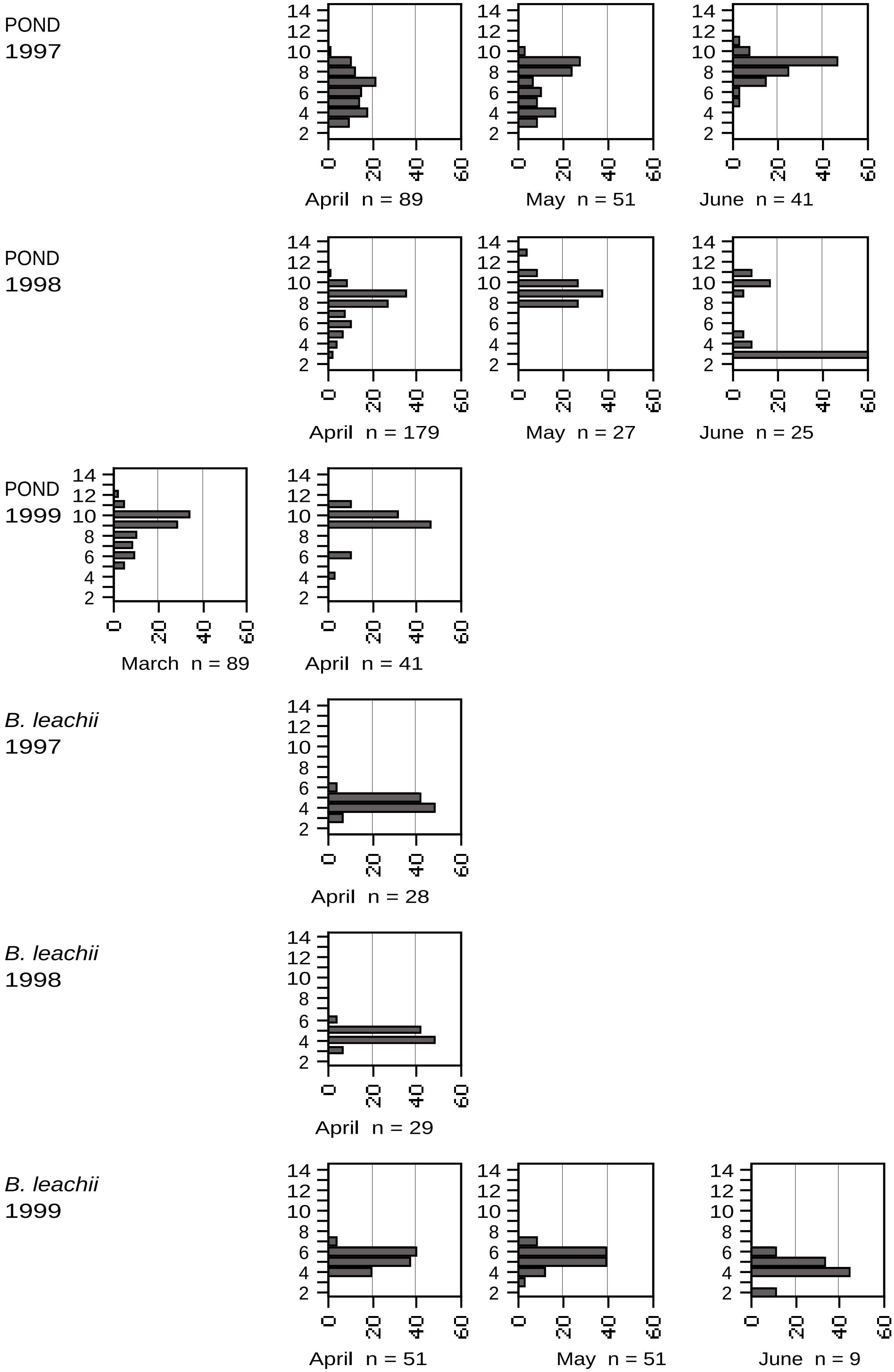
July n = 85
August n = 206
September n = 158
October n = 212

July n = 102
August n = 121
September n = 96

July n = 199
August n = 133
September n = 146
October n = 124

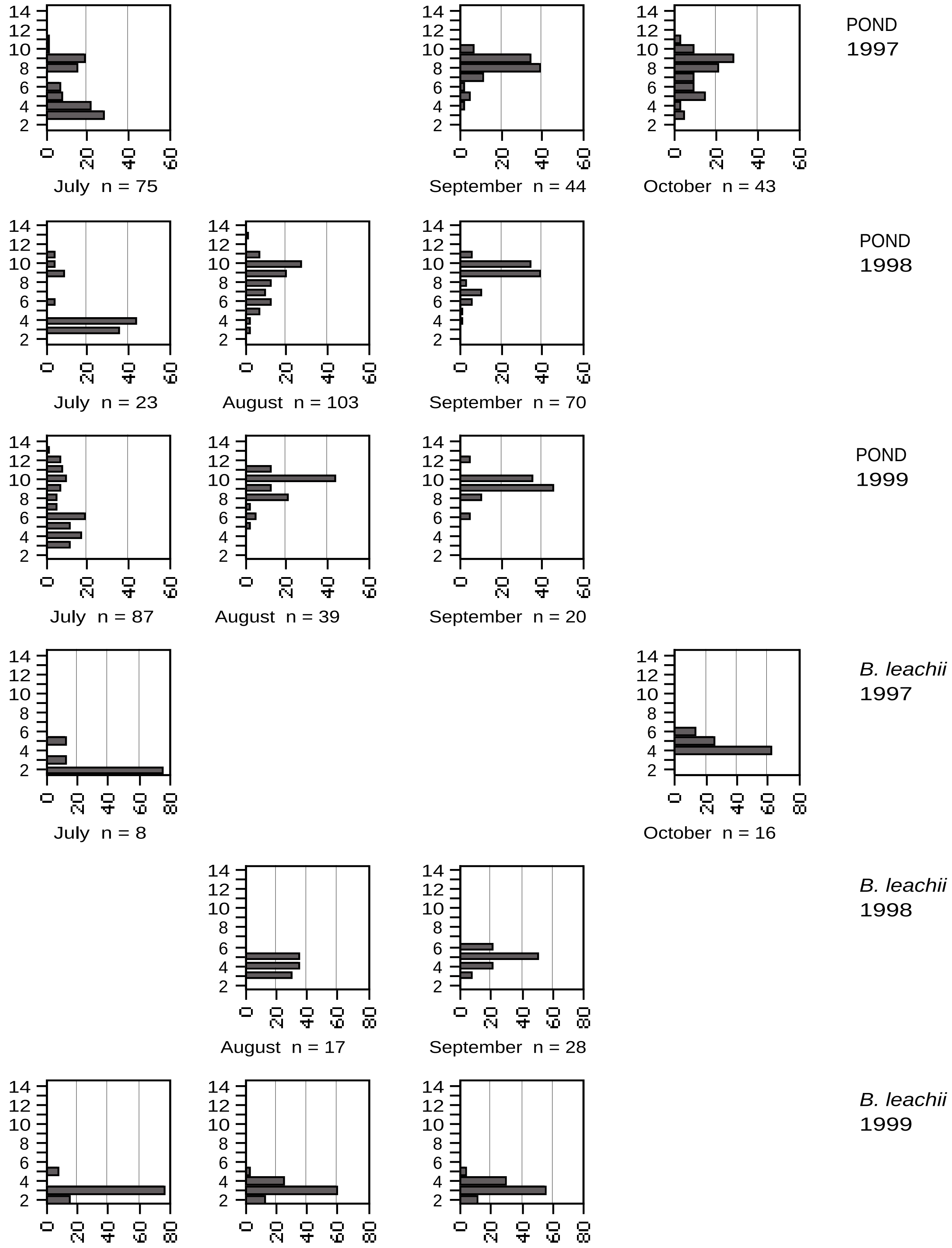
July n = 188 (dif. X-axis)
August n = 99
September n = 141
October n = 91

July n = 169
August n = 132
September n = 128



April n = 89
May n = 51
June n = 41
April n = 179
May n = 27
June n = 25
March n = 89
April n = 41
April n = 28
April n = 29
April n = 51
May n = 51
June n = 9

Fig. 10: Length-frequency graphs for the Pond populations of *B. tentaculata* and *B. leachii*


14
12
10
8
6
4
2
0
20
40
60
80
July n = 75
September n = 44
October n = 43
POND
1997
July n = 23
August n = 103
September n = 70
POND
1998
July n = 87
August n = 39
September n = 20
POND
1999
July n = 8
October n = 16
B. leachii
1997
August n = 17
September n = 28
B. leachii
1998
July n = 13
August n = 40
September n = 27
B. leachii
1999

2.2.3. Years

1997

This was a year with fairly homogeneous tendencies (Fig. 11a). In April the mean shell heights of most populations were between 6 mm and 7 mm. However, there were significant differences (ANOVA, P < ,0001). The Canal population lay somewhat above average and the Small Pond population was clearly larger than all others (Bonferroni/Dunn, P < ,0001). The Small Pond population remained larger than the other populations throughout the year. This was in part due to its lack of reproductive success.

All populations grew moderately during spring. The first juveniles appeared in the Hunte already in June and one month later in the other habitats. With exception of the Ditch there was considerable growth in late summer and autumn. However, the rate of increase in shell height differed between habitats to the effect that in October there were pronounced differences in mean shell height between the populations (Kruskall-Wallis-Test, P < ,0001, a non-parametric test was employed because shell height distribution was bimodal in some cases).

Shell heights fell into 4 groups at the end of the season, the Small Pond population being larger and the Ditch population smaller than all others (Fig. 11a). The Canal and Pond populations were of the same mean height and fairly large with 7,5 mm but their length–frequencies showed differences (Figs. 8 and 10). The Canal population was dominated by the size class of 8 mm which comprised nearly 50% of all snails whereas the Pond population was more evenly distributed and had its maximum with 30% in the 9 mm size class. The river populations (Leine and Hunte) were clearly smaller and lay between them and the Ditch.

1998

This year the course of the mean shell heights was inhomogenous (Fig. 11b). The population differences visible the previous October prevailed throughout overwintering. Only the mean shell height in the Ditch closed up to the river populations, leaving 3 groups of significantly different shell heights (ANOVA, P < ,0001; Bonferroni/Dunn P < ,0001 for differences between groups). The Small Pond snails were by far the largest, the Pond and Canal snails were of intermediate height and the group with the smallest mean heights consisted of the Hunte, Leine and Ditch populations.

3 populations showed rapid growth in spring with an increase of at least 1 mm per month for 1 (Pond) or 2 months (Hunte and Ditch), the others showed a more restrained increase. Juveniles were first present in the Pond, making up the majority of the population from June onwards. Differences were pronounced in July, the river populations of Leine and Hunte consisting almost completely out of juveniles by now whereas hatching commenced only slowly in the other Dümmer populations and no juveniles were found in the Small Pond. Here newborn snails appeared during autumn, comprising now more than 75% of the population.

The mean shell height reached its minimum in August for 2 populations (Ditch and Small Pond), whereas it increased for more than 3 mm in the Pond and the Leine. During autumn the increase in shell size ranged from zero (Canal and Leine) over moderate (Hunte, Small Pond and Pond) to rapid in the Ditch.

At the end of the season the mean shell heights fell again within 3 groups clearly separated from each other (Kruskall-Wallis-Test, $P < ,0001$). However, the grouping differed from the spring situation. The population in the Ditch had now by far the largest mean shell size, the Hunte snails were the smallest and the other 4 populations were intermediate. The picture was even further complicated because of the different size class distributions (uni- and bimodal) within the 6 populations (Figs. 8, 9 and 10).

1999

This year the mean shell heights were again different between the 3 remaining populations (Fig. 11c). Shell heights differed in March (Kruskall-Wallis-Test, $P < ,0001$) when Pond and Leine showed a unimodal size-frequency distribution with a maximum in the 10 mm and 8 mm class, respectively. The Small Pond showed a bimodal distribution with clearly separated juvenile- and adult-sized snails (Fig. 9).

Growth in spring was zero in the Pond, moderate for three months in the Leine and fast until May in the Small Pond population, the latter reaching the mean shell size of the Pond population already in April. The Small Pond population failed successful reproduction again this year. In contrast, the Leine population consisted mainly of juveniles by July (Fig. 9).

Because most snails were killed by the fungal infection in the Pond, sampling was unsuccessful in May and June. In July the Pond population consisted of fast-growing juveniles with no apparent maximum in any size-class (Fig. 10). During late summer rapid

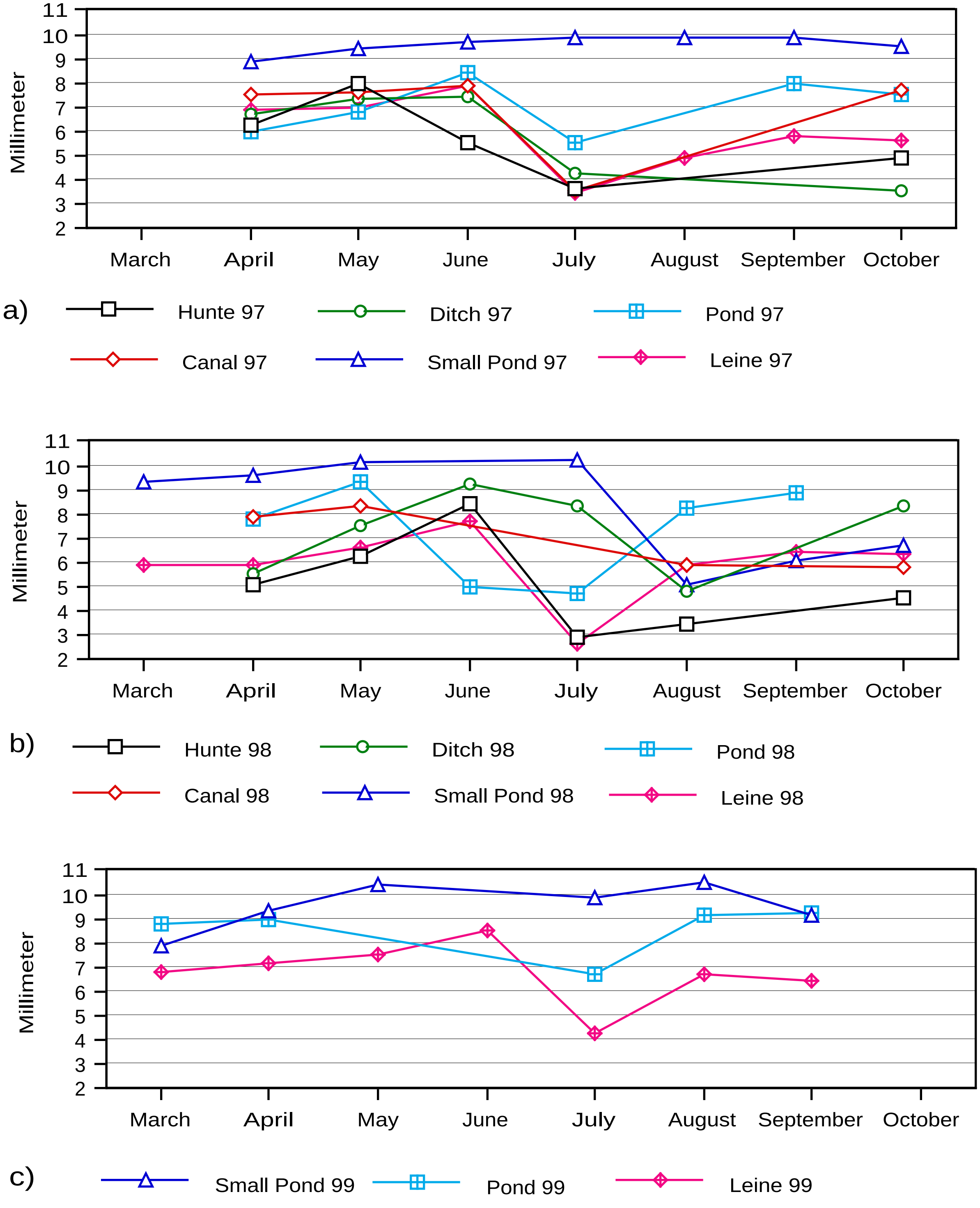


Fig. 11: Mean shell heights for all years and all *B. tentaculata* populations (n = 8920)

growth took place in the Pond and the Leine that stopped already in autumn. In the Small Pond some juveniles were found in September, the adult snails showing no further increase in shell size before winter.

2.2.4. Gender effects on growth

The effect of gender on growth was of minor importance. When the growth data were splitted for gender, the resulting mean shell height graphs were mostly in parallel (Fig. 12). At the Dümmer, only the Canal population showed minor differences between males and females (Fig. 12a). However, this seems to be an artefact of the small sample sizes (Because the sex-ratio fluctuates in time, the number of snails of a given gender was low at some sampling dates. Several samples had to be excluded for this reason).

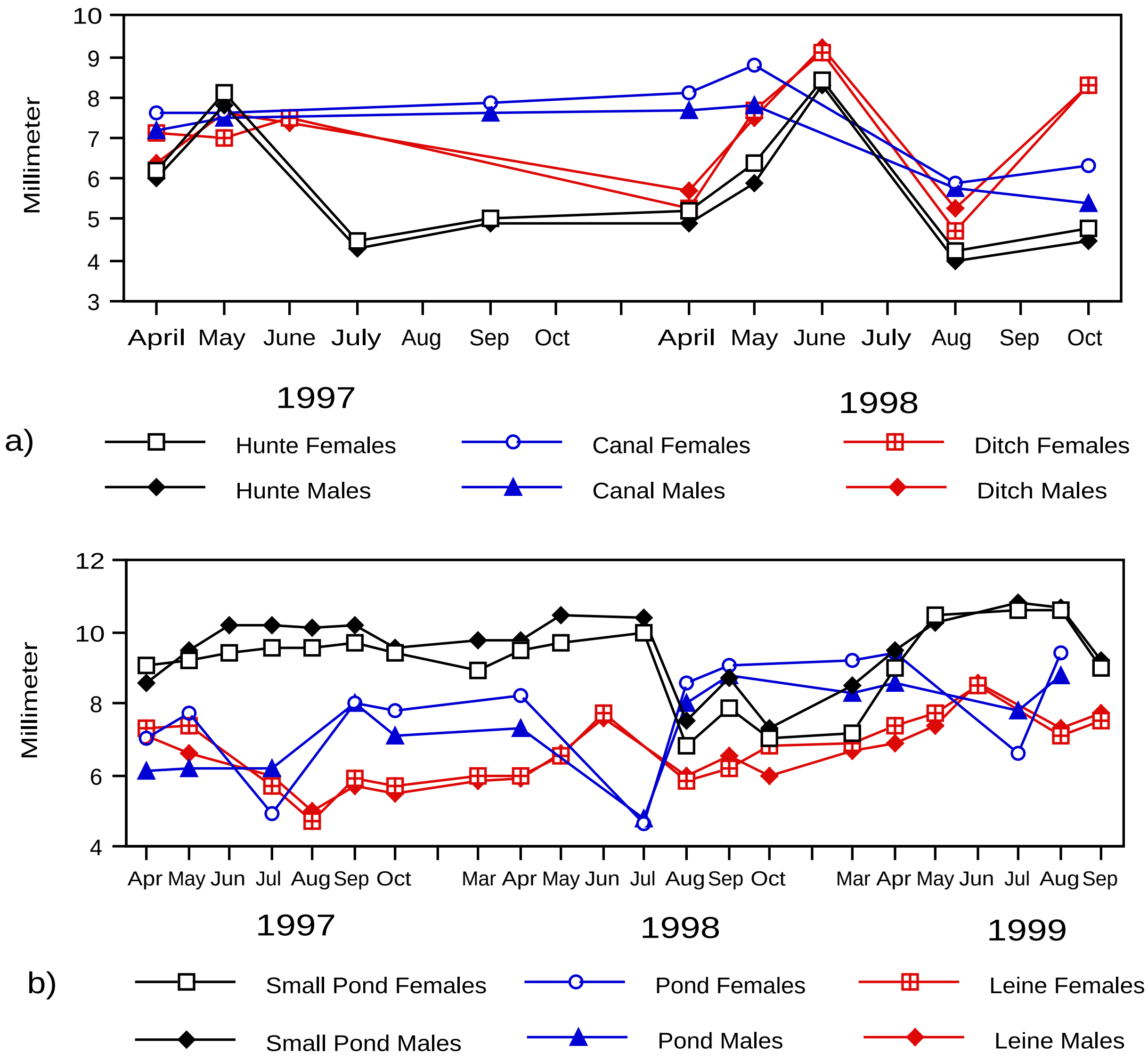


Fig. 12: Mean shell height graphs for all *B. tentaculata* populations, data splitted by gender (n = 8920)

The graphs for the Leine population in Hannover were in parallel for the three years under study (Fig. 12b). Differences between male and female curves are most pronounced in the Pond population. This is most obvious in spring/early summer 1997 and 1999.

Some differences were apparent in the Small Pond (Fig. 12b). During spring 1997 only males grew while females remained on a high level throughout the season. In spring 1998 females started growing a month before males. In 1999 the mean shell height of males increased earlier than that of females. However, this year females reached mean shell heights equal to males for the first time (see next section for further details).

2.2.5. A comparison of gender and habitat

Sexual dimorphism

There is no easy way to answer the question whether there is any sexual dimorphism in the genus *Bithynia*. The data are quite ambiguous. In three *B. tentaculata* populations females were overall bigger than males, in two populations males and females had overall identical mean shell heights and in one population males were larger than females (Tab. 4).
Height differences were most pronounced for the Canal and the Pond populations where the mean shell height of females lay 5% above males. The Small Pond was the only habitat where males were larger than females.

With *B. leachii* gender differences were more pronounced. The mean shell height of females lay 20% above male shell height in this species (Tab. 4).

Tab. 4: Height relations of males to females for all populations (heights of all sampled and sexed individuals > 3,5 mm were pooled for analysis)

Females > Males	**Females = Males**	**Males > Females**
Canal, T-Test P = ,020 Female: **7,9** mm ± 1,3 (n = 156) Male: **7,5** mm ± 1,3 (n = 155)	**Hunte**, T-Test P = ,15 Female: **6,0** mm ± 2,0 (n = 505) Male: **5,9** mm ± 1,8 (n = 432)	**Small Pond,** U-Test P < ,0001 Female: **9,1** mm ± 1,9 (n = 1039) Male: **9,4** mm ± 2,1 (n = 1063)
Pond, T-Test P = ,0005 Female: **8,1** mm ± 2,0 (n = 415) Male: **7,7** mm ± 2,0 (n = 507)	**Ditch**, T-Test P = ,47 Female: **7,3** mm ± 2,2 (n = 318) Male: **7,4** mm ± 2,1 (n = 354)	
Leine, T-Test P = ,017 Female: **6,9** mm ± 1,6 (n = 969) Male: **6,7** mm ± 1,6 (n = 1239)		
B. leachii, U-Test P < ,0001 Female: **4,8** mm ± 1,2 (n = 159) Male: **4,0** mm ± 0,9 (n = 132)		

An analysis of the height to breadth ratio revealed no significant differences between male and female *B. tentaculata*. This means that the height to breadth ratio increases symmetrically with growth for both genders (Fig. 13). This holds true for all 6 habitats. An ANOVA of the height to breadth ratio between habitats (height divided by breadth was used for comparisons) showed that snails originating from the Leine were slimmer than other snails

(ANOVA, P < ,0001; Bonferroni/Dunn, P < ,0033 or smaller for the a posteriori comparisons).

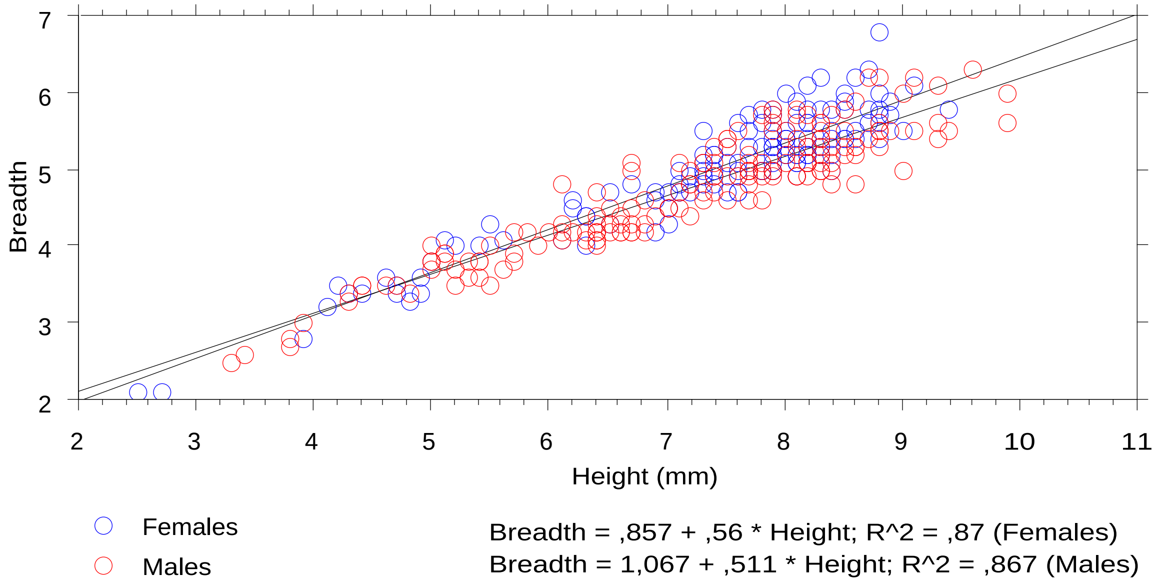


Fig. 13: Regression of breadth on height for *B. tentaculata*, splitted by gender (n = 554)

An ANOVA showed differences between the habitats and the mean shell height of populations (Fig. 14; Tab. 5). The overall smallest snails were found in the rivers with the Hunte population (6,0 mm) being even smaller than the Leine population (6,8 mm). Snails from the Ditch (7,4 mm) were on average larger than river snails but smaller than snails from the Pond (7,9 mm) and the Canal (7,7 mm) which were of equal size. By far the largest snails inhabited the Small Pond (9,3 mm).

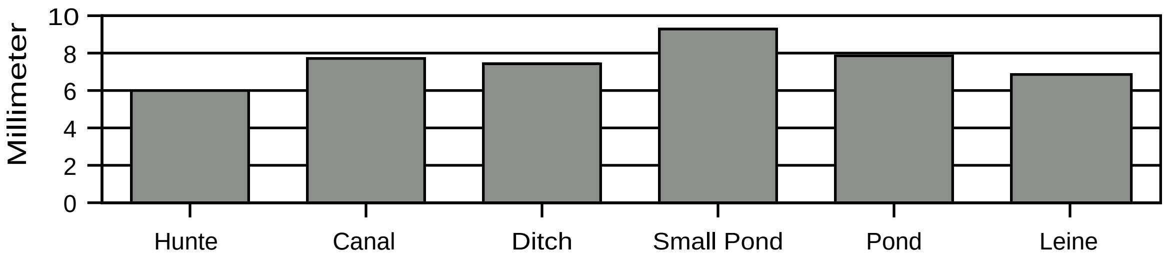


Fig. 14: Mean shell height of the different *B. tentaculata* populations (n = 10920)

When the data are splitted by gender, the ranking between habitats remains unchanged with only one exception: the mean shell height of the Ditch males is equal to that of Canal and Pond males (Tab. 5). This is a consequence of the differences in sexual dimorphism between the populations. The Canal and Pond females were on average larger than males whereas in the Ditch both genders were of equal size.

Tab. 5: Ranking of the mean height of males and females and the population means (for mean height values and n see Tab. 4)

ANOVA: Mean height of whole population/males/females from the different habitats (Bonferroni/Dunn post hoc test, = difference not significant; < difference significant)	
Population P < ,0001	Hunte < Leine < Ditch < Canal = Pond < Small Pond
Females P < ,0001	Hunte < Leine < Ditch < Canal = Pond < Small Pond
Males P < ,0001	Hunte < Leine < Ditch = Canal = Pond < Small Pond

To compare the maximum shell heights between the 6 habitats, an ANOVA for the mean shell height of the largest individuals was calculated (Tab. 6). Individuals from the Small Pond were clearly larger than any other snails. Pond individuals remained on the second position but Canal snails had smaller maximum sizes and fell below the Ditch and even the Leine (males). This signifies that even though the Canal population was a population consisting of large animals, individual snails did not attain maximum sizes above 10 mm. Shell heights of 10 mm and above were frequently encountered in other habitats where the overall population means were lower than in the Canal.

Tab. 6: Ranking of the mean values of the largest male/female *B. tentaculata* per population

ANOVA: Mean height of the largest males/females from the different habitats (n = 20), in millimetre (Bonferroni/Dunn post hoc test, = difference not significant; < difference significant)	
Females P < ,0001	Leine (9,5) = Canal (9,6) = Hunte (9,8) < Ditch (10,5) = Pond (11,1) < Small Pond (12,1)
Males P < ,0001	Hunte (9,3) = Canal (9,3) < Leine (10,0) < Ditch (10,9) = Pond (11,1) < Small Pond (12,1)

2.3. Snail abundance

Different habitat size, habitat structures and varying sampling techniques made it impossible to strictly compare population size between habitats. Instead a comparison based on sampling time is used to rank habitats (Fig. 15). This seems the more reasonable as population size itself is strongly fluctuating and dependent on time of year. Using the mean sample size for one hour of sampling effort is levelling off the seasonal influence.

B. tentaculata was most abundant in the Leine with a mean sample size of 382 snails per hour sampling effort, followed by the second river population, the Hunte, with a mean sample size of 295 snails. The Small Pond population is intermediate with a mean of 189 snails per hour sampling effort. In the other habitats, *B. tentaculata* was far less abundant with a mean sample size of 66 snails in the Canal, 54 snails in the Ditch and 36 in the Pond (Fig. 15). *B. leachii* was even less common than *B. tentaculata* in the Pond, its low numbers preventing any useful calculation of a mean sample size.

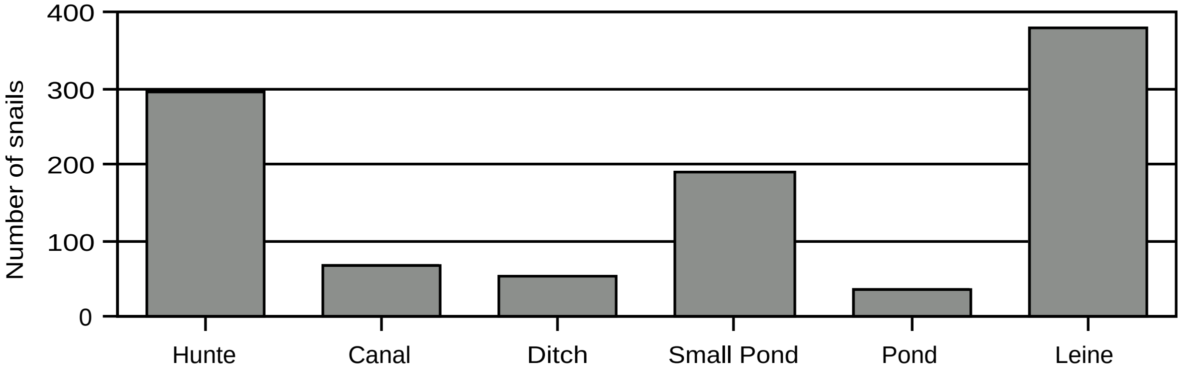


Fig. 15: Number of *B. tentaculata* per hour sampling effort for the different habitats (n = 6754)

Abundance of *B. leachii* in relation to *B. tentaculata* in the Pond

B. leachii was far less abundant than *B. tentaculata* in 1997 and 1998 (Tab. 7). Its numbers increased significantly during 1999 (Fisher's Exact P-Value < ,0001).

Tab. 7: Number of sampled individuals of both co-occuring species in the Pond samples (percentage of total individuals in brakes)

Year	***B. leachii***	***B. tentaculata***
1997	58 (15%)	323 (85%)
1998	84 (16%)	455 (84%)
1999	190 (38%)	313 (62%)

2.4. Sex ratio

2.4.1. Overall sex ratio of the different habitats

The sex-ratio of *B. tentaculata* was balanced (Canal and Small Pond) or males predominated (Fig. 16). Only in the Hunte lived slightly more females than males. Differences between habitats were significant and the overall sex-ratio for *B. tentaculata* is dissimilar from 1:1 (Contingency Table, Chi Square P < ,0001). The predominance of males is clearly visible in the Pond and in the Leine. In contrast to *B. tentaculata*, with *B. leachii* females were more abundant.

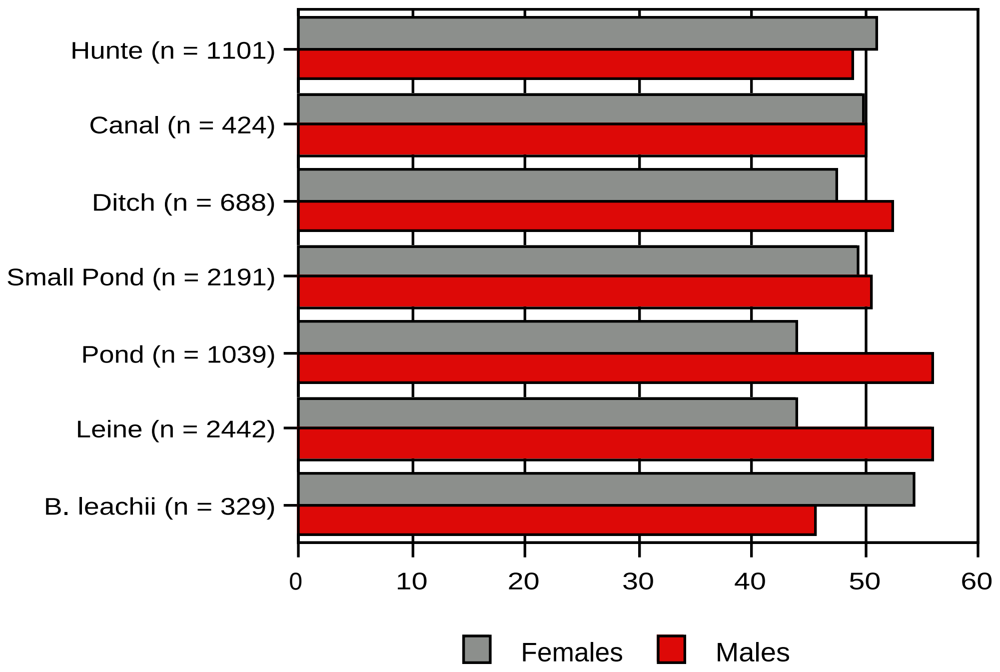


Fig. 16: Sex-ratio of populations of both species, data pooled for all years

2.4.2. Temporal fluctuations in gender abundance

The sex-ratio of male to female *B. tentaculata* was not stable in time but exhibited more or less pronounced fluctuations within years (Figs. 17 and 18).

Hunte

The Hunte population was the only one where there were slightly more females than males (Fig. 16). In the first half of 1997 the percentage of females showed great fluctuations, starting slightly above 50% in April, reaching a maximum in May and a minimum in June (Fig. 17a). After June the percentage of females increased steadily until October.

In 1998 the curve is very smooth, the percentage of females starting with a maximum of 56% in March, decreasing steadily to a low in June and increasing thereafter again above 50% in October.

Canal

Fluctuations in gender abundance were not pronounced. There was a trend towards females being less abundant than males at the end of the season (Fig. 17b).

Ditch

Females made up clearly more than half of the population in April 1997 but then their percentage declined rapidly to below 30% in June (Fig. 17c). Data is lacking afterwards because the population consisted mainly of juveniles to small for sex determination.

In March 1998 females made up 60% of the population. Their percentage dropped to 40% in April and May and increased again to 50% for the rest of the year.

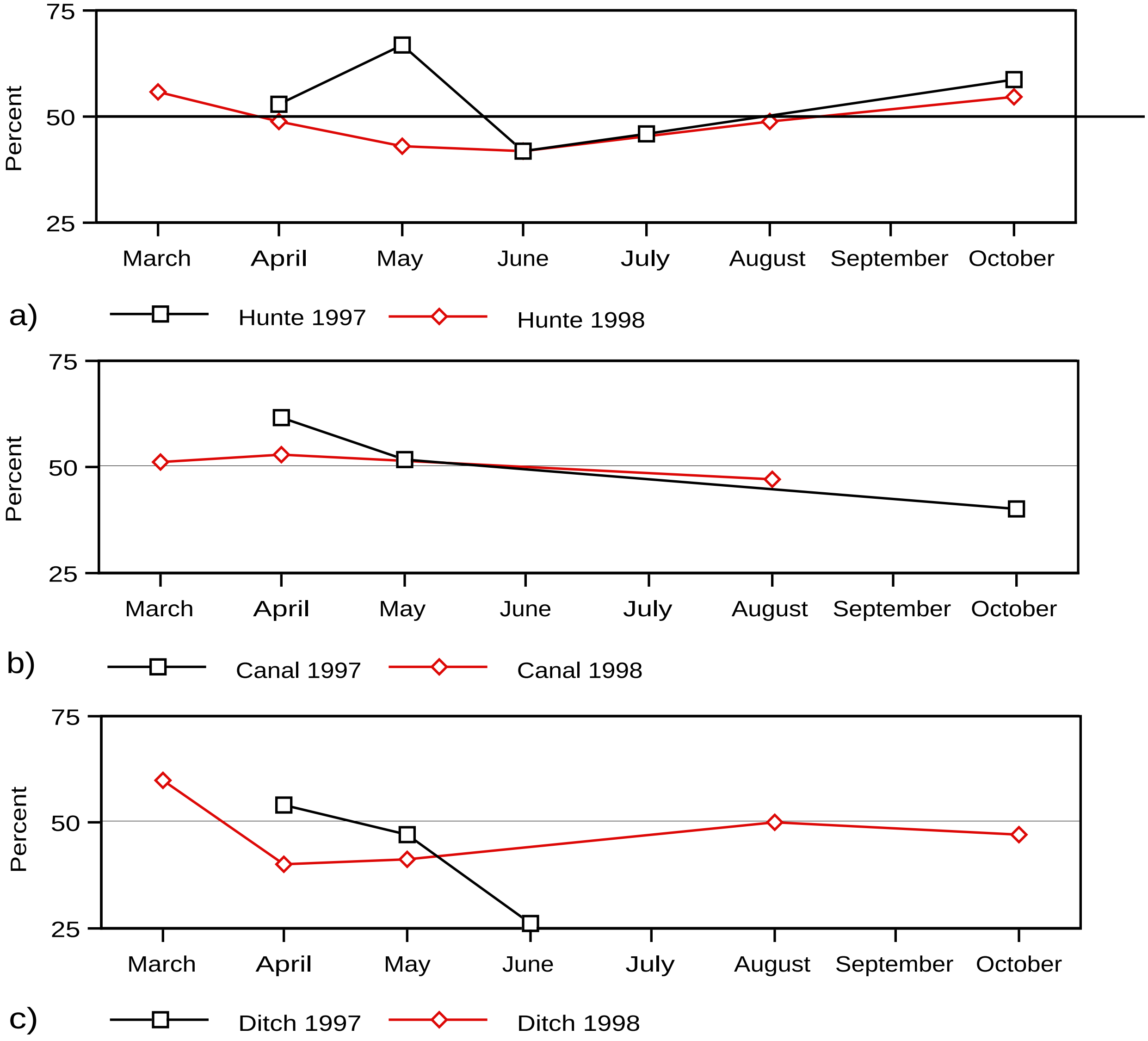


Fig. 17: Percentage of females in samples from the Dümmer

Small Pond

In accordance with an overall sex-ratio of 1:1, the percentage of females in the samples was mostly near 50% (Fig. 18a). The major deviations occured in spring 1997 and in April

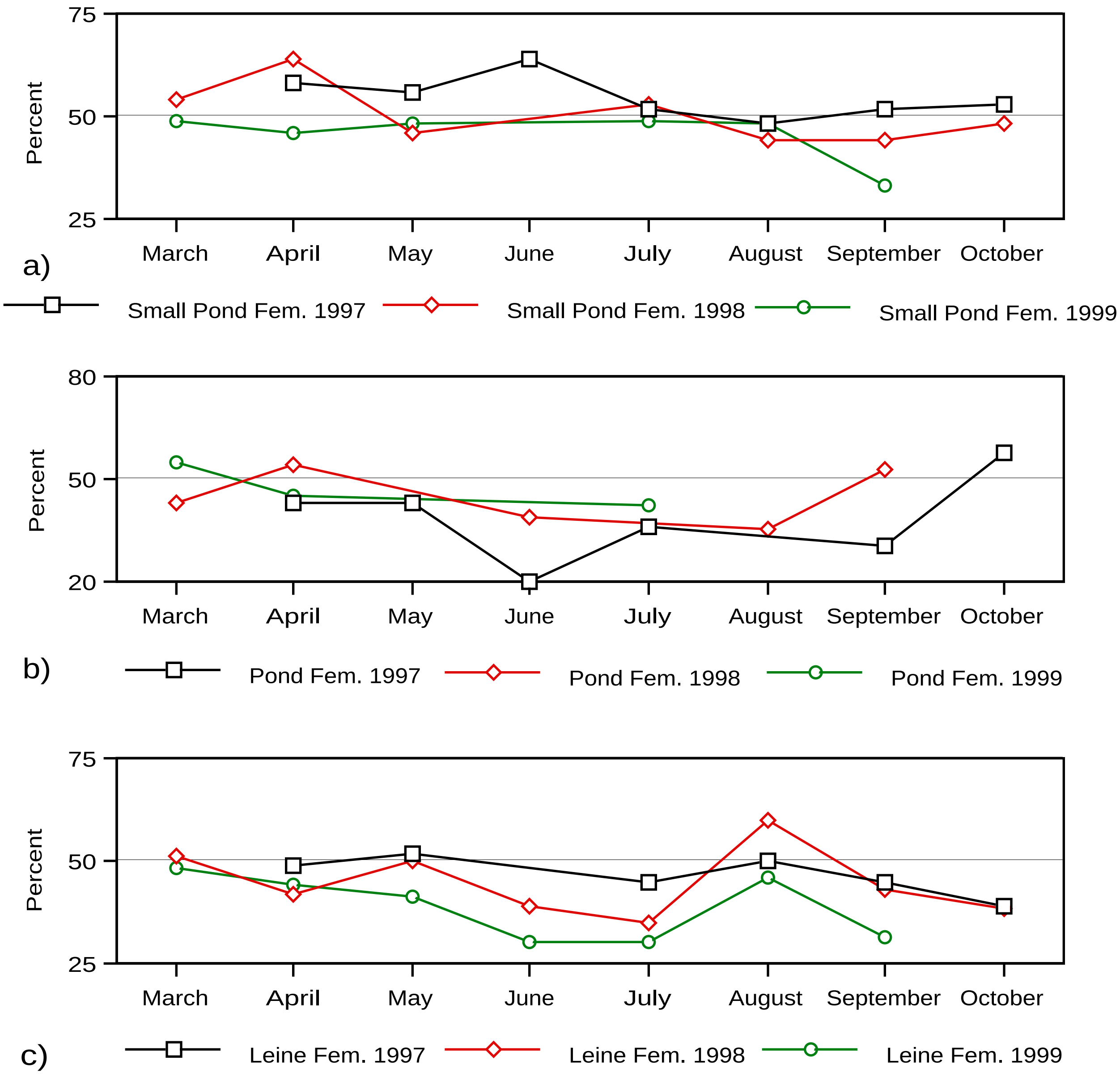


Fig. 18: Percentage of females in samples from Hannover

1998 when there were overproportionally many females in the samples. By far the fewest females were sampled in September 1999. The percentage of females before and after overwintering is in good accordance both times.

Pond

In most samples there were clearly less than 50% females present (Fig. 18b). In general, the percentage of females was higher in spring, diminished during summer and rised again in autumn when it lay above 50% in 1997 and 1998. The lowest number of females was

sampled in June 1997 when they made up only 20% of the population. This points in the direction that adult females were more prone to fungal infections than males.
Leine

In spring females made up half the population in all 3 years (Fig. 18c). During summer their numbers declined every year until a minimum was reached in July. The percentage of females increased in August to around 50% but dropped again during autumn.

2.4.3. Sex-ratio of progeny under laboratory conditions

Introductory remarks

This experiment suffered from problems typically connected with biological studies: the extremely varying outcome.

In several cases all juveniles died after a short spell of time, only sometimes reached the majority of juveniles a sexable size. What was observed more often was that one of the juveniles exhibited rapid growth, several others reached a medium size and most remained very small. This relation remained stable in most cases even if food abundance was improved, animals were transferred in larger aquaria or adult-sized animals were removed from the aquaria. It seems as if some incidence at an early stage determines the further developmental trajectories (this in itself would be an interesting starting point for further studies).

The aforementioned pattern was typically shown by *B. tentaculata*, *B. leachii* offspring grew much more homogenous. Only females with more than 10 juveniles of sexable size were used in analysis.

B. tentaculata

15 females produced 516 juveniles of a size large enough to allow sex identification. 266 (51,5%) were females, 250 (48,5%) were males (Fig. 19).
Out of these, 116 were measured and their shell heights used to test for growth differences between genders (T-Test, P = ,3163). The mean shell height of females was slightly larger but the difference was not significant.

B. leachii

16 females produced 506 juveniles, 260 (51,4%) were females and 246 (48,6%) males (Fig. 19). All juveniles were measured, the females having a mean shell size of 3,1 mm and the males of 2,6 mm. Females grew significantly faster than males (U-test Tied P < ,0001).

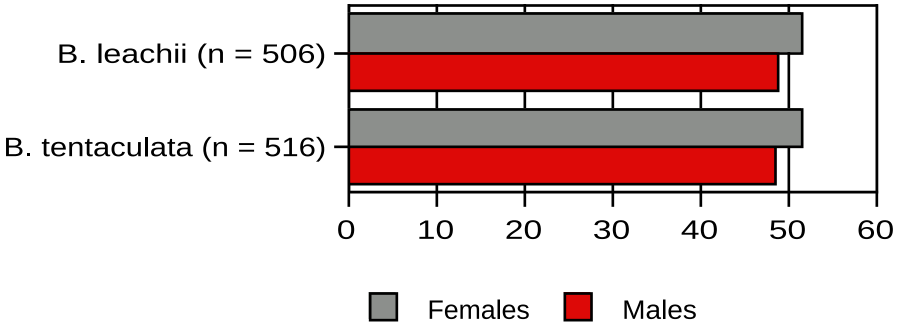


Fig. 19: Sex-ratio of laboratory offspring

The outcome is consistent with the hypothesis that both species have a sex-ratio of 1:1 at birth and there is no bias in favour of one gender. Only for *B. leachii* gender had a significant influence on juvenile growth rate. This is consistent with the pronounced sexual dimorphism encountered in field sample data for *B. leachii*.

Juveniles sampled in the Pond and the Leine in summer 1997

Of several hundred juvenile snails sampled in the Pond 83 reached a size sufficient for sex and species determination in February 1998. 69 (31 females, 38 males) belonged to *B. tentaculata*, 14 (6 females, 8 males) to *B. leachii.* This relation of juveniles (69/14; 83%/17%) is in good agreement with the relation for relative abundance of the two species found throughout direct sampling of the Pond populations in 1997 (323 *B. tentaculata* /58 *B. leachii* ; 85%/15%).

From the juveniles sampled in the Leine, 78 were females and 68 males. This adds up to 109 female and 106 male *B. tentaculata*.

3. PARASITES

The percentage of snails parasitized by trematodes fluctuated with time in all habitats (Figs. 20 and 21). The grade of parasitic infection was examined separately for males and females but differences were only significant in the Small Pond. Here more females than males were infected (Fisher's Exact Test, P = ,0008). Data for males and females are therefore combined for statistical analysis in the other 5 populations.

3.1. Habitats

3.1.1. Dümmer

In the spring of 1998 the percentage of snails parasitized was low in the Hunte and the Ditch and high in the Canal (Fig. 20). The percentage of infected snails increased more or less rapidly until July when approximately 25% of the populations were infected. There are no data for the Canal due to sampling problems. In August percentage of parasitized snails was below 5% in the Canal and the Ditch but remained high in the Hunte. In late autumn parasitation was low in all habitats. Overall parasitation levels were highest in the Hunte (15%), intermediate in the Canal (11%) and low in the Ditch (8%) (Tab. 8).

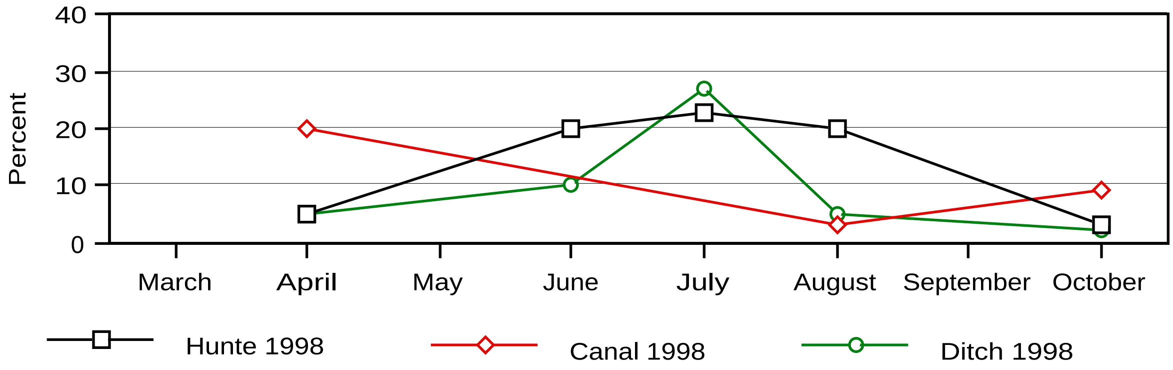


Fig. 20: Percentage of parasitized *B. tentaculata* in the Dümmer populations (n = 550)

3.1.2. Small Pond

The Small Pond exhibited some unusual features. It was the only population showing a gender effect. Furthermore was it possible in 1999 to compare infection levels of older snails to that of snails born the previous year (Fig. 21a). This was possible because of aforementioned differences in the shell structure.

Gender and parasitation

The gender effect was first observed in autumn 1998. In 1997 and in spring/summer 1998 infection levels for males and females were the same. In autumn 1998, out of 62 examined females 47 (76%) were parasitized, but out of 85 males only 44 (52%), the difference being statistically significant (Fisher's Exact Test, P = ,0035). The effect persisted for the older snails (born in 1997 or earlier) in 1999. This year, out of 43 examined females 32 (74%) and out of 62 males 17 (27%) were infected (Fisher's Exact Test, P < ,0001). Interestingly, the number of parasitized snails showed no significant difference between genders for the snails born the previous year (12 parasitized females out of 71 examined and 4 parasitized males out of 70).

Seasonal fluctuations and stage specific parasitation

In July 1997 24% of the Small Pond snails were parasitized and this number doubled until October (Fig. 21a). In May 1998 the number of parasitized snails (25%) was lower than the previous autumn, pointing towards a higher winter mortality of parasitized snails. The infection level increased steadily during summer and autumn until in October more than 70% of the adult population were parasitized (and 24 out of 26 examined adult females!).

In 1999 several processes interact. Old snails started on a high level of parasitation in April (60%) that is retained in May (55%). Then the infection level dropped to 24% in July. This was mostly due to the mortality scheme, almost all of the highly parasitized old females being dead by now. The surviving old males showed a moderate infection level compared to females.

The young snails started on a very low infection level in spring 1999, but the percentage of infected animals increased during summer until 22% are parasitized in August. Because most of the older snails were dead by now, younger snails contributed increasingly to the overall infection level from summer onwards. These interactions led to the observed scheme of parasitic infections with its decline from April to July and its levelling off around 20% in late summer.

The overall infection level (37% of all examined snails) was by far the highest for all habitats under study (Tab. 8).

Tab. 8: Parasitation of snails in per cent (number of parasitized snails/ number of examined snails)

	Hunte		**Canal**		**Ditch**	
	Parasitized	%	Parasitized	%	Parasitized	%
1998	38/261	15	7/66	11	18/223	8

	Small Pond		**Pond**		**Leine**	
	Parasitized	%	Parasitized	%	Parasitized	%
1997	35/96	37	3/11		8/46	17
1998	147/292	50	11/90	12	33/399	8
1999	72/292	25	8/93	9	17/248	7
Sum:	254/680	37	22/194	11	58/693	8

3.1.3. Pond

Parasitation was low in spring in both years (Fig. 21b). Data are very sparse until August because the fungal infection killed nearly all adult snails during spring/early summer and there is no point in examining newly hatched snails for trematode larva.

In 1998 the number of infected snails increased in autumn up to 20%. In 1999 quite a large number of the new generation was parasitized by July. However, no infected snails were found later on. With 11% the overall infection level is moderate in the Pond (Tab. 8).

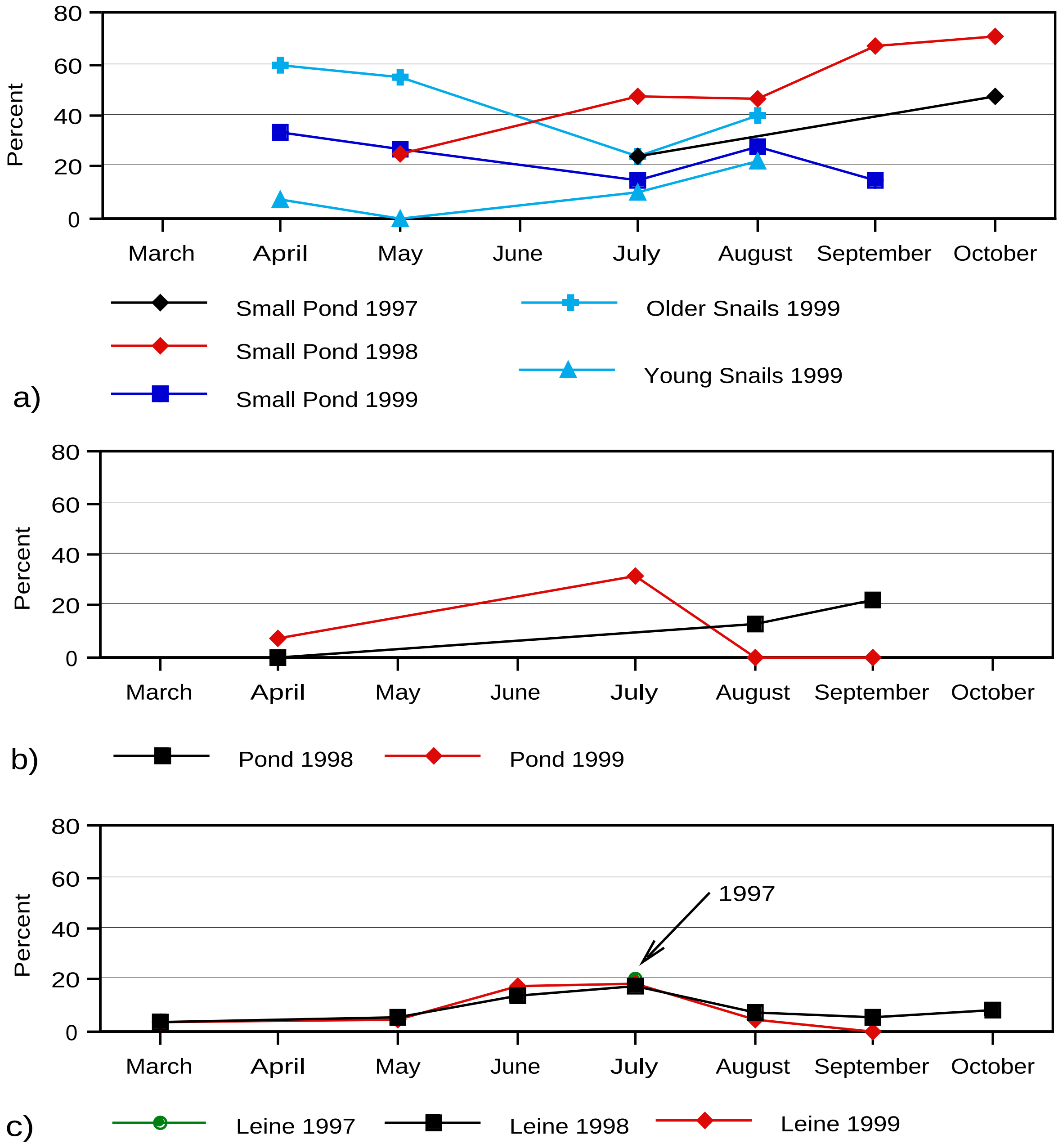


Fig 21: Percentage of parasitized *B. tentaculata* in the populations in Hannover (n: a = 680; b = 194; c = 693)

3.1.4. Leine

The course of parasitation levels was identical in both years. With 3% the infection level was very low in March (Fig. 21c). It remained low until May and increased towards June, reaching nearly 20% in July as in July 1997. The infection level dropped in late summer and was low to zero (September 1999) until overwintering. With 8% the overall infection level of the population was low (Tab. 8).

3.2. Parasitation and gigantism

The mean shell sizes of parasitized and non-parasitized snails were compared to test for increased shell growth in reaction to parasitation. This mechanism is repeatedly documented in the literature. Only snails > 7 mm were used in the analysis since trematode parasitation is often occult in smaller animals. The outcome is equivocal: In the Small Pond and the Leine the mean shell size for both groups is exactly the same; in the Hunte, the Ditch and the Pond the parasitized snails belong to a significantly larger subgroup of the population (Tab. 9). The number of Canal snails examined was too low to allow any statistical analysis.

Tab. 9: Comparison of the mean shell height of parasitized and non-parasitized snails

Origin	**Parasitized**	**Non-parasitized**	**P-value**
Hunte	Ø = **9,0** mm ± 1,2 (n = 27)	Ø = **8,1** mm ± 0,7 (n = 115)	< ,0001; U-test
Ditch	Ø = **9,6** mm ± 1,5 (n = 23)	Ø = **9,0** mm ± 1,0 (n = 131)	,0066; U-test
Small Pond	Ø = **10,1** mm ± 0,8 (n = 181)	Ø = **10,1** mm ± 0,7 (n = 204)	,6485; T-Test
Pond	Ø = **10,5** mm ± 1,0 (n = 21)	Ø = **9,3** mm ± 1,2 (n = 156)	< ,0001; T-Test
Leine	Ø = **7,9** mm ± 0,8 (n = 40)	Ø = **8,0** mm ± 0,6 (n = 279)	,5196; T-Test

4. INDIVIDUAL LIFE HISTORIES AND REPRODUCTION

4.1. Individual life histories and reproduction of females in the field

Introductory remark

To structure the following section there is first a comparison on the population respective species level which gives a picture of the general outline. Field data of all years is pooled for statistical analysis. Afterwards the variance within each population for the 3 (2) years under study is analysed and the legitimacy of the data being pooled will be post hoc established. To round the picture off each years data will be analysed shortly in the concluding section. For a short explanation of box plot graphs used frequently throughout this section, see page 16 in Material and Methods.

4.1.1. Minimal female height for reproduction

Females in the Small Pond (8,6 mm) and the Pond (8,2 mm) attained significantly larger sizes before reproducing than Leine females (7,4 mm) (Fig. 22; ANOVA, P < ,0001; Bonferroni/Dunn post hoc test, P < ,0001 -Small Pond/Leine-; P = ,0010 -Pond/Leine-). Height of *B. leachii* females (4,4 mm) was clearly below that of *B. tentaculata* females (T–Test, P < ,0001).

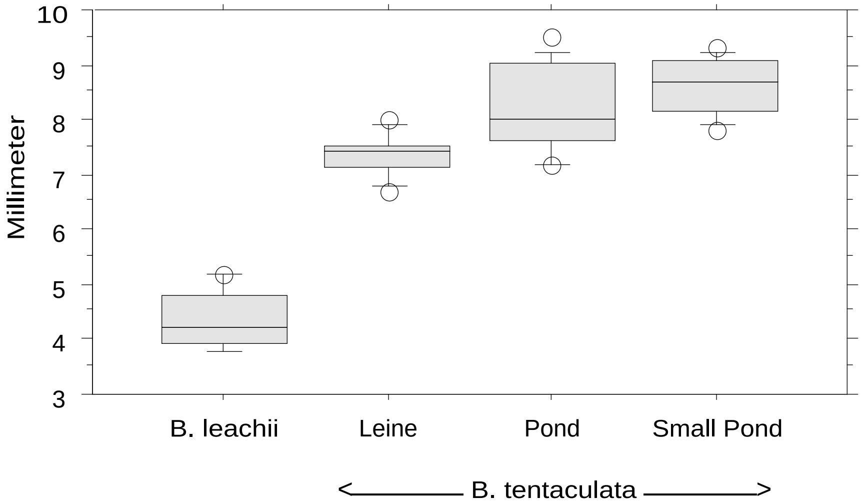


Fig. 22: Height of smallest reproducing females (n = 55)

4.1.2. Start of reproduction

The starting point for reproduction differed for 2 to 4 weeks (that corresponds to differences in water temperature of 2 to 4 °C) between females within each population. The differences were most pronounced for old and young females in the Small Pond in 1999. Here the old females (aged 2 years or older) started to reproduce in April, approximately 1 month earlier than females born the previous summer.

4.1.3. Egg number

The mean number of eggs laid per reproducing female was in the range of 188 to 400 and differed significantly between the populations (Fig. 23; Tabs. 10, 19 and 21).
The mean egg number per female for the Leine population (400 eggs) lay above the other *B. tentaculata* populations and *B. leachii* . The mean egg number for the Small Pond (188 eggs) and the Pond (189 eggs) were the same. The mean egg number for *B. leachii* (228 eggs) lay significantly above the mean for the Small Pond, but the difference to the Pond was not significant (Tab. 10).

The differences between females with a high and a low output of eggs were most pronounced in the Leine population. The total egg number of individual females per reproductive period was below 100 eggs for some females and nearly 900 eggs for others.

The differences between females were in the same order of magnitude in the other 3 populations (Fig. 23).

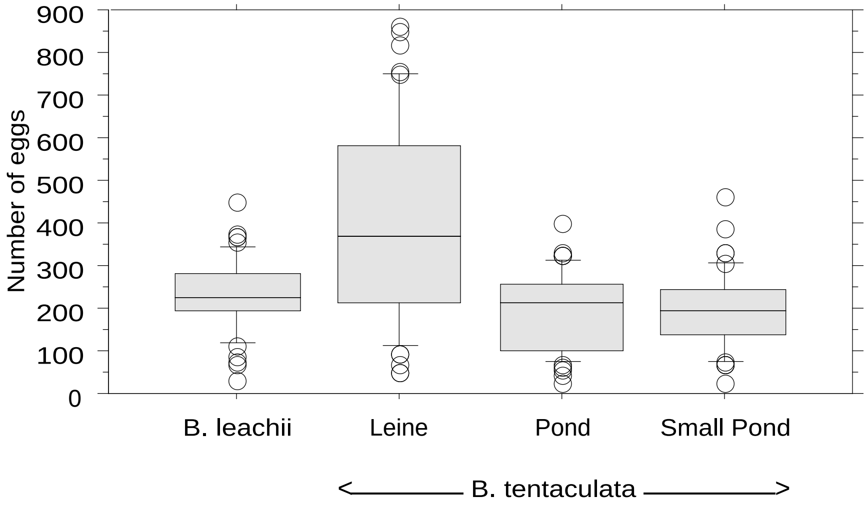


Fig. 23: Mean egg number of reproducing females (n = 221)

Tab. 10: Egg number statistics (The Kruskall-Wallis-Test tested the whole data set for significant differences; the U-Tests are a-posteriori tests to establish significant differences between 2 groups within the data set after a positive Kruskall-Wallis-Test was calculated)

Egg number (n = 221)	Kruskall-Wallis-Test, Tied P < ,0001
Small Pond = Pond	U-Test, Tied P = ,9499
Small Pond < Leine	U-Test, Tied P < ,0001
Small Pond < *B. leachii*	U-Test, Tied P = ,0171
Pond < Leine	U-Test, Tied P < ,0001
Pond = *B. leachii*	U-Test, Tied P = ,0750
Leine > *B. leachii*	U-Test, Tied P = ,0001

4.1.4. Number of spawns

The mean number of spawns per reproducing female was statistically different between the populations (Tabs. 11, 19 and 21; Fig. 24). *B. leachii* females laid on average more spawns (36,2 spawns) than any of the 3 *B. tentaculata* populations. Leine females laid significantly more spawns (29,1 spawns) than females from the Small Pond (11,3 spawns) or the Pond (11,8 spawns). There was no difference between the Small Pond and the Pond.

Differences between individual females for the number of spawns laid per reproductive period were most pronounced within the Leine population, intermediate for *B. leachii* and low for the Small Pond and Pond populations (Fig. 24).

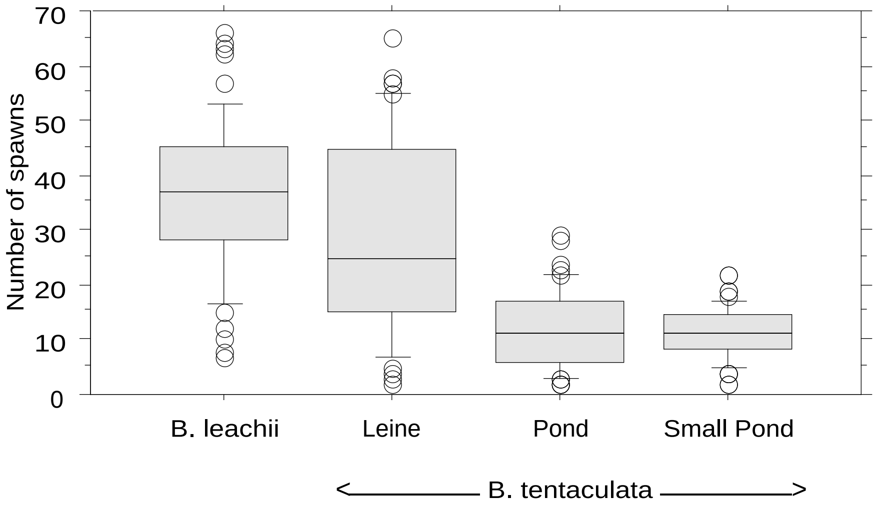


Fig. 24: Mean number of spawns per reproducing female (n = 221)

Tab. 11: Spawn number statistics (The Kruskall-Wallis-Test tested the whole data set for significant differences; the U-Tests are a-posteriori tests to establish significant differences between 2 groups within the data set after a positive Kruskall-Wallis-Test was calculated)

Spawn number (n = 221)	Kruskall-Wallis-Test, Tied P < ,0001
Small Pond = Pond	U-Test, Tied P = ,9332
Small Pond < Leine	U-Test, Tied P < ,0001
Small Pond < *B. leachii*	U-Test, Tied P < ,0001
Pond < Leine	U-Test, Tied P < ,0001
Pond < *B. leachii*	U-Test, Tied P < ,0001
Leine < *B. leachii*	U-Test, Tied P = ,0294

4.1.5. Eggs per spawn

The mean number of eggs per spawn was statistically different between the populations (Tabs. 12, 19 and 21; Fig. 25). *B. leachii* had on average less eggs per spawn (6,7 eggs) than any of the 3 *B. tentaculata* populations. Leine spawns contained on average significantly fewer eggs (14,5 eggs) than spawns from the Small Pond (18,1 eggs) or the Pond (18,9 eggs). Again there was no significant difference between the Small Pond and the Pond populations.

The differences between individual females with regard to mean number of eggs per spawn were low for *B. leachii* and pronounced for the Small Pond and Pond populations (Fig. 25).

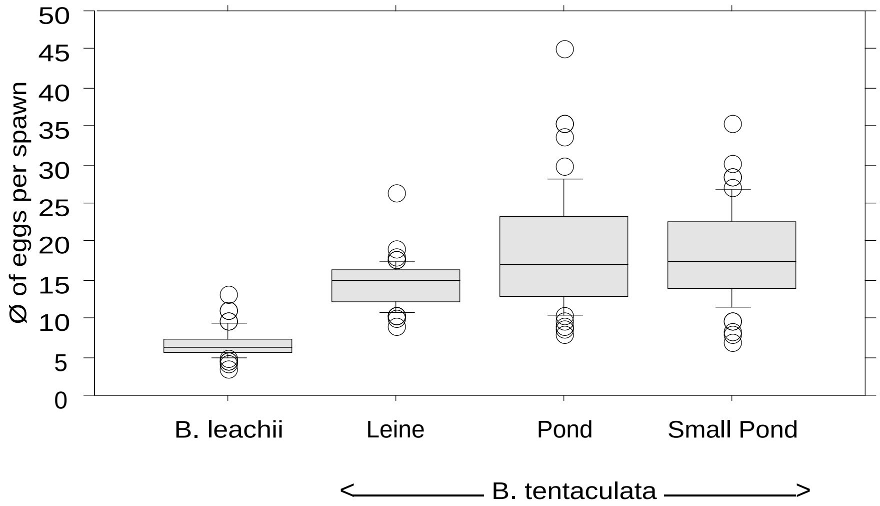


Fig. 25: Mean number of eggs per spawn (n = 221)

Tab. 12: Eggs per spawn statistics (The Kruskall-Wallis-Test tested the whole data set for significant differences; the U-Tests are a-posteriori tests to establish significant differences between 2 groups within the data set after a positive Kruskall-Wallis-Test was calculated)

Eggs per spawn (n = 221)	Kruskall-Wallis-Test, Tied P < ,0001
Small Pond = Pond	U-Test, Tied P = ,9404
Small Pond > Leine	U-Test, Tied P = ,0004
Small Pond > *B. leachii*	U-Test, Tied P < ,0001
Pond > Leine	U-Test, Tied P = ,0022
Pond > *B. leachii*	U-Test, Tied P < ,0001
Leine > *B. leachii*	U-Test, Tied P < ,0001

In all populations of both species the number of eggs per spawn decreased significantly between the onset and the end of the breeding season (Tab. 13). The mean difference between first and last spawns was most pronounced in the Small Pond but also clearly visible in the Pond and the Leine. The decline in egg number per spawn within the breeding period was least distinctive for *B. leachii*.

Table 13: Paired T-Test, egg number of first spawn compared to egg number of last spawn per breeding season for individual females

Origin	Mean difference between first and last spawn	P-value	n
Small Pond	33,68 ± 25,81	< ,0001	59
Pond	23,45 ± 20,87	< ,0001	56
Leine	16,52 ± 13,21	< ,0001	56
B. leachii	9,30 ± 7,42	< ,0001	56

The mean egg number of spawns declined constantly throughout all months of each reproductive season. This is even obvious when mean egg number per spawn started on a low level as is the case with *B. leachii* (Tab. 14).

Tab. 14: Mean egg numbers per spawn for the consecutive months of the reproductive period (the numbers in brackets show egg number of the smallest and biggest spawns)

Origin	**1. Month**	**2. Month**	**3. Month**	**4. Month**	**5. Month**	**6. Month**
Small Pond 1997	**Ø: 16,7** (1-79) n = 132	**Ø: 13,8** (2-36) n = 90	**Ø: 7,4** (2-18) n = 14			
Small Pond 1998	**Ø: 30,9** (1-121) n = 55	**Ø: 19,3** (2-67) n = 81	**Ø: 9,9** (1-34) n = 68			
Small Pond 1999	**Ø: 24,8** (4-60) n = 35	**Ø: 22,0** (1-69) n = 92	**Ø: 10,9** (2-25) n = 52	**Ø: 4,6** (1-13) n = 30		
Pond 1997	**Ø: 31,0** (1-78) n = 19	**Ø: 12,2** (1-36) n = 170	**Ø: 9,0** (3-22) n = 87	**Ø: 8,1** (3-14) n = 13		
Pond 1998	**Ø: 20,6** (1-83) n = 78	**Ø: 15,2** (1-29) n = 37	**Ø: 6,5** (3-12) n = 10			
Pond 1999	**Ø: 24,5** (1-123) n = 121	**Ø: 15,2** (1-30) n = 118				
Leine 1997	**Ø: 15,7** (1-44) n = 68	**Ø: 13,9** (2-34) n = 162	**Ø: 9,1** (1-22) n = 67			
Leine 1998	**Ø: 18,1** (1-60) n = 107	**Ø: 11,6** (1-32) n = 124	**Ø: 10,7** (3-21) n = 11			
Leine 1999	**Ø: 19,6** (5-64) n = 82	**Ø: 15,9** (1-31) n = 303	**Ø: 13,5** (1-37) n = 264	**Ø: 10,7** (1-25) n = 339	**Ø: 13,5** (5-24) n = 38	**Ø: 23,7** (2-46) n = 10
B. leachii 1998	**Ø: 10,3** (1-29) n = 52	**Ø: 8,3** (1-52) n = 320	**Ø: 4,9** (1-19) n = 224	**Ø: 3,4** (1-10) n = 87		
B. leachii 1999	**Ø: 8,3** (1-41) n = 223	**Ø: 6,2** (1-17) n = 619	**Ø: 4,6** (1-21) n = 141	**Ø: 3,1** (1-5) n = 10		

In every year and for all populations the mean egg number per spawn was highest in the first month of the reproductive period. It declined more or less rapidly afterwards. The only exception is the unusual long reproductive period in the Leine in 1999. Mean egg numbers increased during autumn again after a minimum in summer, but only few females took part in the autumnal reproduction (Tab. 14).

4.1.6. Range of eggs per spawn and other spawn characteristics

Mean range of eggs per spawn

The mean range of eggs per spawn was significantly different between the populations (Tab. 15; Fig. 26). This parameter measures the difference between the biggest and smallest spawn for any reproductive female. By this it allows to compare the extent of seasonal shifts in egg number per spawn within and between populations during the course of the reproductive period.

The mean range of eggs per spawn for *B. leachii* (17,1) was less than the mean range for the 3 *B. tentaculata* populations (Tab. 20). The mean range of Small Pond females (44,3) lay significantly above the level in the Leine (29,8) and the Pond (36,1). The difference between the Pond and the Leine was not significant.

Tab. 15: Range of eggs per spawn statistics (The Kruskall-Wallis-Test tested the whole data set for significant differences; the U-Tests are a-posteriori tests to establish significant differences between 2 groups within the data set after a positive Kruskall-Wallis-Test was calculated)

Range of eggs per spawn (n = 221)	Kruskall-Wallis-Test, Tied P < ,0001
Small Pond > Pond	U-Test, Tied P = ,0311
Small Pond > Leine	U-Test, Tied P < ,0001
Small Pond > *B. leachii*	U-Test, Tied P < ,0001
Pond = Leine	U-Test, Tied P = ,1976
Pond > *B. leachii*	U-Test, Tied P < ,0001
Leine > *B. leachii*	U-Test, Tied P < ,0001

The mean range of eggs per spawn declined continuously alongside with mean egg number of spawns throughout the reproductive period (Tab. 14). The only exceptions were the Small Pond in 1999 when the young snails started to reproduce with a delay of 1 month compared to old snails and the *B. leachii* population in 1998. But in general big spawns were laid in the beginning of each season and no more at its end. Nonetheless most spawns laid were small spawns independent of population, year or time of season. Spawns containing few eggs to only 1 were laid continuously throughout the reproductive period in all populations. (Tab. 14).

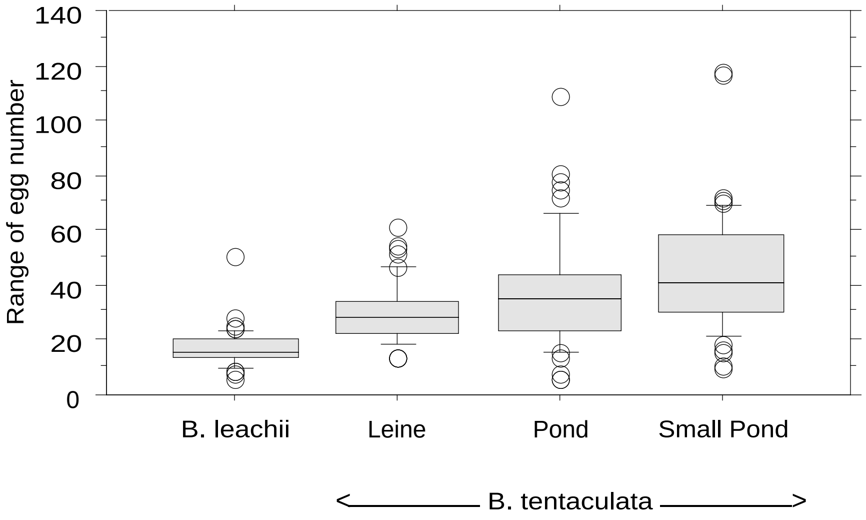


Fig. 26: Mean range of eggs per spawn (n = 221)

Egg number of first spawns

It was of interest to find out wether the first spawn a given female produced during the reproductive period was also the biggest spawn (and therefore the female's biggest per cent investment in reproductive terms).

This was the case more often in the Small Pond and the Pond than in the Leine (Tab. 16; Chi Square P = ,0262). *B. leachii* laid less often the biggest spawn at the start of the reproductive period than *B. tentaculata*, but this was statistically just not significant (Tab. 16; Fisher's Exact P-Value = ,0504). The difference became significant when only the sympatric populations of both species were compared (Fisher's Exact P-Value = ,0048).

Tab. 16: Number of females that laid their biggest spawn at the start of the reproductive season

Origin	**First spawn = Biggest spawn**	**First spawn ≠ Biggest spawn**
Small Pond	40	14
Pond	42	10
Leine	42	29
Sum *B. tentaculata*	124	53
B. leachii	24	21

In general, *B. tentaculata* females laid biggest spawns containing more eggs than *B. leachii* females (Fig. 27; Kruskall-Wallis Test, P < ,0001). Big spawns in the Small Pond and the Pond could contain more than a hundred eggs whereas egg numbers never exceeded 65 eggs in the Leine and 52 eggs for *B. leachii* spawns.

By the same token *B. leachii* females laid on average smallest spawns containing less eggs (1,3 eggs) than *B. tentaculata* females (5,6 eggs) (Kruskall-Wallis-Test; P < ,0001).

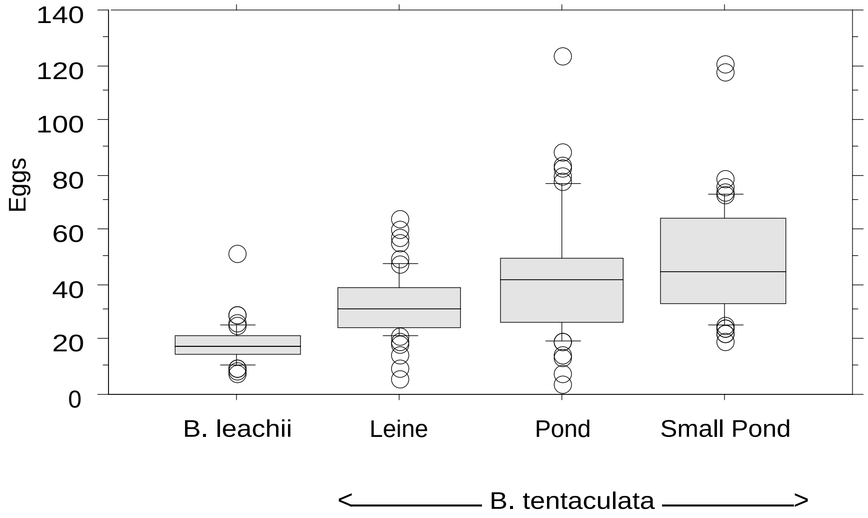


Fig. 27: Egg number of biggest spawn (n = 221)

Female size and egg number of spawns

A significant positive correlation between female shell height at onset of reproduction and the mean egg number of first spawns was only observed for females in the Pond, otherwise these traits were uncorrelated (Tab. 17).

It should be mentioned that even a significant correlation coefficient of ,583 as seen in the Pond explains only one third of the variance encountered in mean egg number of first spawns.

Tab.17: Correlation between female size at the onset of reproduction and mean number of eggs per spawn for the first three weeks of the reproductive period

Origin	**Correlation coefficient**	**P-value**	**n**
Small Pond	,055	,7037	51
Pond	,583	< ,0001	41
Leine	,203	,1832	45
B. leachii	-,128	,3637	53

4.1.7. Size of eggs and juveniles

Egg size

Mean egg size (length by breadth of eggs) proofed significantly different between populations and species (ANOVA, P = < ,0001). *B. tentaculata* eggs laid in the Small Pond and in the Pond had the same size and were significantly larger than eggs from the Leine population and eggs of *B. leachii* (Scheffe's post-hoc-test, P < ,0001).

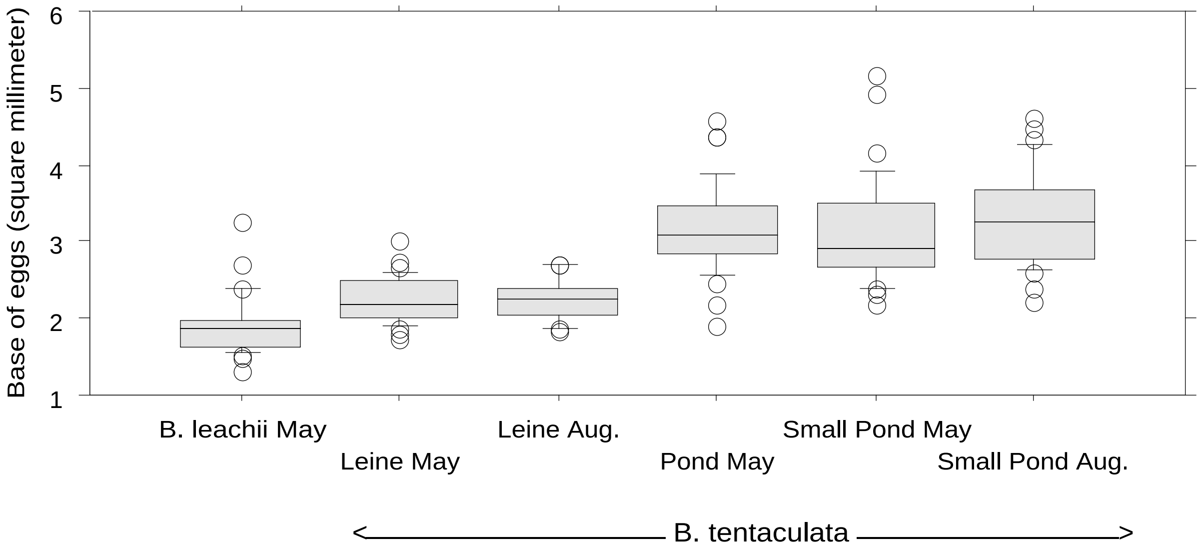


Fig. 28: Mean egg size (length by breadth of egg base) of different snail populations

Most interestingly, eggs of the Leine population and of *B. leachii* were almost the same size with only a small difference that was not statistically significant (Fig. 28).

The mean egg size at the beginning and the end of the reproductive period remained the same for the Small Pond and the Leine.

Juvenile shell height at hatching

An ANOVA revealed significant differences (P = <, 0001) in juvenile shell height at hatching. The hatchlings of *B. tentaculata* in the Pond and the Small Pond were of the same height (about 1,2 mm; Fig. 29) and both were significantly larger than hatchlings from *B. leachii* (Scheffe's post hoc test, P = <,0001). Unfortunately, the situation in the Leine did not allow for sampling of freshly hatched juveniles. Since mean egg size of the Leine population was in the range of *B. leachii* eggs used in analysis, it seems a reasonable interpolation that shell height of juveniles in the Leine should be smaller than in the other habitats of *B. tentaculata*.

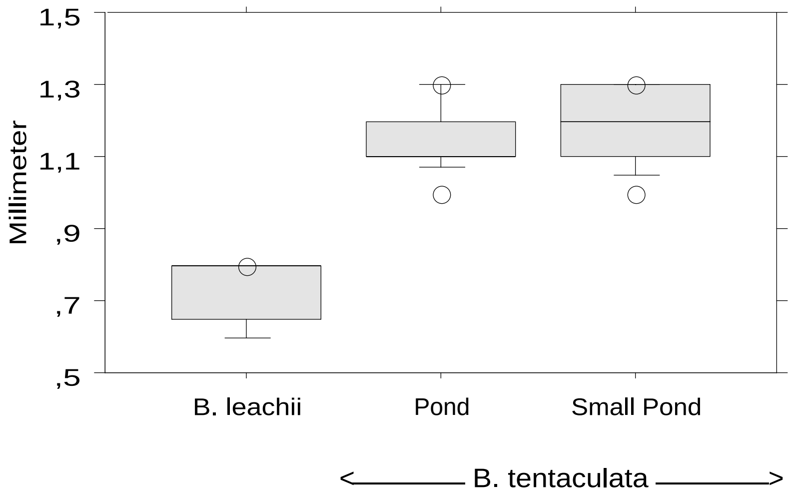


Fig. 29: Juvenile shell height at hatching in millimeter(n = 30)

4.1.8. Length of reproductive period

The mean length of the reproductive period was significantly different between the populations (Fig. 30; Tabs. 18 and 19). Leine females had, with a mean value of 86,7 days, on average the longest reproductive periods. For several females its duration exceeded 4 months. Pond females had a significantly shorter mean length of the reproductive period (37,6 days) than any other population (Tab. 19). This was due to the high mortality caused by the fungal infections every year.

There was no significant difference in the mean length of the reproductive period between the Small Pond (57,7 days) and *B. leachii* (64,4 days).

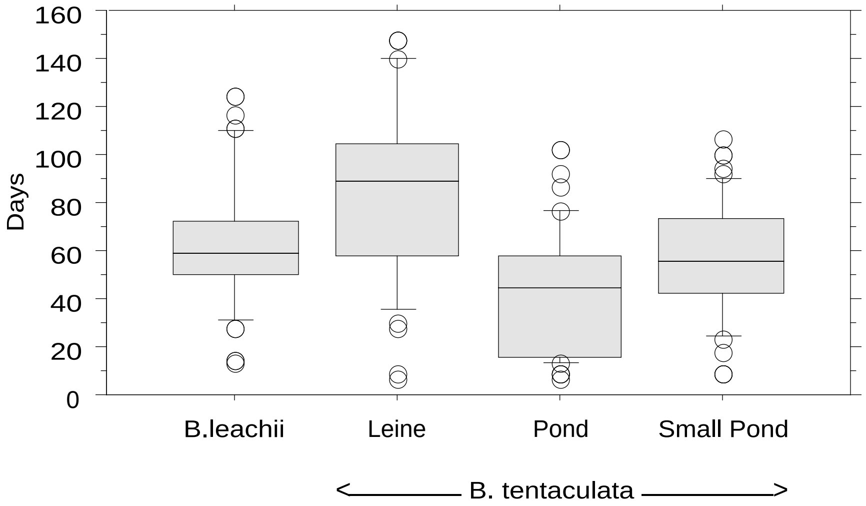


Fig. 30: Mean length of reproductive period in days (n = 191)

Tab. 18: Statistics for length of reproductive period (The ANOVA tested the whole data set for significant differences; the Bonferroni/Dunn tests are a-posteriori tests to establish significant differences between 2 groups within the data set after a positive ANOVA was calculated)

Length of reproductive period (n = 191)	ANOVA, P < ,0001
Small Pond > Pond	Bonferroni/Dunn, P = ,0075
Small Pond < Leine	Bonferroni/Dunn, P < ,0001
Small Pond = *B. leachii*	Bonferroni/Dunn, P = ,2522
Pond < Leine	Bonferroni/Dunn, P < ,0001
Pond < *B. leachii*	Bonferroni/Dunn, P = ,0001
Leine > *B. leachii*	Bonferroni/Dunn, P = ,0006

4.1.9. Hatching rates of eggs

The hatching rate of eggs was generally high in all habitats (Fig. 31; Tab. 19). With more than 97% of all eggs hatched the mean hatching rate was highest for *B. leachii* and with 90,6% it was somewhat lower for the coexisting *B. tentaculata* population in the Pond. The hatching rate of *B. leachii* females never dropped below 90% in a single case with data for more than 50 females included (Tab. 19).

Differences between the hatching rates of individual females were most pronounced in the Small Pond, but also in this population more than 85% of all eggs hatched on average.
Hatching rates were not obtained for the Leine population because of aforementioned difficulties due to silt sedimentation in the cages.

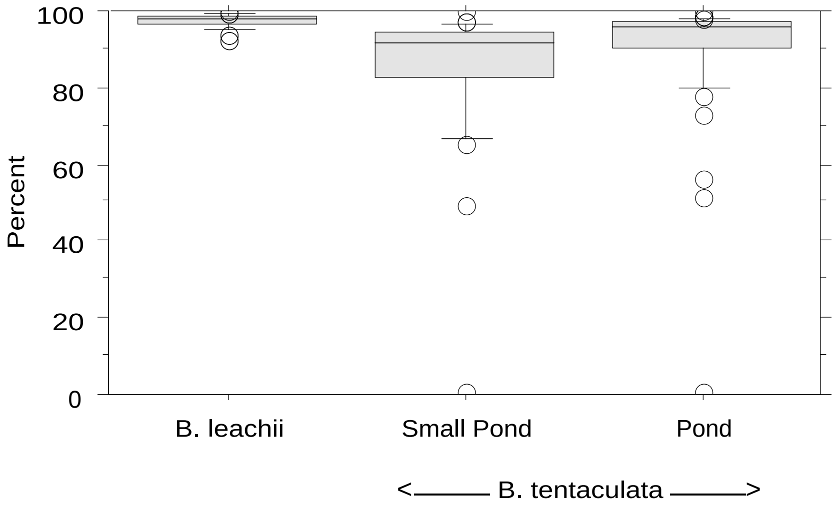


Fig. 31: Mean hatching rates of eggs in per cent, data for all reproductive females pooled per population (n = 151)

Tab. 19: Population means ± 1 standard deviation for several parameters connected to reproduction (the first 2 numbers in the boxes are the lowest and highest data points of observed parameters)

Origin	Egg number	Spawn number	Ø of eggs per spawn	Range of eggs per spawn	Hatching rate in per cent	Length of reproductive season (days)
Small Pond	23 - 460 **Ø: 188,0** ± 85,6 (n = 59)	2 - 22 **Ø: 11,0** ± 4,6 (n = 59)	6,2 - 35,5 **Ø: 17,7** ± 6,0 (n = 59)	10 - 118 **Ø: 49,0** ± 22,2 (n = 59)	0,0 - 100 **Ø: 85,7** (n = 43)	9 - 107 **Ø: 57,7** ± 24,5 (n = 48)
Pond	20 - 403 **Ø: 189,4** ± 91,6 (n = 56)	5 - 29 **Ø: 11,7** ± 7,0 (n = 56)	3,8 - 45,0 **Ø: 18,6** ± 7,7 (n = 56)	6 - 109 **Ø: 35,7** ± 20,7 (n = 56)	0,0 - 100 **Ø: 90,6** (n = 56)	9 - 92 **Ø: 37,6** ± 25,8 (n = 56)
Leine	50 - 862 **Ø: 400,1** ± 229,9 (n = 54)	2 - 67 **Ø: 29,0** ± 17,4 (n = 54)	9,1 - 26,5 **Ø: 16,7** ± 3,1 (n = 54)	14 - 61 **Ø: 29,0** ± 10,8 (n = 54)		7 - 148 **Ø: 86,7** ± 37,5 (n = 37)
B. leachii	31-453 **Ø: 228,4** ± 84,0 (n = 52)	7 - 66 **Ø: 35,6** ± 14,2 (n = 52)	3,5 - 13,1 **Ø: 6,8** ± 1,9 (n = 52)	6 - 51 **Ø: 17,2** ± 6,8 (n = 52)	92,2 - 100 **Ø: 97,4** (n = 52)	13 - 125 **Ø: 64,4** ± 28,0 (n = 50)

4.1.10. Variance within populations between years

Annotation:

Box plots showing descriptive statistics for each discussed parameter, population and year are included in the concluding section "Years" (4.1.13.). For reasons of clarity there are no further references to individual graphs in this section.

Small Pond

There were very few significant differences between years observed in this population (Tab. 21). Spawn number as mean number of eggs per spawn and range of eggs per spawn were, within some limits, the same in all years. The mean number of eggs was highest in 1999 but this was not significant either.

There was a difference for length of reproductive period (ANOVA, P = ,0230), the reproductive season of 1999 being longer than that of 1997 (Bonferroni/Dunn, P = ,0065). The hatching rate was lowest in 1997.

Small Pond 1999

This year it was possible to tell apart snails born the previous year and older ones by differences in shell features. Generally being of equal sizes, young snails had thin, transparent shells whereas shells of older snails were thick, opaque and corroded. 15 of the caged females were born in 1998 (called younger) and 15 were at least one year older (called older).

Tab. 20: Means of reproductive traits for older and younger females from the Small Pond in 1999

	Old females (n = 5)	**Young females** (n = 11)	
Egg number	257,4 ± 54,9	209,5 ± 149,1	U-test, P = ,4615
Spawn number	16,2 ± 2,2	11,6 ± 6,7	U-test, P = ,1731
Ø eggs per spawn	15,9 ± 2,1	17,0 ± 5,6	U-test, P = ,6917
Range	38,2 ± 12,1	38,3 ± 20,0	T-Test, P = ,9942
Length of reproduction (days)	84 ± 23,8	58 ± 31,5	T-Test, P = ,1234
Hatching rate (%)	94,7	88,5	

Out of the 16 reproducing snails, 5 were older and 11 younger females. Younger females started to reproduce about 4 weeks later than older ones. There was a strong tendency towards older females having a longer reproductive period and producing more spawns and eggs than younger females but this tendency was not significant (Tab. 20). This was partially due to the low numbers of reproducing old females, most older females being castrated by trematodes. Mean egg number per spawn and range of eggs per spawn were the same for both groups. Hatching rate of older females lay slightly above that for younger ones.

Tab. 21: Yearly population means ± 1 standard deviation for several reproductive traits (the first 2 numbers in the boxes are the lowest and highest data points of observed parameters)

Origin	Egg number	Spawn number	Ø of eggs per spawn	Range of eggs per spawn	Hatching rate in per cent	Length of reproductive season (days)
Small Pond 1997	23 - 305 **Ø: 161,7** ± 75,0 (n = 22)	2 - 22 **Ø: 10,7** ± 4,8 (n = 22)	7,7 - 35,5 **Ø: 15,7** ± 6,0 (n = 22)	17 - 72 **Ø: 41,7** ± 16,8 (n = 22)	0,0 - 97,1 **Ø: 82,6** (n = 20)	9 - 84 **Ø: 49** ± 22,2 (n = 23)
Small Pond 1998	68 - 300 **Ø: 187,4** ± 62,1 (n = 21)	4 - 19 **Ø: 9,7** ± 3,5 (n = 21)	6,8 - 30,3 **Ø: 20,5** ± 6,4 (n = 21)	16 - 118 **Ø: 51,0** ± 27,8 (n = 21)	72,2 - 93,2 **Ø: 84,1** (n = 7)	27 - 85 **Ø: 59** ± 19,8 (n = 10)
Small Pond 1999	28 - 460 **Ø: 224,8** ± 126,5 (n = 16)	2 - 22 **Ø: 13,1** ± 6,0 (n = 16)	6,2 - 19,3 **Ø: 16,7** ± 4,7 (n = 16)	10 - 65 **Ø: 38,3** ± 17,5 (n = 16)	75,7 - 100 **Ø: 90,4** (n = 16)	23 - 107 **Ø: 70** ± 26,7 (n = 15)
Pond 1997	20 - 326 **Ø: 209,0** ± 81,8 (n = 17)	5 - 29 **Ø: 17,0** ± 5,8 (n = 17)	3,8 - 16,8 **Ø: 12,0** ± 3,3 (n = 17)	6 - 75 **Ø: 32,8** ± 17,0 (n = 17)	92,3 - 100 **Ø: 97,3** (n = 17)	13 - 92 **Ø: 49** ± 17,3 (n = 17)
Pond 1998	28 - 324 **Ø: 117,5** ± 78,2 (n = 19)	2 - 24 **Ø: 6,6** ± 6,0 (n = 19)	10,3 - 45,0 **Ø: 21,6** ± 9,7 (n = 19)	6 - 64 **Ø: 25,1** ± 15,7 (n = 19)	56,5 - 97,8 **Ø: 90,0** (n = 19)	9 - 77 **Ø: 25** ± 20,2 (n = 19)
Pond 1999	96 - 403 **Ø: 241,1** ± 75,1 (n = 20)	6 - 28 **Ø: 12,1** ± 5,4 (n = 20)	9,1 - 33,6 **Ø: 21,4** ± 5,5 (n = 20)	23 - 109 **Ø: 48,1** ± 22,5 (n = 20)	0,0 - 98,0 **Ø: 85,5** (n = 20)	14 - 51 **Ø: 42** ± 6,4 (n = 20)
Leine 1997	53 - 633 **Ø: 325,1** ± 152,0 (n = 12)	2 - 48 **Ø: 24,8** ± 12,8 (n = 12)	10,5 - 26,5 **Ø: 14,5** ± 4,7 (n = 12)	17 - 41 **Ø: 27,2** ± 7,1 (n = 12)		7 - 102 **Ø: 61** ± 28,0 (n = 12)
Leine 1998	50 - 441 **Ø: 204,0** ± 119,1 (n = 17)	3 - 31 **Ø: 13,8** ± 8,5 (n = 17)	10,1 - 19,0 **Ø: 15,3** ± 2,3 (n = 17)	14 - 47 **Ø: 28,5** ± 9,6 (n = 17)		
Leine 1999	185 - 862 **Ø: 569,6** ± 196,3 (n = 25)	11 - 67 **Ø: 41,3** ± 15,1 (n = 25)	9,1 - 17,8 **Ø: 14,1** ± 2,4 (n = 25)	14 - 61 **Ø: 30,2** ± 11,5 (n = 25)		28 -148 **Ø: 101** ± 31,8 (n = 25)
B. leachii 1998	31 - 453 **Ø: 214,9** ± 104,6 (n = 26)	7 - 66 **Ø; 33,4** ± 18,2 (n = 26)	3,5 - 13,1 **Ø: 7,0** ± 2,3 (n = 26)	6 - 51 **Ø: 19,3** ± 8,0 (n = 26)	92,4 - 100 **Ø: 97,4** (n = 26)	13 - 125 **Ø: 67** ± 38,2 (n = 24)
B. leachii 1999	142 - 366 **Ø: 241,8** ± 55,2 (n = 26)	18 - 57 **Ø: 37,8** ± 8,7 (n = 26)	4,3 - 9,2 **Ø: 6,5** ± 1,2 (n = 26)	8 - 22 **Ø: 15,0** ± 4,2 (n = 26)	92,2 - 99,5 **Ø: 97,3** (n = 26)	35 - 108 **Ø: 62** ± 13,4 (n = 26)

Pond

The mean length of the reproductive period, the mean spawn number and the mean egg number were lower in 1998 than in both other years (Tab. 21; ANOVA, P = ,0001 for each of 3 comparisons).

The mean spawn number in 1999 was also lower than the mean number in 1997. The mean number of eggs per spawn was lower in 1997 than in both other years (Kruskall-Wallis–Test, Tied P < ,0001). The hatching rate declined from 97,3% in 1997 over 90,0% in 1998 to 85,5% in 1999 (Tab. 21).

Leine

The mean egg number and the mean number of spawns were exceptionally high in 1999, the differences being significant (Tab. 21; ANOVA, P < ,0001 for mean egg number; Kruskall–Wallis-Test, Tied P < ,0001 for mean spawn number). The reproductive period lasted longer in 1999 than in 1997 (T-Test, P = ,0002). Due to building activities at the site which led to major disturbances, data for 1998 are not included.

Although differences between 1997 and 1998 were pronounced (these are to some extent a consequence of the building activities), these differences are not statistically significant. The mean number of eggs per spawn and the range of eggs per spawn were the same in all years.

B. leachii

There were no apparent differences between both years (Tab. 21). Only the mean range of eggs per spawn lay slightly higher in 1998 (U-test, P = ,0169).

4.1.11. Correlations

Only few parameters are correlated in any meaningful way. Unexpectedly, the egg number of females is only weakly positive (*B. tentaculata*) or not at all (*B. leachii*) correlated to shell height of females (Tabs. 22-25). This means that larger females did not lay significantly more eggs than smaller females.

The only real strong positive correlations existing for the populations of both species are between egg number, number of spawns and length of reproductive period. The correlation coefficients are near or above ,8 in all cases (Fisher's r to z P-value < ,0001 for every single correlation between these three parameters). Are partial correlation coefficients calculated instead of correlation coefficients, coefficient values decline clearly showing that

Tab. 22: Small Pond, correlation matrix (n = 46)

	Height May	Egg number	Spawns	Ø per spawn	Range	Length/rep. period
Height May	1,000	,382	,275	,198	,288	,303
Egg number	,382	1,000	,787	,220	,623	,796
Spawns	,275	,787	1,000	-,331	,374	,789
Ø per spawn	,198	,220	-,331	1,000	,254	-,009
Range	,288	,623	,374	,254	1,000	,417
Length/rep. period	,303	,796	,789	-,009	,417	1,000

46 observations were used in this computation.

Tab. 23: Pond, correlation matrix (n = 59)

	Height April	Egg number	Spawns	Ø per spawn	Range	Lenght/rep. period
Height April	1,000	,429	-,003	,381	,563	,015
Egg number	,429	1,000	,772	,102	,645	,787
Spawns	-,003	,772	1,000	-,407	,308	,853
Ø per spawn	,381	,102	-,407	1,000	,270	-,211
Range	,563	,645	,308	,270	1,000	,318
Lenght/rep. period	,015	,787	,853	-,211	,318	1,000

59 observations were used in this computation.

Tab. 24: Leine, correlation matrix (n = 56)

	Height April	Egg number	Spawns	Ø per spawn	Range	Length/rep. period
Height April	1,000	,308	,277	,141	,432	,034
Egg number	,308	1,000	,951	-,018	,287	,845
Spawns	,277	,951	1,000	-,228	,156	,811
Ø per spawn	,141	-,018	-,228	1,000	,432	-,094
Range	,432	,287	,156	,432	1,000	,286
Length/rep. period	,034	,845	,811	-,094	,286	1,000

Tab. 25: *B. leachii*, correlation matrix (n = 50)

	Height May	Egg number	Spawns	Ø per spawn	Range	Length/rep. period
Height May	1,000	,192	,007	,202	-,152	-,127
Egg number	,192	1,000	,819	,037	,138	,805
Spawns	,007	,819	1,000	-,451	-,042	,864
Ø per spawn	,202	,037	-,451	1,000	,380	-,250
Range	-,152	,138	-,042	,380	1,000	-,025
Length/rep. period	-,127	,805	,864	-,250	-,025	1,000

50 observations were used in this computation.

the 3 parameters are closely interconnected. In the end this has no further meaning than that an increasing length of the reproductive period leads to increasing spawn and egg numbers. The range of eggs per spawn is positively correlated with number of eggs in the Small Pond and the Pond (Fisher's r to z P-value < ,0001), but there is no correlation for the Leine and *B. leachii* (Tabs. 22-25).

The only other interesting correlation is a weak but significant negative correlation between number of spawns and mean number of eggs per spawn. This confirms a trend for females laying many spawns to decrease the egg number per single spawn.

4.1.12. An analysis of cumulative egg numbers

Small Pond

The curves are of a different shape each year (Fig. 32a). In 1997 it was a parabolic curve, its slope diminishing with time. One third of all eggs were laid in the first week, after 2 weeks 50% were laid. The egg number per week then decreased steadily. 90% of all eggs were laid within the first 7 weeks, contributions to total egg number later on were only marginal. The breeding period was short and lasted for 12 weeks.

In 1998 the curve has a more or less linear appearance. 18% of all eggs were laid during the first week, nearly no eggs during the second and 20% during the third. 50% of all eggs were laid within the first 4 weeks. After that there is a more or less steady weekly increase of approximately 10% until more than 90% of all eggs have been laid in week 9. The last 4 weeks contribute nearly nothing to the total egg number.

In 1999 the curve was sigmoid with a slope that increases steadily until it is steepest between weeks 6 and 8 and decreases afterwards. In the first 4 weeks only 25% of all eggs were laid. 50% were reached after 6 weeks. Another 25% of eggs were laid after week 8. With 16 weeks the reproductive period lasted longer than the other years.

Pond

The curves are more or less linear in all years (Fig. 32b). The slope largely remained the same throughout most of the time. An interesting detail is the contribution of the first week to the total egg number which increased throughout the years from 14% (1997) over 20% (1998) to more than 30% in 1999. The last value is the major exception from linearity within the first weeks. 50% of all eggs were laid after 2-3 weeks (1998 and 1999) or 3-4

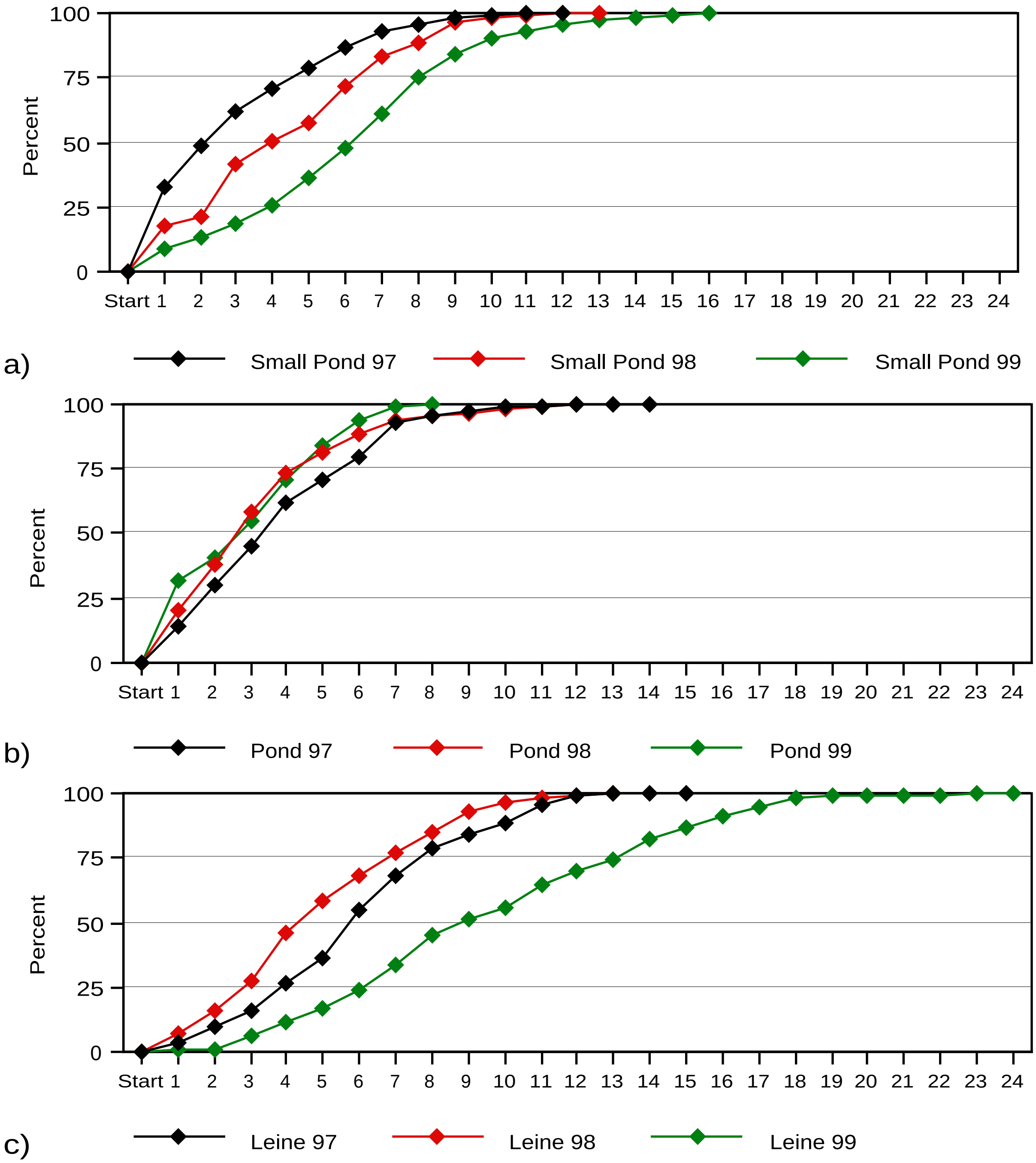


Fig. 32: Cumulative egg numbers for the *B. tentaculata* populations in Hannover (numbers signify consecutive weeks of the reproductive period)

weeks (1997). Egg numbers decreased quite abruptly after 6 or 7 weeks when the die-off of snails started.

With a duration of only 8 weeks, the reproductive period was shortest in 1999. The longest reproductive period lasted for 14 weeks in 1997 while the contributions to total egg number was near zero during the last 5 weeks.

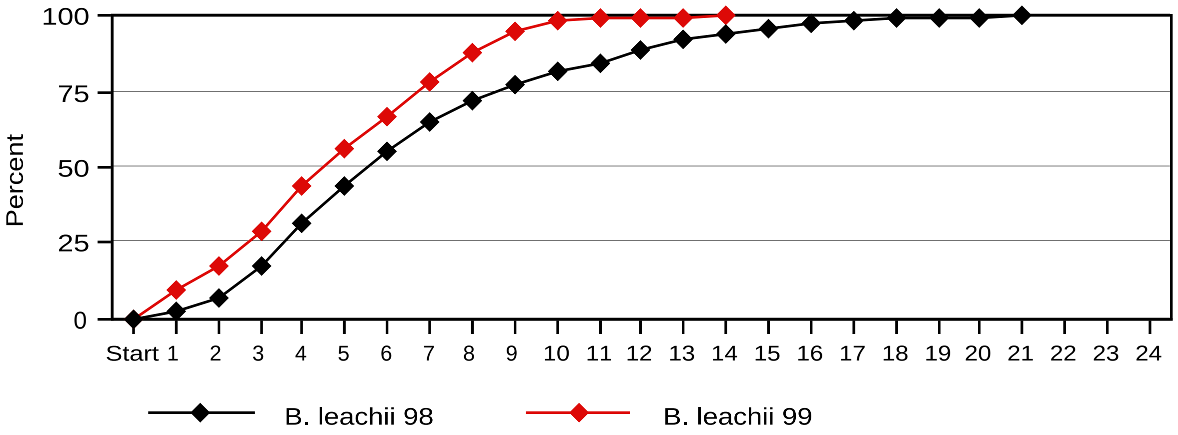


Fig. 33: Cumulative egg numbers for the B. leachii population (numbers signify consecutive weeks of the reproductive period)

Leine

The curves were sigmoid every year but were differentiated by their slopes (Fig. 32c). In 1997 egg numbers increased steadily for the first 6 weeks with 25% of all eggs laid after 4 weeks. The steepest slope was reached during weeks 6 and 7 after which nearly 70% of all eggs were laid. The slope gradually decreased afterwards until almost all eggs were laid after 11 weeks. Reproduction continued for one month but the number of eggs was nearly zero.

In 1998 the slope increased faster than in 1997, reaching its maximum already between weeks 3 and 5. Nearly half the eggs were laid during the first month. Egg numbers decreased with week 6 and 90% of all eggs were laid within two months. The reproductive period lasted 13 weeks while in the last weeks almost no further eggs were laid.

In 1999 egg laying started very restrained. It took 6 weeks for 25% of all eggs to be laid and only after 9 weeks the 50% mark was reached. Maximum egg laying occurred during week 8 and it continued on a medium level for another 10 weeks. Due to this, weekly contributions to total egg number were extremely low this year, never exceeding 10% per week with exception of week 8 (11,5%). It took 18 weeks for more than 95% of all eggs to be laid. The reproductive period continued for a further 6 weeks. With more than 5 months this year's reproductive period was by far the longest observed in the field.

B. leachii

Egg laying started restrained in 1998 but increased after week 2 (Fig. 33). The weekly output lay around 10% for the following 5 weeks. After week 7 the slope decreased but egg

laying continued steadily on a lower level for another 8 weeks. The reproductive period lasted altogether 21 weeks with the last 6 weeks not contributing much to total egg number.
In 1999 egg laying started more rapidly than the previous year and it took one week less until half the eggs were laid. The slope remained on a high level throughout most of the reproductive period and only went down when more than 95% of all eggs were laid after week 9. Reproduction continued for another 5 weeks but almost no further eggs were laid. The reproductive period lasted for only 14 weeks this year.

4.1.13. Differences between years

Number of reproducing females

A higher percentage of adult *B. leachii* (98%) than *B. tentaculata* females (69%) reproduced (Tab. 26). The percentage of reproducing females showed differences between years for all populations with exception of *B. leachii*. A higher percentage than usual reproduced in the Small Pond in 1997 (85%) and in the Leine in 1999 (93%). In 1999 fewer females reproduced in the Pond (70%) than in the other years.

Tab. 26: Number of reproductive females as portion of adult females for the different years and mortality of females from one reproductive period to the next

Origin	Reproductive females	Living at overwintering	Living at next year's reproductive period
Small Pond 1997	24/28	17/30	7/17
last years in 1998	6/7	0/7	-
Small Pond 1998	15/30		
Small Pond 1999	16/30	13/30	11/13
Pond 1997	17/22	0/30	-
Pond 1998	22/25	0/30	-
Pond 1999	21/30	0/30	-
Leine 1997	16/26	7/30	6/7
Last years in 1998	3/6	0/6	-
Leine 1998	15/30	1/30	1/1
Leine 1999	25/27	21/27	
B. leachii 1998	26/26	4/26	2/4
last years in 1999	1/2	0/2	-
B. leachii 1999	28/28	1/28	

Origin	Reproductive females	Living at overwintering	Living at next year's reproductive period
Small Pond	61/95	30/60	18/30
Pond	60/77	0/90	-
Leine	59/89	29/87	
B. leachii	55/56	5/54	2/4

There was a trend towards more female *B. tentaculata* reproducing in the Pond (78%) than in the other habitats (Small Pond: 64%; Leine: 66%), but the overall percentage of reproducing females was not significantly different between the populations (Chi Square P–Value = ,1263).

Egg number

The mean egg number of reproducing Leine females was higher than that of the other *B. tentaculata* populations and *B. leachii* in 1997 (325,1 eggs) and 1999 (569,6 eggs) (Tabs. 21 and 27). Egg number was generally high in all populations in 1999 (Fig. 34).

The lowest mean egg numbers had the Small Pond population in 1997 (161,7 eggs) and the Pond population in 1998 (117,5 eggs).

Tab. 27: Comparison of mean egg numbers per year and population (n = 221)

	Year		Kruskall-Wallis-Test
Egg number	1997	Small Pond < Pond < Leine	Tied P = ,0031
	1998	Pond < Small Pond = Leine = *B. leachii*	Tied P = ,0041
	1999	Small Pond = Pond = *B. leachii* < Leine	Tied P < ,0001

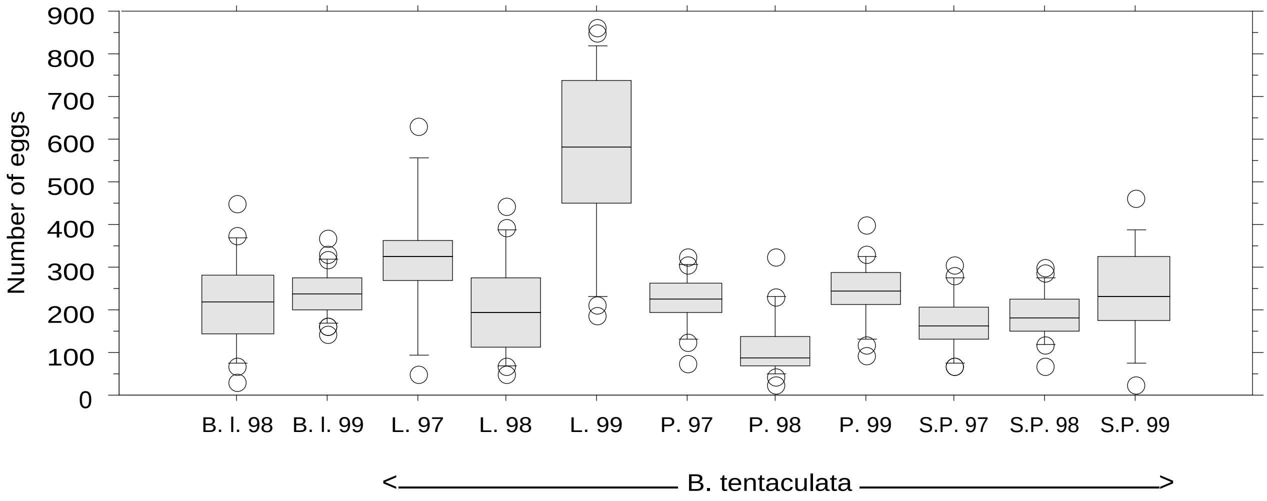


Fig. 34: Egg number of females (n = 221) (B. l. = *B. leachii*; L. = Leine; P. = Pond; S.P. = Small Pond)

Spawn number

The mean spawn number was highest in 1997 for the Leine population (24,8), 1998 for *B. leachii* (33,4) and 1999 for *B. leachii* (37,8) and the Leine population (41,3) (Tabs. 21 and 28). The number of spawns was generally low in the Small Pond and also in the Pond population (Fig. 35).

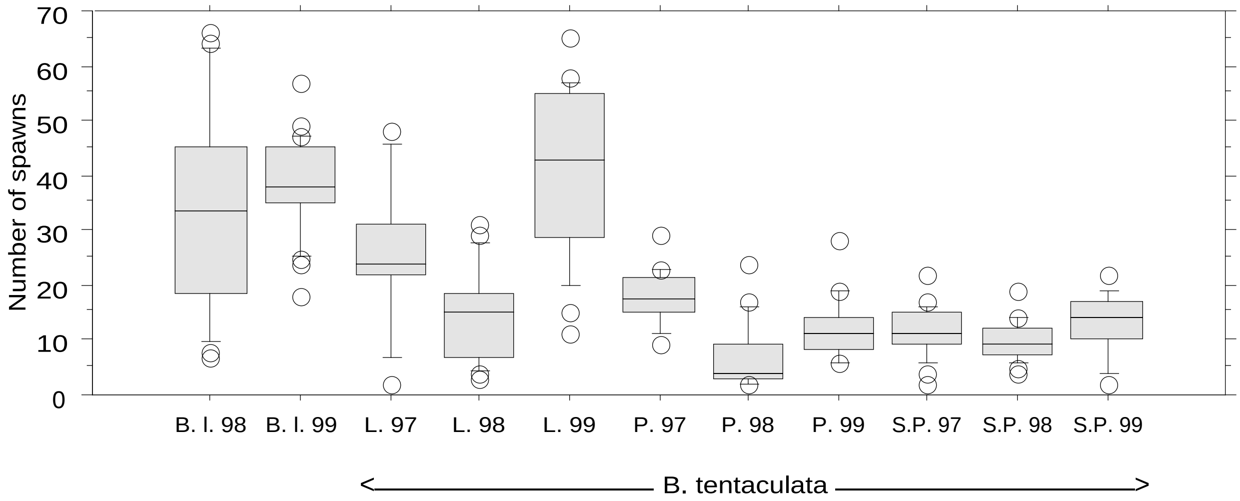


Fig. 35: Number of spawns (n = 221) (B. l. = *B. leachii*; L. = Leine; P. = Pond; S.P. = Small Pond)

Tab. 28: Comparison of mean spawn number per year and population (n = 221)

	Year		Kruskall-Wallis-Test
Spawn number	1997	Small Pond < Pond < Leine	Tied P = ,0002
	1998	Small Pond = Pond = Leine < *B. leachii*	Tied P < ,0001
	1999	Small Pond = Pond < Leine = *B. leachii*	Tied P < ,0001

Mean number of eggs per spawn

The mean number of eggs per spawn was generally highest for the Small Pond and/or Pond populations in all years (Tabs. 21 and 29; Fig. 36). It was lowest for *B. leachii* in both years, the Leine population being on an intermediate level.

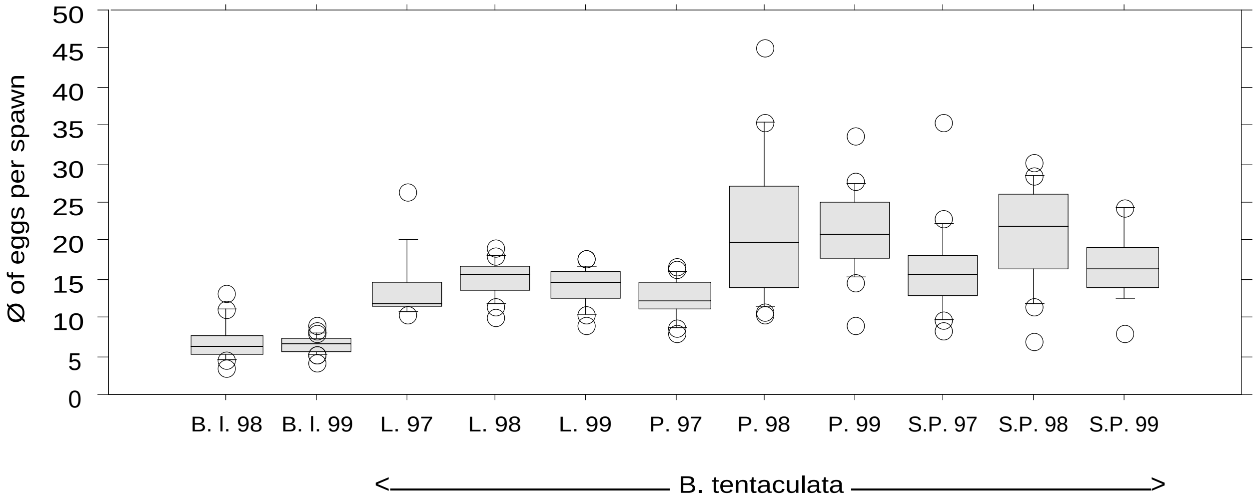


Fig. 36: Mean number of eggs per spawn (n = 221) (B. l. = *B. leachii*; L. = Leine; P. = Pond; S.P. = Small Pond)

Tab. 29: Comparison of mean number of eggs per spawn (n = 221)

	Year		Kruskall-Wallis-Test
Ø of eggs per spawn	1997	Small Pond > Pond; Small Pond = Leine; Pond = Leine	Tied P = ,0436
	1998	Small Pond = Pond > Leine > *B. leachii*	Tied P < ,0001
	1999	Pond > Small Pond = Leine > *B. leachii*	Tied P < ,0001

Length of reproductive period

The mean length of the reproductive period was shortest in the Pond in 1998 (25 days) and 1999 (42 days) (Tabs. 21 and 30; Fig. 37). The duration of the reproductive period was exceptionally long in the Leine in 1999 (101 days) and for B. leachii in 1998 (67 days).

Tab. 30: Comparison of mean length of reproductive period between years and populations (n = 161)

	Year		Kruskall-Wallis-Test
Mean length of reproductive period	1997	Small Pond = Pond = Leine	Tied P = ,4278
	1998	Small Pond = *B. leachii* > Pond	Tied P = ,0001
	1999	Pond < Small Pond = *B. leachii* < Leine	Tied P < ,0001

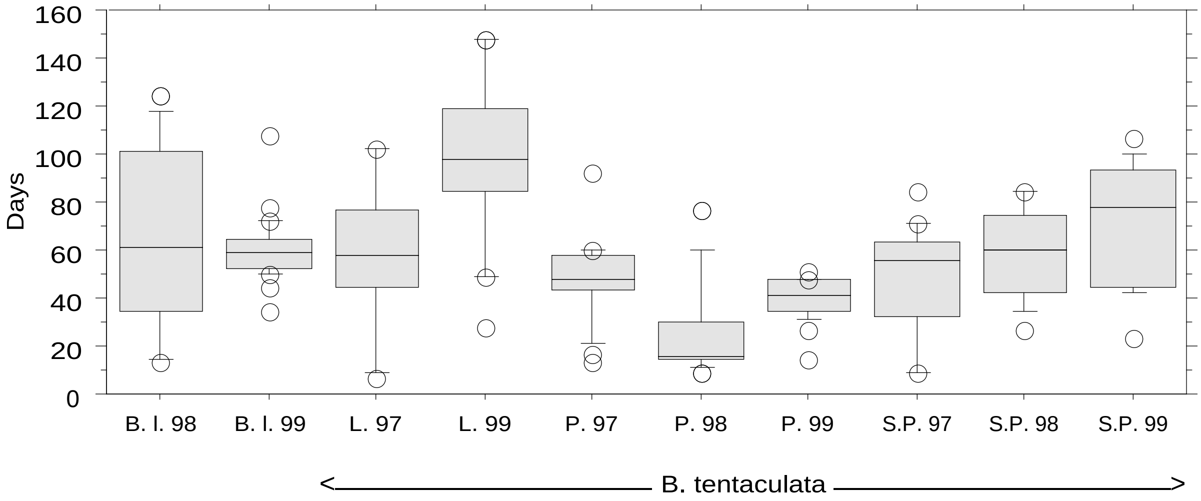


Fig. 37: Length of reproductive period in days (n = 161) (B. l. = *B. leachii*; L. = Leine; P. = Pond; S.P. = Small Pond)

4.2. Trait combinations and individual reproductive strategies

The females exhibited differences in their individual strategies within the populations. In direct comparison within the populations, there were females that laid many spawns with few eggs, others that laid few spawns containing many eggs and females adopting a strategy inbetween. This trade-off between spawn size and -number combined with other traits like start of reproduction, range of spawn size and length of the reproductive period led to individual trait combinations. I have compiled some of the data for different years (Tab. 31).

I used egg number as the common denominator since it demonstrates most convincingly that any given investment in a similar number of eggs can be partitioned in a different spatio–temporal pattern.

Tab. 31: Combinations of reproductive traits in several individual females

Origin	Egg number	Spawn number	Ø of eggs per spawn	Range of spawn size	Length of reproductive period	First spawn is greatest spawn of season
Small Pond 1997	186	15	12,4	58 (5-63)	56	Yes
	197	15	13,1	49 (3-52)	71	Yes
	196	11	17,8	47 (5-52)	56	Yes
	194	9	21,6	46 (5-52)	63	Yes
Small Pond 1999	307	22	14,0	32 (2-34)	86	Yes
	334	18	18,6	58 (1-59)	100	No
	330	14	23,6	61 (6-67)	78	Yes
Pond 1999	254	28	9,1	23 (1-24)	48	No
	275	19	14,5	37 (5-42)	41	Yes
	250	11	22,7	81 (7-88)	41	Yes
	237	10	23,7	39 (16-55)	48	Yes
	251	9	27,9	36 (14-50)	48	Yes
Leine 1997	366	32	11,4	21 (2-23)	102	No
	333	28	11,9	24 (1-25)	102	No
	327	22	14,9	21 (2-23)	51	No
	363	23	15,8	33 (2-35)	65	No
	348	17	20,5	41 (3-44)	49	Yes
Leine 1999	435	48	9,1	14 (1-15)	84	No
	455	31	14,7	27 (6-33)	84	Yes
	451	28	16,1	27 (3-30)	112	Yes
	408	25	16,3	27 (3-30)	77	No

4.3. Transplant experiment

Of the 10 transplanted *B. leachii* snails (5 females/5 males) one female was lost and one died before the onset of the reproductive period. The remaining 3 females reproduced. All females grew during the reproductive period and died in late summer of 1998.

One male died shortly after the start of the experiment, the others grew during the summer. Two males died in late summer of 1998, the remaining 2 in early spring of 1999. Mean shell height at death was similar to the pond population.

The mean egg number per reproducing females in the Leine lay slightly higher than the egg number of *B. leachii* females in the Pond, but the difference was not significant (T-Test; P = ,5796). All other reproductive parameters like spawn number etc. showed no major differences between transplanted and Pond females (Tab. 32). The eggs developed into hatchable juveniles in the Leine and hatching was observed but not quantified due to aforementioned problems with silt sedimentation in the cages.

Tab. 32: Mean values ± 1 standard deviation for some reproductive parameters of transplant females (n = 3)

	Egg number	Spawn number	Ø of eggs per spawn	Range of eggs per spawn	Length of reproductive period (days)
B. leachii Transplant 1998	236 - 284 **Ø: 261,7** ± 24,2	27 - 30 **Ø: 29,0** ± 1,7	7,9 - 10,5 **Ø. 9,1** ± 1,3	21 - 30 **Ø: 24,0** ± 5,2	50 - 93 **Ø: 69,7** ± 21,7

4.4. Reproduction and parasitation

Field evidence

Of all females recovered dead during field experiments, 16 were in a condition good enough to be examined for trematode larval stages. Of these snails 9 were not parasitized and had successfully reproduced. 6 females were strongly parasitized. 5 of these snails had not reproduced at all and 1 had made an attempt at egg laying but the eggs were not viable. 1 of the parasitized females belonged to *B. leachii* and was the only female of this species in the field experiments that did not reproduce.

Laboratory evidence

Out of the 33 Hunte females kept in the laboratory in this experiment, 2 died in the first 2 weeks and 1 non-reproductive female in August. An unusual high number of 27 out of the 30 living females reproduced, leaving only 3 non-reproductive females. Of this 3 females 1 was severely parasitized, the others were not parasitized and had normally developed gonads. The result is therefore not in agreement with the hypothesis that non-reproducing females are always parasitized.

4.5. Individual life histories and reproduction of females in laboratory culture

4.5.1. Minimal female height for reproduction

The mean height of the smallest reproducing snails was different between habitats (Fig. 38). With the height of the 5 smallest reproducing snails per habitat an ANOVA analysis was calculated showing significant differences between groups ($P < ,0001$). Because of the small number a Fisher's PLSD was preferred over more conservative post-hoc tests in this case. Snails from the Leine (Ø: 6,8 mm) and the Hunte (Ø: 7,0 mm) started reproducing at the smallest size. They were significantly smaller than those from the Canal (Ø: 7,6 mm), which were themselves smaller than those from the Pond (Ø: 8,1 mm). Snails from the Small Pond (Ø: 8,8mm) and the Ditch (Ø: 9,2 mm) had to reach a significantly larger size than all others before being able to reproduce.

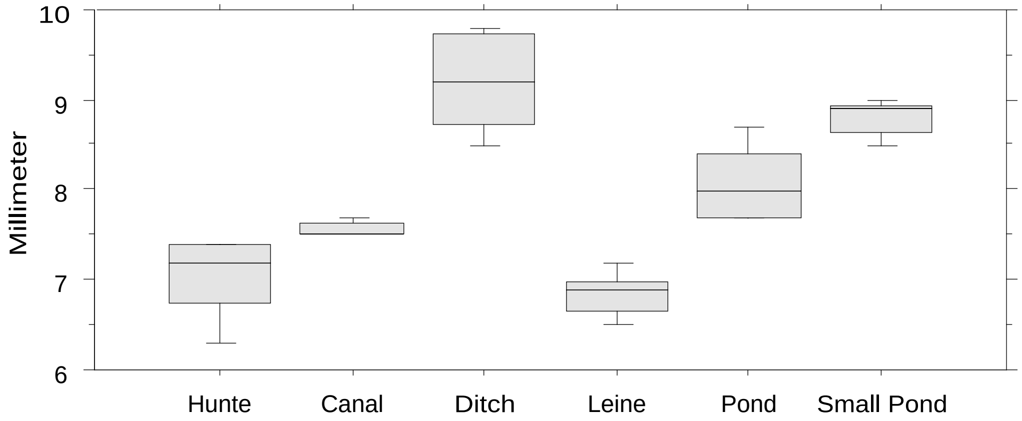


Fig. 38: Shell height of smallest reproducing *B. tentaculata* females under laboratory conditions (n = 30)

Critical shell height for reproduction in further laboratory experiments

Pond

All males and females grew throughout spring and summer and reached normal adult sizes. None of the 9 females reproduced. It seems reasonable to argue that Pond females must have reached a shell height of at least 7,0 mm in early spring to be able to reproduce.

Leine

8 males and 5 females grew during the experiment. 3 out of the 10 females reproduced. The reproducing females were the largest ones, being of a shell height of 6,4 mm (2x) and 6,6 mm. All females smaller than 6,4 mm in early spring failed to reproduce irrespective of the size they attained during spring and summer. Therefore the critical shell height for Leine females seems to be 6,4 mm.

4.5.2. Shell height of females

The mean height of females at start of laboratory culture (which largely reflects the population's composition in the field in spring 1997) was different (Kruskall-Wallis-Test: P < ,0001) between habitats (Tab. 33).

Females from the Ditch (Ø: 8,1 mm) and the Small Pond (Ø: 8,9 mm) were largest, females from the Canal (Ø: 7,7 mm) and the Leine (Ø: 7,4 mm) were of a medium size and Pond (Ø: 6,6 mm) and Hunte (Ø: 6,2 mm) females were the smallest.

Tab. 33: Shell height of *B. tentaculata* females at start of experiment and at their deaths

	Start (April 1997)			Death		
FEMALES	Ø	min	max	Ø	min	max
Hunte (n = 40)	6,2	3,3	9,2	7,7	6,0	9,3
Canal (n = 30)	7,7	4,7	9,0	8,4	7,1	10,0
Ditch (n = 18)	8,1	4,7	10,1	9,6	8,7	10,6
Small Pond (n =32)	8,9	6,3	10,7	9,2	7,7	10,7
Pond (n = 33)	6,6	3,5	10,1	8,5	6,4	10,4
Leine (n = 50)	7,4	4,6	9,0	7,7	5,0	9,1

The mean shell height at death showed significant differences between habitats (Tab. 33; ANOVA, P = ,0001). Females from the Ditch (Ø: 9,6 mm) and the Small Pond (Ø: 9,2 mm) grew up to equal sizes and were significantly larger than females from the Canal (Ø: 8,4 mm) and the Pond (Ø: 8,5 mm). Females from all 4 population were significantly larger than females from the river populations (Hunte and Leine Ø: 7,7 mm; Bonferroni/Dunn post-hoc test, P = ,0033).

4.5.3. Egg number

The mean egg number of reproducing females was significantly different between populations (ANOVA, P = ,0001). The females from the Ditch (Ø: 101 eggs) and the Small Pond (Ø: 105 eggs) laid significantly more eggs in 1997 than those of the other populations which showed no significant differences between each other (Tab. 34; Bonferroni/Dunn post-hoc-test, P = ,0033).

No significant differences were found for mean number of spawns (Tab. 34; Kruskall–Wallis-Test, P = ,336)

4.5.4. Hatching rate of eggs

The hatching rates of *B. tentaculata* females originating from Dümmer populations were higher than those of females originating from populations out of Hannover (Tab. 34). The hatching rates of the latter were dramatically lower than those observed in the field for this populations (see Tab. 19).

Tab. 34: Population mean values ± 1 standard deviation for several reproductive traits (the first 2 numbers in the boxes are the minimum and maximum values of observed parameters)

Origin	Egg number 1997	Egg number 1998	Spawn number 1997	Spawn number 1998	Ø per spawn 1997	Ø per spawn 1998	Hatching rate 1997 (%)
Hunte	12 - 100 **Ø: 61,4** ± 24,8 (n = 13)	4 - 126 **Ø: 37,4** ± 40,6 (n = 12)	1 - 11 **Ø: 7,1** ± 3,3 (n = 13)	1 - 24 **Ø: 5,6** ± 6,6 (n = 12)	5,2 - 21,0 **Ø. 9,8** ± 4,5 (n = 12)	2,0 - 11,5 **Ø: 6,9** ± 3,1 (n = 9)	4,9 - 100 **Ø. 83,1** (n = 13)
Canal	36 - 115 **Ø: 63,1** ± 23,4 (n = 16)	55 - 110 **Ø: 78,2** ± 23,8 (n = 5)	1 - 10 **Ø: 5,8** ± 3,2 (n = 16)	5 - 31 **Ø: 12,6** ± 10,5 (n = 5)	5,0 - 34,5 **Ø: 12,9** ± 7,2 (n = 15)	3,1 - 13,8 **Ø: 8,6** ± 4,4 (n = 5)	13,9 - 100 **Ø: 61,3** (n = 16)
Ditch	8 - 194 **Ø: 101,2** ± 60,2 (n = 6)	-	1-25 **Ø: 10,5** ± 8,4 (n = 6)	-	4,4 - 19,8 **Ø: 12,5** ± 6,8 (n = 5)	-	90,7 - 98,7 **Ø: 95,9** (n = 6)
Small Pond	50 - 187 **Ø: 105,0** ± 38,7 (n = 21)	34 - 63 **Ø: 48,0** ± 11,9 (n = 4)	1 - 15 **Ø: 6,8** ± 3,2 (n = 21)	3 - 5 **Ø: 3,8** ± 1,0 (n = 4)	7,2 - 16,7 **Ø: 16,9** ± 6,1 (n = 20)	8,5 - 21 **Ø: 13,7** ± 5,9 (n = 4)	0 - 78,2 **Ø: 21,1** (n = 20)
Pond	10 - 120 **Ø: 61,5** ± 34,9 (n = 10)	14 - 64 **Ø: 46,6** ± 20,8 (n = 7)	2 - 16 **Ø: 6,4** ± 4,0 (n = 10)	1 - 9 **Ø: 4,1** ± 2,8 (n = 7)	2,0 - 29,5 **Ø: 11,5** ± 8,1 (n = 10)	6,9 - 15,0 **Ø: 9,7** ± 3,0 (n = 9)	0 - 90,0 **Ø: 52,0** (n = 10)
Leine	13 -115 **Ø: 50,8** ± 23,2 (n = 27)	14 - 105 **Ø: 54,4** ± 28,4 (n = 8)	1 - 13 **Ø: 7,8** ± 3,4 (n = 27)	1 - 17 **Ø: 7,1** ± 5,2 (n = 8)	2,8 - 16,0 **Ø: 7,2** ± 3,4 (n = 26)	4,6 - 26,5 **Ø: 10,1** ± 7,8 (n = 7)	0 - 95,7 **Ø: 54,5** (n = 27)

4.5.5. Length of reproductive period

No significant differences were found for mean length of reproductive period (ANOVA, P = ,903; Fig. 39; Tab. 35).

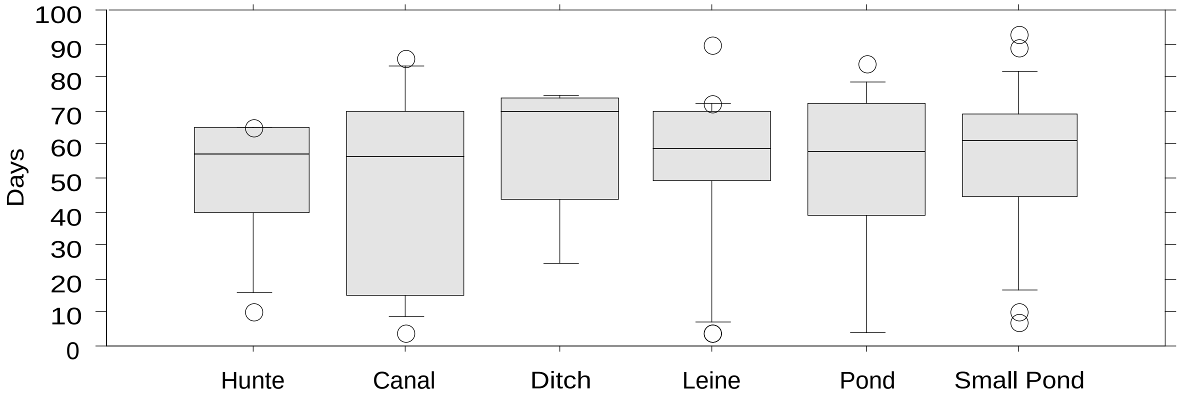


Fig. 39: Length of reproductive period for laboratory *B. tentaculata* females in 1997 (for n see Tab. 35)

Tab. 35: Length of the reproductive period ± 1 standard deviation in laboratory culture in days

Hunte 97	Hunte 98	Canal 97	Canal 98	Ditch 97	Ditch 98
Ø = 46 ± 23 (1-65) (n = 13)	**Ø = 13** ± 18 (1-60) (n = 12)	**Ø = 46** ± 31 (1-86) (n = 16)	**Ø = 34** ± 21 (1-52) (n = 5)	**Ø = 49** ± 30 (1-75) (n = 6)	-

Small Pond 97	Small Pond 98	Pond 97	Pond 98	Leine 97	Leine 98
Ø = 51 ± 27 (1-93) (n = 21)	**Ø = 24** ± 12 (14-38) (n = 4)	**Ø = 50** ± 27 (4 - 84) (n = 10)	**Ø = 33** ± 34 (1 - 89) (n = 7)	**Ø = 52** ± 23 (1 - 90) (n = 27)	**Ø = 20** ± 20 (1 - 52) (n = 8)

Out of these observations a common pattern emerges (Tab. 36). The females from the smallest and most ephemeral habitats delay their reproductive activity until they reach a shell size well above that of most of the females from other populations. This difference in shell size found at the turning point from exclusive investment in somatic growth to investment both in growth and reproduction is preserved throughout further live. Females of this habitat type remain significantly larger than females from other habitats until death. This larger size pays off in a significantly larger number of eggs.

Tab. 36: Statistical tests for several traits connected with reproduction under laboratory conditions (ANOVA, P < ,0001 for each analysis; Bonferroni/Dunn Post Hoc Test, = no significant difference; < significant difference, P < ,0033 at least)

Smallest reproducing females	Leine = Hunte < Canal < Pond < Small Pond = Ditch
Height at death (Females)	Leine = Hunte < Canal = Pond < Small Pond = Ditch
Height at death (Males)	Hunte < Leine < Ditch = Canal = Pond < Small Pond
Egg number of females (1997)	Leine = Hunte = Canal = Pond < Small Pond = Ditch

With regard to the size at first reproduction and the shell size at death the females from the Pond and the Canal (which clearly resembles a pond) were in a medium position. However, their larger size did not pay off in egg numbers compared to river populations. The females from both river habitats started to reproduce at the smallest size and showed only moderate growth afterwards. They attained only smaller adult sizes than females from other populations. This smaller size did not lessen their reproductive output compared to the pond type of habitat.

4.5.6. Differences between years

The significant differences in egg number found in 1997 between populations did not persist in laboratory culture in 1998 (ANOVA, P = ,192; Tab. 34). In contrast to females from the other populations, the females from the Ditch did not reproduce a second time in the laboratory. Due to the small number of reproducing females no further statistics were performed with the data from 1998, but it seems remarkable that in almost every case reproductive success and related traits were lower in 1998 than in 1997. It seems also obvious that laboratory culture levelled off differences between populations (Tab. 34). The only exception were the females from the Canal, which laid more spawns with more eggs in 1998 than in 1997 (but notice that number of reproducing snails was very low in 1998).

5. OVIPOSITION SITE CHOICE

The females of the 4 populations clearly preferred macrophytes for spawn deposition (Tab. 37). Wood and gravel were not used by 3 populations. Dead leaves were used for spawn deposition by 3 populations, but egg numbers were sparse. This is even more remarkable since females preferred other substrata than macrophytes for foraging (Tab. 38). Egg laying behaviour therefore does not simply reflect the feeding preferences of females. Females are discriminating actively between sites for foraging and locations for egg laying.

Tab. 37: Egg numbers on different substrat types

Origin	Egg number/ wood	Egg number/ gravel	Egg number/ macrophytes	Egg number/ dead leaves
Pond	–	–	195	21
Small Pond	–	31	309	–
Canal	–	–	229	10
Ditch	18	–	148	23
Count:	**18**	**31**	**881**	**54**

Tab. 38: Location of females at recovery

Origin	Wood	Gravel	Macrophytes	Dead leaves	Water surface	Dead females
Pond	1	–	6	6	–	–
Small Pond	2	2	2	2	1	6
Canal	4	3	1	1	–	–
Ditch	4	1	–	4	2	–
Count:	**11**	**6**	**9**	**13**	**3**	**6**

6. REPRODUCTIVE SUCCESS OF *B. TENTACULATA* UNDER THE INFLUENCE OF *L. STAGNALIS*

6.1 Preliminary study

Spawn deposition by *B. tentaculata* was observed in all aquaria. However, juveniles were only found in the controls without *L. stagnalis* and also in one aquarium containing gravel and one containing gravel and macrophytes.

Direct consumption of spawns laid by *B. tentaculata* was observed in several cases but *L. stagnalis* did not feed on spawns systematically. This means that snails encountering a spawn did not consume it as a whole, but consumed that part of the spawns that lay in their way during grazing movements. In the long run, due to intensive grazing activities of *L. stagnalis*, most spawns were consumed completely during several chance encounters.

Direct consumption of juveniles was not observed. In consideration of the observation that at least some juveniles hatched in aquaria containing *L. stagnalis*, but mostly could not be found at the end of the experiment and the large size difference between adult *L. stagnalis* and *B. tentaculata* juveniles, consumption should be a common cause of mortality for the latter.

6.2 Main experiment

Out of 160 adult *B. tentaculata* present at the start of the experiment, 136 (85%) were recovered after 6 months. Of these snails 91 (33 males, 33 females, 25 gender unknown) were alive and 45 (19 males, 17 females, 9 gender unknown) were dead.

Living juveniles of *B. tentaculata* were found in 4 tubs, living juveniles of *L. stagnalis* in all tubs where this species was established. Altogether 142 juvenile *B. tentaculata* were found in the 2 control tubs. In the 6 tubs containing *L. stagnalis* there were 20 juvenile *B. tentaculata* and 526 juvenile *L. stagnalis* (Tab. 39).

The outcome showed clearly that the reproductive success of *B. tentaculata* is influenced negatively by *L. stagnalis* and that this influence is a strong one. Surprisingly, experimental conditions (habitat diversity, number of adult *L. stagnalis*) seemed not to influence the reproductive success in the presence of *L. stagnalis* (Tab. 39). Reproduction was low to zero in all cases. This is not in favour of the hypothesis that predicted increasing numbers of surviving juveniles under lower feeding pressure and higher structural habitat diversity. A possible explanation is that the feeding pressure by *L. stagnalis* on small juvenile stages was underestimated and that the gravel layer at the bottom of the tubs did not improve habitat structure sufficiently to offer *B. tentaculata* protection from *L. stagnalis*.

Tab. 39: Number of living juvenile *B. tentaculata* at end of experiment

	Experimental conditions			
	Controls	10 *L. stagnalis*, no gravel	5 *L. stagnalis*, with gravel	10 *L. stagnalis*, with gravel
Number of juveniles	133	12	–	–
	9	–	–	8
Count:	**142**	**12**	**–**	**8**

7. GROWTH

7.1. Females

7.1.1. Growth of *B. tentaculata* females under field conditions

The females of the 3 populations showed overall more similarities than differences in regard to their growth pattern.
In the Small Pond and the Leine 20% of all females grew, whereas in the Pond 30% grew, but this difference was not significant. On the other hand it should not be overlooked that differences within the 3 populations between years can be pronounced (Tab. 40).

Reproduction and growth are correlated traits. Significantly more non-reproducing females grew than reproducing ones (Fisher's exact test, P = ,0005), but in all populations a substantial fraction (every sixth female) grew while reproducing (Tab. 40). This comes close to the laboratory data, were every fifth reproducing female grew (see chapter 7.1.2.).

Overall only 35% of the non-reproducing females grew, but there is a difference between populations: In the Pond a larger fraction (57%) grew than in the Small Pond (27%) and the Leine (24%) (Contingency Table, Chi Square P = ,0140). There is one further difference: Subadult females grow more often than adult ones. Out of a total number of 20 females below the critical shell height for reproduction, 17 grew whereas only 17 out of 77 adult-sized females grew.

Overall 63 (23%) out of a total of 275 observed individuals grew. It is obvious that most females grew in the period from spring to early summer (49 out of 63), some during summer until autumn (14 out of 63) and none grew in autumn or during winter (Tab. 41). An even smaller fraction of those females observed a second year after successful overwintering grew. This makes it clear that the main increase in shell size occurs directly after birth until the first winter, some during the following spring and only a little bit later on.

When comparing mean shell height at start and at death of females, it is apparent that in most habitats and years there is almost no to only moderate increase (Tab. 42). Exceptions are the Small Pond in 1999, the year when there was a substantial fraction of young snails after a successful reproductive period the year before, the Pond in 1997 when there were more small females in the spring than usual and the Leine in 1999 when females reached unusual large shell heights during summer.

Tab. 40: Number of females with a given trait as fraction of females that could show this trait

Origin	Growing females	Growing reproductive females	Growing non-reproductive females
Small Pond 1997	4/30	1/24	3/6
last years in 1998	0/7	0/6	0/1
Small Pond 1998	2/30	1/15	1/15
Small Pond 1999	13/30	7/16	6/14
Pond 1997	17/28	8/17	9/11
Pond 1998	6/28	1/22	5/8
Pond 1999	3/30	1/21	2/9
Leine 1997	6/30	3/16	3/14
Last years in 1998	1/6	0/3	1/3
Leine 1998	3/29	0/15	3/14
Leine 1999	8/27	7/25	1/2
B. leachii 1998	25/26	25/26	-
last years in 1999	1/2	0/1	1/1
B. leachii 1999	12/28	12/28	-

Origin	Growing females	Growing reproductive females	Growing non-reproductive females
Small Pond	19/97	9/61	10/36
Pond	26/86	10/60	16/28
Leine	18/92	10/59	8/33
B. leachii	38/55	37/55	1/1

Small Pond 1999

This year 13 out of 30 females grew. Out of the growing females 11 were born the previous year and only 2 were older snails. All the 4 non-reproducing younger females grew also.

Out of 16 reproducing females 7 grew which were all younger individuals.The growth of young snails led to the result that 1999 was the only year when mean shell height increased in the Small Pond between the start of experiment and the death of females (Tab. 42). These findings underline the former notion that most increment in shell size occurs directly after birth until the first winter, some during the following spring or early summer and only few females grow when more than 1 year old.

Tab. 41: Growth patterns of females for all years and populations

Date	**Small Pond 1997**			**Small Pond 1998**			**Small Pond 1999**		
Start	Grown	Not grown	Dead	Grown	Not grown	Dead	Grown	Not grown	
->May				–	11		9	21	5
->June	2	26	1	1	10	1	7	18	–
->July	2	25	1	–	10	8	–	25	4
->August	2	23	2	–	2	1	1	20	2
->Sept.	–	24	7	–	1	–	2	17	3
->Oct.	–	17	1	–	1	–	–	16	3
->March	–	16	9	–	1	1	–	13	2
Sum:	**4**	**24**	**21**	**1**	**10**	**11**	**13**	**17**	**19**

Date	**Pond 1997**			**Pond 1998**			**Pond 1999**		
Start	Grown	Not grown	Dead	Grown	Not grown	Dead	Grown	Not grown	Dead
->May				5	24	26	3	27	17
->June	17	13	20	1	2	1	3	10	13
->July	–	10	10	–	2	2			
Sum:	**17**	**13**	**30**	**6**	**23**	**29**	**3**	**27**	**30**

Date	**Leine 1997**			**Leine 1998**			**Leine 1999**		
Start	Grown	Not grown	Dead	Grown	Not grown	Dead	Grown	Not grown	Dead
->May				1	35	15	–	27	2
->June	2	23	10	2	19	9	3	22	1
->July	2	13	5	1	11	10	1	23	1
->August	2	8	2	–	2	1	3	20	–
->Sept.	1	7	1	–	1	–	–	23	1
->Oct.	–	7	–	–	1	–	–	22	1
->March	–	7	1	–	1	–			
Sum:	**6**	**19**	**19**	**3**	**33**	**35**	**7**	**20**	**6**

Date				***B. leachii* 1998**			***B. leachii* 1999**		
Start				Grown	Not grown	Dead	Grown	Not grown	Dead
->May				17	7	6	10	18	2
->June				12	6	6	–	26	24
->July				–	12	1	–	2	1
->August				–	11	5	–	1	–
->Sept.				4	2	1	1	–	–
->Oct.				2	3	1			
->March				–	4	1			
Sum:				**20**	**1**	**21**	**11**	**17**	**27**

Tab. 42: Shell height of females in millimeter at start of experiment and at their deaths (n = 30; exceptions: *B. leachii* 1998, n = 27; *B. leachii* 1999, n = 28)

	Start			Death		
FEMALES	Ø	min	max	Ø	min	max
Small Pond 1997	9,2	5,6	10,4	9,2	7,9	10,3
Small Pond 1998	9,6	8,4	11,1	9,5	8,3	11,1
Small Pond 1999	9,5	7,6	11,0	10,2	8,8	11,6
Pond 1997	7,7	4,9	12,5	8,8	7,8	12,5
Pond 1998	8,4	6,1	10,1	8,8	7,3	10,4
Pond 1999	10,0	9,1	12,0	10,0	9,1	12,0
Leine 1997	7,8	4,9	9,0	8,0	5,4	10,0
Leine 1998	7,7	6,6	8,7	7,8	6,6	10,0
Leine 1999	8,2	7,5	9,1	8,6	7,5	11,8
B. leachii 1998	4,5	3,8	5,7	5,5	4,7	6,9
B. leachii 1999	5,7	4,4	6,6	5,9	5,1	6,7

7.1.2. Growth of *B. tentaculata* females under laboratory conditions

The populations exhibited significant differences in their overall growth patterns during the experiment (Contingency Table, Chi Square P < ,0001). On average more females from the Hunte, the Ditch and the Pond grew until their deaths while growth for the Leine population was significantly below average (Tab. 43). This also can be seen when comparing the mean shell height at start and at death for the 6 populations. The mean shell height of the Hunte, the Ditch and the Pond is increasing most profoundly (Tab. 44).

It is also obvious that most females grew in the period from mid-April to early summer (80 females out of an overall sum of 97 growing females), some in late summer to autumn and almost none grew between mid-September and April (Tab. 43).

In 1997, 67 out of a total of 203 females proofed to be below the critical shell size for reproduction. Out of the 67 small females, almost all (93%, 62 females) grew in 1997. The same year 130 females reproduced while only 19% (25 females) grew.
Fewer females grew during their second spring (23 out of 102) than during their first (80 females out of 203; Fisher's Exact Test, P = ,0032).

These results point out two things: First, nutrition during lab culture was good enough to allow for growth. Second, most females curbed their growth in favour of reproduction when reaching an adult size. However, a substantial fraction of females (every fifth female) continued to grow.

Tab. 43: Growth patterns for females under laboratory conditions (n = 203)

Date	Hunte			Canal			Ditch		
Start: 16.4.97	Grown	Not grown	Dead	Grown	Not grown	Dead	Grown	Not grown	Dead
-> 9.7.	20	18	2	9	21	3	13	3	2
-> 16.9.	11	25	4	8	19	5	4	12	–
-> 16.12.	1	33	6	2	20	4	–	16	3
-> 11.4.	–	28	3	–	18	4	–	13	4
-> Death	7	18	25	3	11	14	1	8	9
Sum:	**25**	**15**	**40**	**13**	**17**	**30**	**14**	**2**	**18**

Date	Small Pond			Pond			Leine		
Start: 26.4.97	Grown	Not grown	Dead	Grown	Not grown	Dead	Grown	Not grown	Dead
-> 7.7	9	22	3	21	10	2	8	42	9
-> 15.9.	2	25	4	7	23	4	4	37	10
-> 16.12.	1	23	2	1	26	5	–	31	6
-> 11.4.	1	22	2	–	22	4	–	25	10
-> Death	2	19	21	5	13	18	5	10	15
Sum:	**12**	**20**	**32**	**22**	**11**	**33**	**11**	**39**	**50**

Tab. 44: Shell height of *B. tentaculata* females at start of experiment and at their deaths (n = 203)

	Start (April 1997)			Death		
FEMALES	Ø	min	max	Ø	min	max
Hunte (n = 40)	6,2	3,3	9,2	7,7	6,0	9,3
Canal (n = 30)	7,7	4,7	9,0	8,4	7,1	10,0
Ditch (n = 18)	8,1	4,7	10,1	9,6	8,7	10,6
Small Pond (n =32)	8,9	6,3	10,7	9,2	7,7	10,7
Pond (n = 33)	6,6	3,5	10,1	8,5	6,4	10,4
Leine (n = 50)	7,4	4,6	9,0	7,7	5,0	9,1

7.1.3. Growth of *B. leachii* females under field conditions

The females of this species exhibited a different growth pattern. They started their growth earlier in spring than females of *B. tentaculata* and curbed their growth completely during the reproductive period (Tab. 41). For the females surviving the summer, there was a second growth period after they stopped to reproduce.

In general, there were significantly more growing *B. leachii* females compared to *B. tentaculata* (Fisher's Exact Test, P < ,0001). With one exception, all females that grew also reproduced (Tab. 40) and this one female was severely parasitized. This is significantly different from *B. tentaculata*, too (Fisher's Exact Test, P < ,0001).

7.2. Males

7.2.1. Growth of male *B. tentaculata* and *B. leachii* under field conditions

In the Small Pond only 11% of the observed males grew whereas 42% of the Pond and 38% of the Leine male population grew. The difference between habitats was significant (Contingency Table, Chi Square P = ,0004). Differences between years can be pronounced as is seen for the Leine population (Tab. 45).

Tab. 45: Number of males with a given trait as fraction of males that could show that trait

Origin	Growing males	Living at overwintering	Living at next years reproductive period
Small Pond 1998	6/30	3/30	2/3
last years in 1999	0/2	2/2	2/2
Small Pond 1999	1/30	16/30	12/16
Pond 1998	11/30	1/30	1/1
Pond 1999	14/30	2/30	
Leine 1998	3/30	1/30	1/1
Leine 1999	18/26	22/26	
B. leachii 1998	16/21	9/27	6/9
last years in 1999	0/6	0/6	-
B. leachii 1999	2/21	1/25	

Origin	Growing males	Living at overwintering	Living at next years reproductive period
Small Pond	7/62	21/62	16/21
Pond	25/60	3/60	1/1
Leine	21/56	23/56	
B. leachii	18/48	10/52	6/9

The overall growth pattern of males was mostly similar to that of females in that most growth took place during spring and summer (Tab. 46).

When comparing mean shell height at start and at death of males, it is apparent that there was almost no increase in the Small Pond in both years (Tab. 47). For the Pond and the Leine, differences between years are obvious (there is a strong temporal component involved). During 1998 there was nearly no growth increment whereas in 1999 males from both populations showed rapid growth. The latter year females also reached shell heights well above average values in both populations (Tab. 41).

Tab. 46: Growth patterns of males for all years and populations

Date	**Small Pond 1998**			**Small Pond 1999**			**Pond 1998**			**Pond 1999**		
Start	Grown	Not grown	Dead	Grown	Not grown	Dead	Grown	Not grown	Dead	Grown	Not grown	Dead
->May	3	38	5	2	30	2	9	20	24	12	18	9
->June	6	30	15	1	29	2	2	3	3	7	14	19
->July	4	17	8	–	28	1	–	2	1	1	1	–
->Aug.	2	11	8	–	27	6	–	1	–	–	2	–
->Sept.	–	5	1	–	21	1	–	1	–	–	2	–
->Oct.	–	4	–	–	20	1	–	1	–	–	2	–
->Mar.	–	4	–	1	18	4	–	1	–	–	2	–
Sum:	**8**	**33**	**37**	**3**	**29**	**17**	**10**	**19**	**28**	**14**	**16**	**28**

Date	**Leine 1998**			**Leine 1999**			***B. leachii* 1998**			***B. leachii* 1999**		
Start	Grown	Not grown	Dead	Grown	Not grown	Dead	Grown	Not grown	Dead	Grown	Not grown	Dead
->May	–	29	12	–	25	–	10	10	6	1	26	4
->June	3	14	8	11	14	–	8	6	–	–	23	22
->July	1	8	6	13	12	1	1	13	4	–	1	–
->Aug.	–	3	2	1	23	–	2	8	–	–	1	–
->Sept.	–	1	–	–	24	1	8	2	1	1	–	–
->Oct.	–	1	–	–	23	–	–	9	–			
->Mar.	–	1	–				–	9	5			
Sum:	**3**	**26**	**28**	**18**	**7**	**2**	**16**	**4**	**16**	**2**	**25**	**26**

Tab. 47: Shell height of males at start of experiment and at their deaths

	Start			Death		
MALES	Ø	min	max	Ø	min	max
Small Pond 98 (30)	10,0	8,8	11,3	10,1	8,8	11,4
Small Pond 99 (30)	10,3	8,6	11,6	10,3	8,9	11,6
Pond 98 (n = 30)	7,8	6,4	9,7	8,2	6,4	10,0
Pond 99 (n = 30)	8,8	6,4	10,3	9,7	8,1	11,5
Leine 98 (n = 30)	8,0	6,9	10,2	8,2	7,0	10,2
Leine 99 (n = 30)	7,8	6,6	8,8	9,2	7,6	10,3
B. leachii (n = 27)	3,9	3,4	4,7	4,7	3,5	5,8
B. leachii (n = 28)	4,6	3,7	5,7	4,8	3,8	5,8

7.2.2. Growth of male *B. tentaculata* under laboratory conditions

Growth patterns of males were more homogenous than those of females. Males from most habitats did not grow until death (108 males out of 125) with exception of Hunte males were 13 out of 30 grew (Tab. 48). The Hunte population is also the only one where an increase in mean shell height between the start and the death was observed (Tab. 49). No contingency table could be calculated for differences between male groups because the expected value for several cells lay below the required minimum value of 5.

The result seems to be mostly a consequence of the starting point of laboratory culture and hence of limited scientific value. Males were sampled in autumn, and, as was seen for females, almost all growth occurs during spring and summer within the first year of an individual's life. Seen in retrospect, only limited growth could be expected therefore. The few growing males grew almost all in the spring and summer of 1998 (Tab. 48). This is in good agreement with the growth pattern observed for females.

Tab. 48: Growth patterns for males in laboratory culture (n = 125)

Date	**Hunte**			**Canal**			**Ditch**		
Start: 3.10.97	Grown	Not grown	Dead	Grown	Not grown	Dead	Grown	Not grown	Dead
-> 16.12.	3	27	8	2	19	5	1	25	2
-> 11.4.	7	15	3	1	15	4	–	24	7
-> Death	7	12	19	1	11	12	2	15	17
Sum:	**13**	**17**	**30**	**3**	**18**	**21**	**3**	**23**	**26**

Date	**Small Pond**			**Pond**			**Leine**		
Start: 18.9.97	Grown	Not grown	Dead	Grown	Not grown	Dead	Grown	Not grown	Dead
-> 16.12.	–	24	2	–	26	2	–	28	1
-> 11.4.	–	22	4	–	24	9	–	27	3
-> Death	5	13	18	2	13	15	4	20	24
Sum:	**5**	**19**	**24**	**2**	**24**	**26**	**4**	**24**	**28**

Tab. 49: Shell height of males at start of experiment and at their deaths in laboratory culture (n = 125)

	Start (September/October 1997)			Death		
MALES	Ø	min	max	Ø	min	max
Hunte (n = 30)	5,3	4,0	7,1	6,2	4,1	8,9
Canal (n = 21)	8,1	7,1	9,4	8,2	7,2	9,5
Ditch (n = 26)	8,0	6,1	9,6	8,1	6,1	9,7
Sm. Pond (n =24)	9,9	8,0	11,6	9,9	8,2	11,6
Pond (n = 26)	8,5	7,6	9,3	8,5	7,7	9,3
Leine (n = 28)	7,0	5,7	8,0	7,0	5,7	8,2

7.3. Growth differences between sexes

B. tentaculata

For the Small Pond and the Pond populations there were no significant differences in regard to growth regime between males and females (Fisher's Exact Test, P = ,19 and P = ,16; respectively). In the Leine more males grew than females (Fisher's Exact Test, P = ,0210). This difference is due to an unusual high number of growing males in 1999 (Tabs. 41 and 46).

B. leachii

More females grew than males (Fisher's Exact Test, P = ,0016). This is in accordance with the pronounced sexual dimorphism in this species (Tab. 4).

7.4. Shell growth marks

Of the 46 juvenile snails without growth marks sampled in October 1997, 28 snails > 5 mm (11 females, 17 males) could be recovered after 20 weeks at constant room temperature. Out of these, the shells of 15 snails showed 1, the shells of 5 snails 2 and the shells of 8 snails no growth marks. Therefore growth marks do not seem to be reliable markers for age determination in *B. tentaculata*.

8. MORTALITY

8.1. Mortality pattern of females under field condition

8.1.1. Habitats

Small Pond

The survival of females was high throughout the reproductive season in 1997 but numbers dropped at its end in August (Fig. 40a). More than half of the females lived at the onset of overwintering but a substantial fraction died during winter. 20% of the females lived for a second reproductive season in 1998 but were all dead towards its end (Tab. 26).

The curve for 1998 is missing because most of the females died when their containment dropped accidentally in the anaerobic zone at the end of the reproductive season.

In 1999 survival was good during spring but the numbers started declining steadily from June onwards. 40% of the females lived in October and nearly all overwintered successfully.

Pond

The survival curves are characterised by the sudden death of all females in early summer (Tab. 26; Fig. 40b). This die-off was caused by an aquatic fungus, supposedly a member of the Saprolegniales. The hyphae were already protruding out of still living animals, showing that the fungus was a real pathogen and not just infesting dead snails. The sectioning of dead snails under a stereomicroscope revealed that they were mostly healthy and not particularly weakened individuals. Females were not over proportionally often parasitized. Most females carried a yolk supply, showing that they died well before the end of reproductive activities. In no year any females were alive after July.

The only major difference between years was the timing of the die-off. Numbers declined later in 1997 than the other years whereas the die-off started already in April in 1998 leading to an exceptionally low reproductive success. All females died within 1 month in 1999, bringing reproduction to an end within May. As a consequence, no females lived through the entire reproductive season.

Leine

In 1997 and 1998 numbers of females declined profoundly after a short delay in early spring (Fig. 40c). As a consequence, 3 out of 4 females were dead at the end of August in 1997 and virtually all in August 1998. In 1997, every fifth female survived for another breeding season in 1998 (Tab. 26).

The survival curve for 1999 is completely different. Numbers were stable throughout spring, followed by a very moderate decline during summer and autumn. 80% of the females were alive at the onset of overwintering.

B. leachii

Survival curves were different in 1998 and 1999 (Fig. 41). 1998 approximately 20% of the females died per month from April onwards till August. Numbers were then stable during autumn and winter. 15% of the females survived to a second reproductive period but all were dead by July (Tab. 26).

In 1999 virtually no females died in spring but then 90% died within 4 weeks leading to an unusual short reproductive period.

8.1.2. Years

1997

Pond and Leine snails showed a more or less rapid decline during late spring/early summer with no or few females alive after July (Fig. 42a). In contrast, survival was high in the Small Pond with more than half of the females alive at the end of the season.

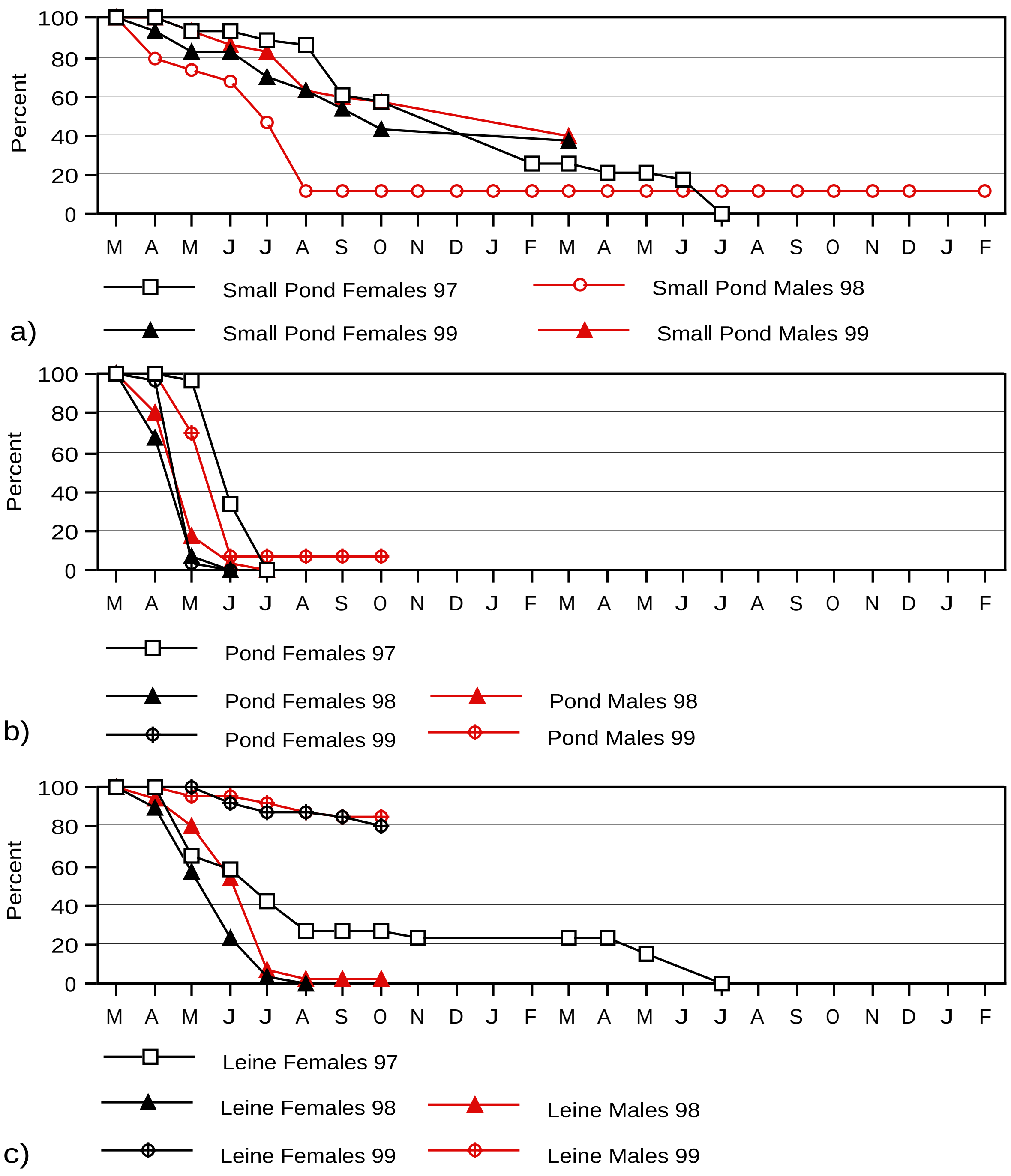


Fig. 40: Mortality scheme of *B. tentaculata* in Hannover under field conditions (n = 420)

1998

Pond and Leine snails again showed a rapid decline in numbers which was somewhat faster in the Pond (Fig. 42b). Here all females were dead by June whereas it took 2 months longer in the Leine until all females were dead. *B. leachii* numbers declined steadily but less rapid and nearly 20% of the females survived till winter.

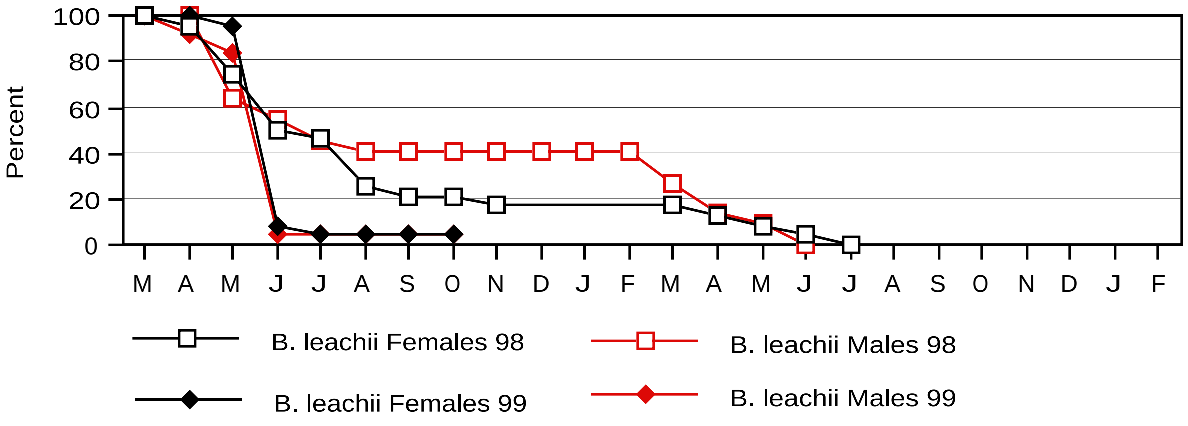


Fig. 41: Mortality scheme of *B. leachii* under field conditions (n = 102)

1999

This year both *B. tentaculata* and *B. leachii* numbers collapsed in the Pond during May and June (Fig. 42c). Survival was unusual high in the Leine and also good for Small Pond females.

8.2. Mortality pattern for female *B. tentaculata* in laboratory culture

The survival curves of all 6 populations were congruent with a minor deviation for the Leine. Here the mortality in July was above-average (Fig. 43). The mortality was moderate throughout the season and was also low during winter.

Females from the populations in Hannover lived significantly longer in the laboratory than under field conditions (ANOVA, P < ,0001). More than half of all females survived their first breeding season and from 30% to 60% took part in a second one. The number of females surviving to a second reproductive season was highest for the Hunte and the Small Pond and lowest for the Ditch and the Leine. Nearly all females died after their second reproductive season. No fungal infections as observed each year in the Pond were observed under laboratory conditions.

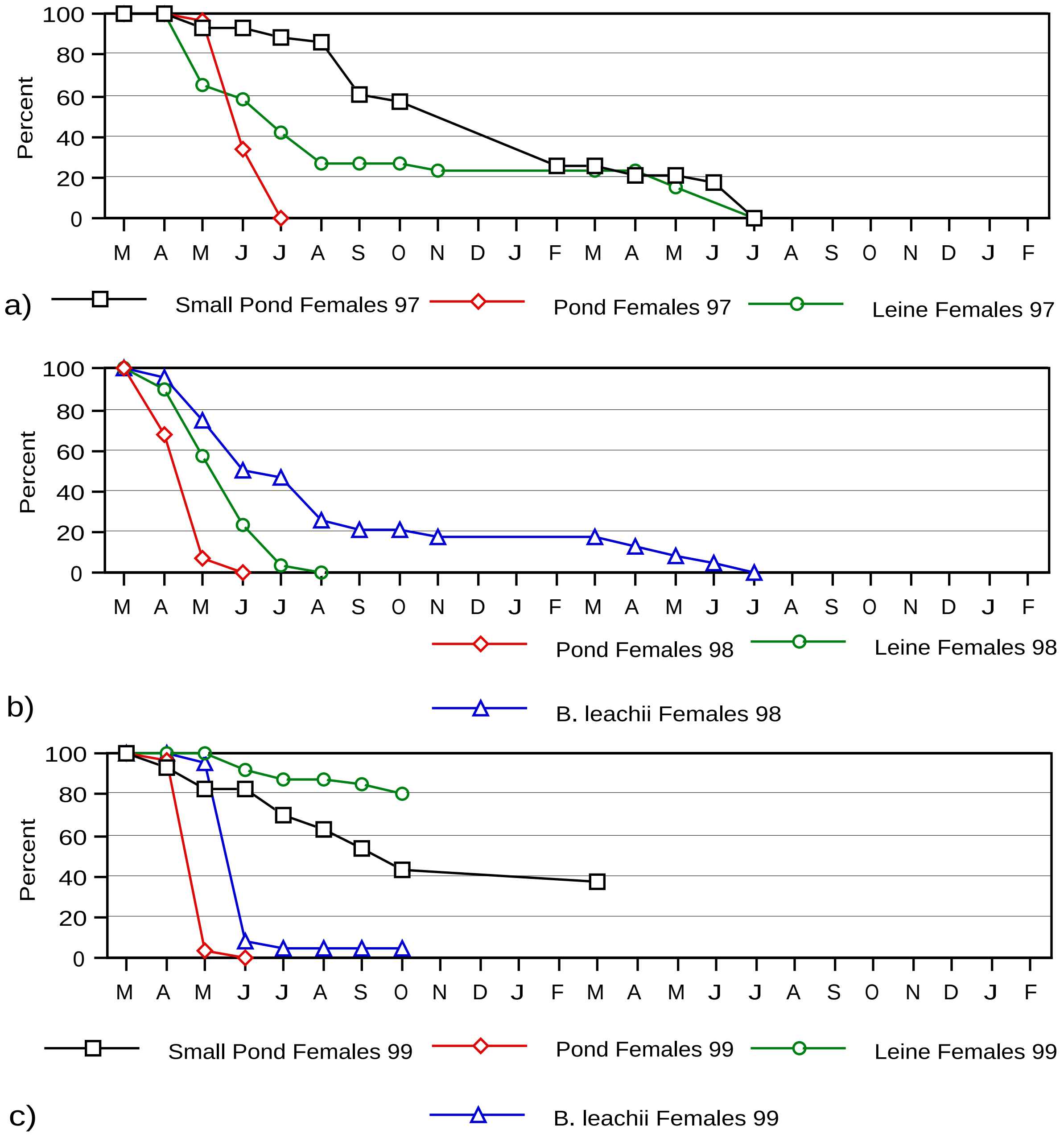


Fig. 42: A comparison of yearly female mortality patterns under field conditions for both species (n = 295)

8.3. Mortality pattern of males under field conditions

8.3.1. Habitats

Small Pond

In 1998 20% of all males died within the first 4 weeks (Fig. 40a). This rapid decline then stopped until June but continued during July and August. The few males left in autumn lived until the end of the experiment in December 1999.

In 1999 there was a much more slow decline in the number of surviving males. Within the first 4 months 20% died and during August another 20%. Numbers were stable then and at the onset of overwintering more than half of all males were living (Tab. 45).

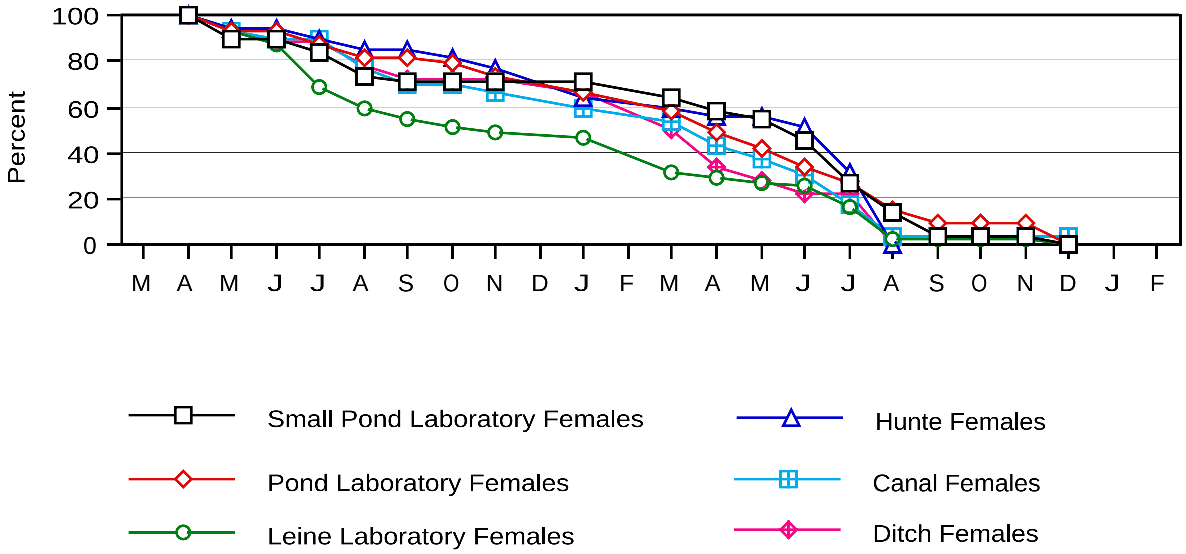


Fig. 43: Mortality scheme for *B. tentaculata* females in laboratory culture

Pond

In both years there was a rapid decline after fungal infections started in spring/early summer (Tab. 45; Fig. 40b). Male mortality matched female mortality patterns. All males were dead by July 1998. The following year the impact of the die-off was as hard during May and June but a small fraction of males survived until the end of the experiment.

Leine

In 1998 the number of males declined fast and in July almost all snails were dead (Fig. 40c). No males were alive at the end of the season.

In 1999 the mortality pattern was totally different. There was a steady but very moderate decline from April onwards. At the end of October more than 80% of all males were alive (Tab. 45).

B. leachii

The curves were different for both years (Fig. 41). After a rapid decline in April 1998 the number of dead snails lessened and no males died from August onwards until next year's spring. The remaining males died during the summer of 1999.

In contrast, there was at first a modest decline in the spring of 1999 followed by a collapse of the population during May. Almost all males were dead by June. The few surviving males stayed alive until the onset of overwintering (Tab. 45).

8.3.2. Years

1998

Differences between habitats were pronounced this year (Fig. 44a). The course of events ranged from a rapid spring decline of *B. tentaculata* males from the Pond population over a nearly as rapid decline in the Leine during early summer to a more steady die-off in the Small Pond.

B. leachii numbers were stable from August onwards and 40% of the males survived until winter.

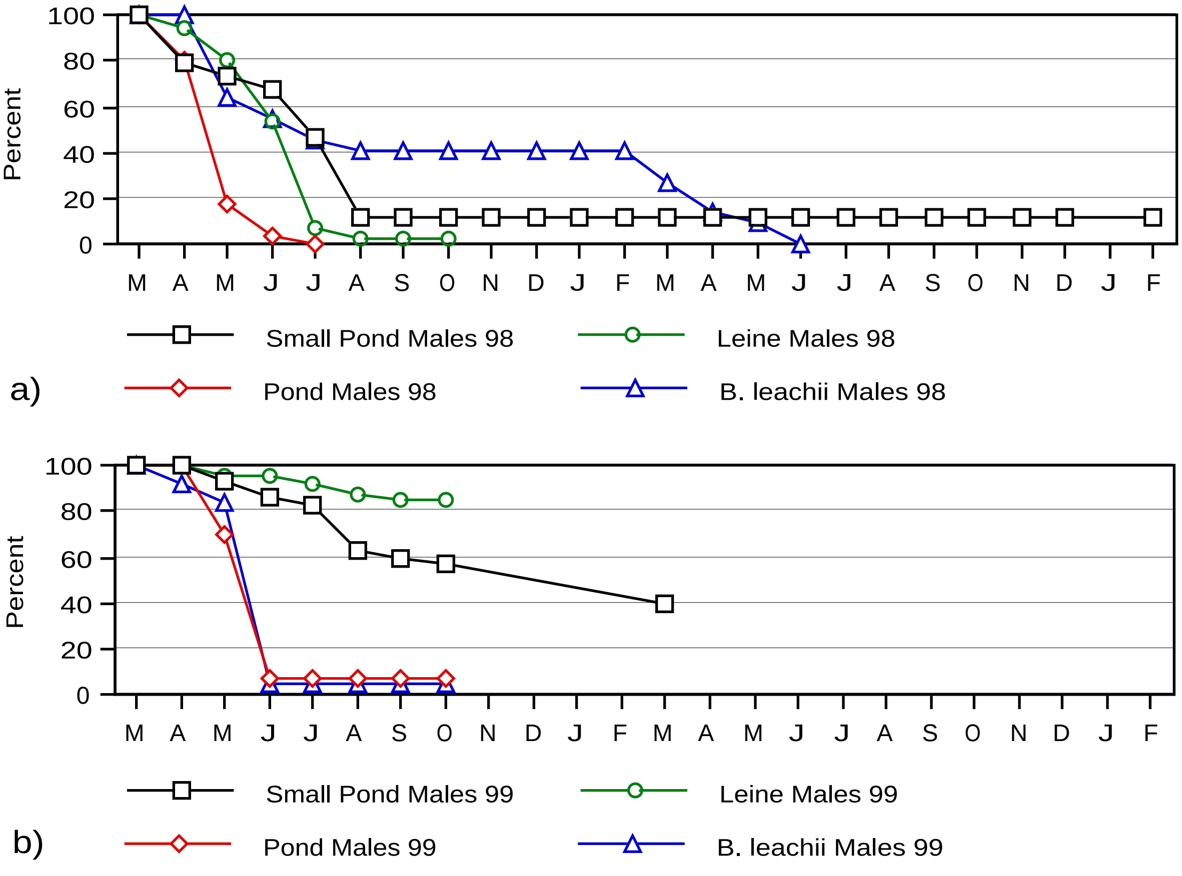


Fig. 44: Mortality pattern of males under field conditions (n = 225)

1999

This year the graphs of both Pond populations were congruent, almost all males being dead by June (Fig. 44b). Survival of the other *B. tentaculata* populations was high throughout most of the year. Male numbers only went down in July in the Small Pond. 40% of the males survived the winter in the Small Pond.

8.4. Male mortality under laboratory conditions

Due to differing sampling dates and the marked seasonal influence on survival, male laboratory data were not analysed.

8.5. Differences in the mortality patterns between sexes

Survival patterns of males and females were mostly congruent for all populations in the field (Figs. 40 and 41). However, there was a tendency for *B. tentaculata* females to die a bit earlier than males during the reproductive season or towards its end (e.g. Pond 1999, Leine 1998). This was also the case for *B. leachii* in 1998 when the graphs were congruent until July, but then 20% of females died whereas male numbers remained stable (Fig. 41).

9. A SIMULATION OF SEVERE DRY PERIODS

After the aquaria had dried up for 4 weeks, living snails were found in each one (Tab. 50). Most snails were active again within 24 hours after adding fresh water, some even within a few hours.

The loss of snails was very small to moderate (Hunte; *B. leachii*) with exception of one aquarium containing snails from the Leine. Since the experimental conditions did not allow to attribute a given death to the dry period because some deaths will have occured in the 4 months it took the aquaria to dry up, the number of living snails at the end of the experiment is not discussed (exact numbers of snails prior to drying up could not be determined, see Material and Methods).

The main aim of the experiment was to test for tolerance of dry periods. It could be demonstrated that snails, regardless of origin, gender and species, survived severe dry periods. This ability was even distinct in snail populations that never encounter a dry period under normal conditions (like river populations). Furthermore, 6 out of the 14 aquaria contained altogether 37 living juvenile snails of both species. Resistance to dry periods is therefore not an exclusive trait of adults.

For *B. tentaculata,* there were no significant differences between sexes with regard to mortality (Tab. 51: Contingency Table, Fisher's exact P-value = ,28). However, there was a significant difference for *B. leachii* (Tab. 52: Contingency Table, Fisher's exact P-value = ,035). *B. leachii* females showed a higher mortality during the dry period than males

Tab. 50: Number of living snails in the aquaria at the beginning and the end of the experiment (A, B: Ditch; C, D: Canal; E, F: Pond; G, H: Small Pond; I, J: Leine; K, L: Hunte; M, N: *B. leachii*)

	A	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**	**L**	**M**	**N**
Start	11	12	10	10	12	12	10	10	10	9	11	10	28	28
End	11	11	9	7	11	11	8	9	10	1	7	5	17	12

Tab. 51: Number of living and dead *B. tentaculata* at end of experiment

	Females	**Males**
Living	49	51
Dead	17	10

Tab. 52: Number of living and dead *B. leachii* at end of experiment

	Females	**Males**
Living	12	17
Dead	19	8

IV. DISCUSSION

Introductory remarks

The principal concerns of this study are an in-depth description of the life histories of *Bithynia tentaculata* and *Bithynia leachii*, to bring out the differences in the life cycle strategies of both species and to discuss the differences in female life histories between and within populations.

It is self-evident that data could not be collected at all levels and for all processes involved and that the following section sets off from rather firm ground were reasoning is supported by data over areas were this basis is dwindling to fields that are more or less speculative.

Since the interdependence of the patterns and processes involved can not be described conclusively in a simple way, I have decided to present things in a modular manner: First, as a foundation, there will be a rough description of the life cycle of *Bithynia* in Central Europe followed by the main factors and traits shaping the life cycle. In succession, factors and traits are then discussed separately, observed and possible consequences are mentioned and interactions and feed-back mechanisms with other factors are discussed. As a synthesis based on the first section follows a detailed description of the similarities and differences in the life histories of both species and of the observed populations. In conclusion, these findings are then discussed under the focus of molluscan life histories and current thinking in life history theory.

1. A ROUGH DESCRIPTION OF THE LIFE CYCLE OF *BITHYNIA* SP. IN CENTRAL EUROPE

Snails surviving the winter at the bottom of water bodies end their inactivity with rising water temperatures in spring. They reenter the upper, warmer water levels in the following weeks. Shell heigth increases markedly during spring.

The reproductive period starts when water temperatures rise to 12°C or above for some days. This happens mostly during late April or early May. Spawning activities increase rapidly with rising temperatures and continue on a high level during May and June. The spawning can continue with decreasing intensity during July and August.

The mortality of adult snails increases in the course of the reproductive period and decreases in autumn. Juvenile hatching starts in June and has its peak in late June and July. Depending on the length of the reproductive period, newly hatched snails may be present also in autumn. While juveniles grow rapidly during late summer and autumn, adults mostly show no further shell growth after the reproductive period.

With decreasing water temperatures in autumn, the snails leave the upper water levels and move towards the bottom of the water body. The snails withdraw within their shells and close the shell opening with their operculum. They remain inactive approximately from November to March. Snails live for 1 to 3 years under natural conditions.

2. FACTORS AND TRAITS SHAPING THE LIFE HISTORIES OF AQUATIC ORGANISMS

There are several important abiotic factors. In general, there exists no feed-back mechanism from the organism onto this factors. I will mention temperature, oxygen content of water, habitat structure and - size, water level and desiccation, water current/velocity and catastrophic events.

Biotic interactions are typically characterised by their feed-back mechanisms. I will discuss predation, parasitation, competition. Food abundance, foraging and co-occurring molluscan species are shortly mentioned.

Discussed traits of the life cycle include growth, reproduction, paternal effects, population structure and sex ratio, mortality and related topics like the distribution of snails in space and time.

2.1. ABIOTIC FACTORS

Temperature

Traditionally, freshwater snail distributions have been explained by physicochemical factors like calcium concentration of waters, but this concept was challenged recently (Lodge et al. 1987) after several studies failed to find meaningful correlations between water chemistry and snail abundance (e.g. Dussart 1979). Former authors strongly emphasised the importance of abiotic factors as temperature and oxygen in combination with biotic ones in explaning snail distributions. Temperature is thought to be the single most influential factor in ecology (Begon et al. 1998). Most biological processes show a more or less linear relationship to temperature throughout a favourable temperature range (Laudien 1973).

Winter temperatures determine the length of inactivity for both *Bithynia* species and thereby strongly influence mortality during overwintering. A sometimes apparent shift in the size frequency distributions of populations towards larger shells between the onset and the end of overwintering was several times attributed to slow shell growth during winter (Lilly 1953; Pinel-Alloul and Magnin 1971). This shift in size frequencies is more reasonably explained by higher winter mortality of small snails since none of the individually caged snails showed any growth during winter. Thereby low temperatures in winter cause size-specific mortality. Winter mortality was also higher for smaller individuals in helicid land snails (Baur 1990).

Rising water temperatures end the inactivity of snails and lead to a shift in the habitat used since snails leave the bottom regions and enter the upper, warmer water levels. In general, rising temperatures increase activity in *Bithynia* and other freshwater snails (e.g. Costil and Bailey 1998; MacRae and Leptizki 1994). The filtration rate of *B. tentaculata* increases with increasing temperatures (Brendelberger and Jürgens 1993).

Rising temperatures exceeding a certain threshold have been confirmed as the major trigger for reproduction in diverse molluscs (e.g. Aldridge 1983; Cáceres-Martínez and Figueras 1998, Costil and Daguzan 1995b; Fretter 1984; Russel-Hunter 1964), but in *Littorina brevicula* spawning is triggered by decreasing temperatures in winter (Son and Hong 1998). In aquatic environments, temperature seems more reliable than photo period whereas for insects photo period is dominant over temperature in timing life history events (Albrecht et al. 1999; Gotthard et al. 1999).

Temperatures of approximately 12°C trigger the start of spawning in *B. tentaculata*. Temperature (and not day-length) is the single cause to trigger spawning since a population in an underground water supply of a large chemical plant started to reproduce when water temperatures rose above 12°C, even in complete absence of light (Richter 1996). The temperature effects were also clearly more important for reproductive stimulation than photo period in *Helix aspersa* (Jess and Marks 1998).

The length of embryonic development is dependent on temperature in *B. tentaculata*. Time between egg laying and hatching drops from 35-45 days in April and May over 20-30 days in June to 10-15 days in July and August. Hatching success was not influenced by different temperatures (Richter and Wächtler 1999).
In the St. Lawrence River, Canada, varying temperatures lead to a change between a long and a short developmental cycle in *B. tentaculata* (Vincent and Harvey 1985).

Temperature was only measured on a regular basis in the 3 habitats in Hannover. There were strong fluctuations between summer maxima and winter minima, but temperatures never exceeded 24°C and seldom dropped below 4°C. The coldest temperatures (1°C) were encountered in the Leine whereas the Pond had the highest temperatures during summer. The temperature profiles were not significantly different between habitats and the temperature regime is fairly homogenous for all populations.

Oxygen

The oxygen demands of organisms generally increase with rising temperatures. This is especially important in aquatic environments since the oxygen tension in water decreases with increasing temperature (Wetzel 1983). The availability of oxygen determines the usable habitat size for prosobranch snails. Since they respire by means of their ctenidium (and to some degree via their epithelia), they depend on sufficiently aerated water. Under low oxygen levels or anaerobic conditions pulmonate snails have a clear advantage over prosobranchs since they can respire atmospheric air via their lung cavity (e.g. Aldridge 1983; Boycott 1936). Oxygen had a major effect on *Bithynia* mortality as was seen by the deaths of caged snails due to hypoxic conditions in the Ditch, Canal and Small Pond.

Sufficient dissolved oxygen is necessary for embryonic development. Lack of oxygen leads to a developmental arrest and lengthens time till hatching. Longer periods of lacking oxygen increase egg mortality of aquatic snails dramatically (Lee and Strathmann 1998). Older embryonic stages are more sensitive to hypoxygenation than younger ones. Death of *Bithynia* spawns occurred as a consequence of oxygen depletion in all habitats. This leads to a strong selection pressure on females to find appropriate places for spawn deposition.

The time needed for oxygen to diffuse through egg capsules constrains their maximum size and influences the spacing of eggs in capsules. Increasing capsule size leads to an increase in the percentage of resources per egg that has to be invested in the costly matrix of the capsule and limits thereby capsule size (Lee and Strathmann 1998).

Habitat structure and -size

Parasitation is strongly influenced by size and structure of aquatic habitats. Both determine the spectrum of definite trematode hosts shedding eggs into the water body. Definite hosts that discriminate strongly by the size and structure of water bodies include mammals like muskrat, beaver and smaller rodents, birds, amphibians and fish.
It is known that both prevalence of parasites and parasitic load can vary strongly on a small scale within habitats (Coy et al. 1982; Fernandez and Esch 1991b). For *B. tentaculata*, infection levels differed approximately 1000 times between 3 sites within 20 m (Lepitzki and Scott 1994). Infection levels differed with the type of vegetation for *Lymnaea elodes* (Sorensen and Minchella 1998).

Habitat structure has an influence on the amount of sites suitable for spawn deposition, probability of predator contact and overwintering possibilities. Due to their size difference, *B. tentaculata* and *B. leachii* differ in their ability of habitat use. The smaller *B. leachii* can use a higher percentage of the total surface area. As was demonstrated in this study, *Lymnea stagnalis* has a severe negative influence on *Bithynia* spawns and juveniles. Habitat structure mediates the outcome of this interaction by excluding the large-bodied *Lymnea* from fine–scaled parts of the habitat that are usable by the smaller *Bithynia*. The same holds true for predators as fish and crayfish that can be limited by their size in entering hollow spaces and crevices under stones and rocks. The effect of predation on freshwater snails is known to be dependent on the type of habitat (Lodge et al. 1987).

Habitat size further influences the degree of mobility that is necessary for *Bithynia,* because the snails use different parts of the habitat for feeding, mating, egg laying and overwintering.

Water levels and habitat desiccation

Varying water levels lead to changes in the usable habitat size. They force strictly aquatic organisms to migrate with their fluctuations. Falling water levels pose a severe threat to immobile life cycle stages as spawns. *Bithynia* spawns can withstand desiccation only for very short periods and are irreversibly damaged after few hours of exposition to air.

Periods of draught can lead to a complete desiccation of a habitat, this being the most extreme form of changing water levels. Complete desiccation forms a strong selection pressure on aquatic organisms to develop resting stages capable of surviving dry periods (Williams 1987). Desiccation increased mortality and decreased fecundity in *Biomphalaria glabrata* (Vianey-Liaud 1996). *Biomphalaria* snails were able to survive desiccation for up to 6 weeks and resumed egg-laying shortly after desiccation ended (Simões and Lopes 1996).

Both *Bithynia* species can withstand desiccation for more than a month in dry mud. Even river populations of *B. tentaculata* that never experience desiccation were able to survive in numbers equal to the only ephemeral habitat, the Ditch. *B. tentaculata* is known to occur in temporal ponds in Germany and Northern India (Heitkamp 1982; Mattison et al. 1995).

Water currents and water velocity

Habitats with standing and running waters show some fundamental differences. In general, running waters are better aerated, but the aggregation of nutrients is impeded or prevented that is typical for standing waters. Most running waters experience periods of high waters and flood that can differ in predictability and affect habitat stability negatively (Brehm and Meijering 1990; Lampert and Sommer 1993). Both the Leine and the Hunte experienced high waters and floods during the observation period. During flood, all three Dümmer habitats were connected in spring 1998. Flooding may thereby facilitate the transport of individuals between populations that are separated otherwise.

Both water currents and -velocity influence the usable habitat size. Increasing water velocity increases energetic demands of surface adherence for snails and increases the risk of drifting. Above a threshold, snails lose surface contact and are subject to drift. Due to this, snail distribution is patchy in rivers. Most parts of the river habitats were devoid of *B. tentaculata* whereas areas with reduced water velocity were the most densely populated of all habitat types. Shells of the Leine population were significantly slimmer than those of the other ones. This is likely to be an adaptation to reduce resistance to water currents.
Perturbations of the substrate in running waters select for thicker snail shells that are able to withstand the abrasive and crushing action of pebbles and stones. This is also known for habitats with different degrees of wave exposition.

Because of their small size even in only moderately flowing waters trematode eggs and miracidia are subject to drift. This reduces the risk of becoming parasitized for snails in streams and rivers and hot spots of trematode infections (e.g. muskrat dens, breeding colonies of birds) are of a more limited size compared to standing waters. By this, infection levels fluctuate on a very small scale in running waters (Lepitzki and Scott 1994).

Disturbance

Disturbance plays a major role in structuring biocoenoses (Sousa 1984). Examples relevant for aquatic molluscs include periods of severe draught or flood, prolonged frost and ice cover in winter, reductions in macrophyte abundance, food shortage and pollution (Lodge et al. 1987). Pollution has been recognised to change the life histories of gastropods (e.g. Liu and Morton 1998). Detrimental effects of fungicides and other chemical substances on *B. tentaculata* are documented (van Wijngarden et al. 1998).

Disturbance played a major role in both rivers where every year there was at least one flood. The occurrence of disturbance is therefore highly predictable in the rivers, but timing and duration of these events is highly unpredictable. The Ditch did not dry out in the observation period, but water levels fluctuated strongly with temperature and the intensity of precipitation. In addition, there were long periods with anoxic conditions during summer. In the other habitats, water levels were fairly stable (in spring 1998, the high water at the Dümmer flooded also the Ditch and the Canal) and winters were generally mild.

2.2. BIOTIC INTERACTIONS

Predation

There is a vast amount of literature concerned with predation and predator-prey interactions in ecology (e.g. Begon et al. 1998). Predation risk is known to change almost every single life history trait. Most features of the sometimes bizarre shaped and commonly thick-walled shells of marine prosobranchs are considered as antipredator structures as are the thick shells of freshwater prosobranchs which mostly lack sculpturing (Vermeij and Covich 1978). These authors attribute the thin shells of pulmonates and the thicker shells of prosobranchs to differences in longevity and general life history strategy.

Constitution of shells strongly influences the outcome of predation pressure by crayfish. Two crayfish species fed predominantly on *Lymnaea stagnalis* and *Lymnaea* (*Radix*) *peregra* when *B. tentaculata* was also present (Nyström et al. 1999). Because a decrease in *L. stagnalis* abundance lessens the predation of *Bithynia* spawns, crayfish may even have a positive influence on *B. tentaculata* abundance and may alter the outcome of competition between both species. Molluscivorous fish can also change the species composition from thin-shelled *L. stagnalis* to thick-shelled *B. tentaculata* (Brönmark and Weisner 1996).

In freshwater systems, predator presence has been observed to change age and size at maturity of snails via changes in their energy allocation (Crowl and Covich 1990; Lam 1994). Snail behaviour also changes with presence or absence of predators. Snails show escape reactions in the presence of predatory crayfish and leeches (Alexander and Covich 1991; Crowl and Covich 1990). Snails can even distinguish between the presence or absence of different types of predators and behave accordingly, in this case between fish and crayfish (Turner et al. 1999).

In this study, the effect of predation was only circumstantially investigated. Habitats differed in predator presence. Predatory fish were absent from the Ditch and the Small Pond. Crayfish and fish were present in the Leine and the Pond and may have been a cause for low pulmonate numbers. Dabbling ducks were common on the Leine, present in small numbers in the other habitats but never observed on the Ditch. From the shore of the smaller water bodies thrushes fed on pulmonates that often forage attached to the water surface. Invertebrate predators were common in all habitats.

In general, prosobranchs can escape shell-invading predators like leeches better than pulmonates. I found commonly small hemolymphe-sucking *Glossiphonia* sp. inside *Bithynia* shells, but due to their small size they are rather parasites than predators. Nothing is known about their possible role as vectors for snail diseases. Cerfolli and Rossi (1995) found that the survival of *B. tentaculata* under predation pressure by leeches increased when a second predator level (represented by fish) was introduced in experiments.

The very small oligochaet *Chaetogaster limnaei* consumed not only trematode miracidia and cercaria, but also caused erosion of the mantle and gill epithelia in *Dreissena* sp. (Conn et al. 1996). I found *Chaetogaster* sp. regularly when crushing snails to look for trematode stages, most often in snails from the Canal and the Ditch. Ditch snails could harbour up to 30 specimen within their shells. I can not say whether their presence was detrimental or beneficial to snails, but it is an interesting coincidence that the lowest infection level in standing waters was correlated with the highest prevalence of *Chaetogaster* sp.. Cercaria were seen in their stomachs on several occasions.

On the level of the individual, growth can be of special significance. In some cases, when predators forage preferably on juvenile and small individuals, rapid growth facilitated by delayed sexual maturity helps to escape predation pressure in pulmonates (Crowl and Covich 1990; Lam 1994). Mean shell height of *B. tentaculata* was larger when predatory crayfish were present in experiments in plastic pools. This was most likely due to size-selective predation of crayfish and not to a growth response by *Bithynia* (Nyström et al. 1999).

Increased mobility due to mate searching and active site selection for mating, reproduction and egg laying increases the predation risk. Foraging possibilities also influence mobility and thereby predation risk. In *Bithynia*, individuals with a sufficient supply of algae and detritus for filter feeding should in general be in lower danger by predators than more mobile grazing snails. Apart from the energetic plus of filter feeding over grazing this would be a second advantage.

Parasitation

-Parasitation

Parasitates have only more recently become a focus of interest in life history and ecological studies (Zander 1998). For several decades, competition and predation were predominant and parasites were virtually absent from the ecological agenda (Lauckner 1986). Several scientists who claimed the general importance of parasites for ecological thinking were concerned with marine and freshwater molluscs (Brown 1991; Lauckner 1984; Lodge et al. 1987). Today, parasites are well integrated in modern ecological thinking. Their role in shaping the life histories of their hosts, host-parasite coevolution, the invention and maintenance of sex in natural populations and their costs and possible benefits to their hosts are investigated (e.g. Begon et al. 1998; Dobson et al. 1992; Huxham et al. 1993; Michalakis et al. 1992; Toft and Karter 1990).

The success of invasive species can be partially attributed to their incompatibility to local parasites as was demonstrated in invading *Mytilus galloprovencalis* in South Africa (Calvo–Ugarteburu and McQuaid 1998).
Bithynia is a host for a broad variety of trematode species (e.g. Mattison et al. 1995; Pike 1967). In *Bithynia* as in other molluscs, infections with larval stages of trematodes most often lead to irreversible castration and reproductive death of infected individuals by direct destruction of the gonad (via ingestion by redia or pressure caused by larval stages) and/or gonadal atrophy due to energetic demands of the parasites (e.g. Goater et al. 1989; Gorbushin and Levakin 1999; Lauckner 1986; Mouritsen and Jensen 1994; Taskinen et al. 1997).

After early researchers thought invasion of the gonad and castration to be a rare event (review in Wright 1966), the castration of the host has long been seen as a strategy of the parasite (review in Baudoin 1975). The complete castration of hosts is mostly achieved within few weeks post infectionem. The reproductive investments of the host can be altered by chemical interference by the parasite within days (e.g. Hodasi 1972; Sorensen and Minchella 1998; Wilson and Denison 1980). Due to parasitic castration, several potentially iteroparous molluscan species were found to be effectively semelparous under field conditions (Holopainen et al. 1997). Among other effects, the preference of the gonad over other host organs enhances host and therefore parasite survival. The longer the potential life-span of the host, the more often the gonad was the site mainly infected (review in Taskinen et al. 1997).

The histological and pathological consequences of infections in *Bithynia* were investigated in several studies (Adam et al. 1995; Neuhaus 1949; Reader 1971a,b, 1976). When snails are crushed under a dissection microscope, it can be seen that in the terminal stages of an infection almost the whole body consists of parasitic stages. The only exceptions are the foot region and the head. In heavy infected populations, a great deal of the biomass attributed to the host should therefore be attributed to the biomass of the parasite. It is clear that trematode infections thereby can change trophic interactions in ecosystems dramatically (Lauckner 1984, 1986).

The prevalence of infections fluctuated strongly with time in the 6 habitats. Prevalence showed also significant differences between the populations with the Small Pond being the most affected habitat of all. Here nearly 4 out of 10 adult snails were parasitised. The infection levels reached their high in October 1998 when three quarters of the adult snails were parasitized. All other habitats showed an overall infection level close to 10% of the adult population. This number becomes more dramatic when it is taken into account that infection levels rised to their high during the reproductive period of *B. tentaculata*. They lay above 20% in July for the Hunte and the Ditch (data for the Canal are missing due to sampling difficulties). The prevalence was near 20% in all 3 years in June and July in the Leine that had otherwise very low infection levels. Data for the Pond are sparse but one third of all snails were parasitized in July 1999.

These results show unequivocally that parasites have a profound effect on the reproductive capacity of *B. tentaculata* individuals and populations. Infection levels for *B. tentaculata* range from 2% from a Spanish population, 10% - 35% in Berlin, Germany, 18% - 37% in Northern India to 57% in Quebec, Canada (Emmel 1942; Mattison et al. 1995; Ménard and Scott 1987; Toledo et al. 1998). According to Mattison et al. (1995); *B. tentaculata* was the heaviest infected snail in their survey in Northern India. Infection levels for *B. leachii* were 1,2% in Brandenburg and 5% - 35% in Berlin and are thought to be generally low (Emmel 1942; Hering-Hagenbeck and Schuster 1996). In sympatric populations of both species, *B. leachii* was less parasitized (Emmel 1942). Ménard and Scott (1987) and also Emmel (1942) found that infection levels fluctuated strongly between seasons for *Bithynia*. A strong seasonality of infections was also found for other snail and bivalve species (e.g. Fernandez and Esch 1991a; Taskinen and Valtonen 1995; Woolhouse 1989).

When it is taken into account that infections persist in snails and that infection levels mostly dropped markedly during autumn, it becomes clear that parasitation has also a major influence on snail mortality and thereby on population structure. Infections seem to negatively influence winter survival of snails since I found that infection levels in spring lay in every case below the pre-winter levels. Reader (1976) also found higher winter mortality in parasitized *B. tentaculata*. This is not astonishing since parasites deplete the energy stores of their hosts. However, Goater et al. (1989) found no effect of parasites on winter survival of *Helisoma anceps* (Pulmonata).

Minchella and Loverde (1981) found that parasites increased mortality in *Biomphalaria glabrata* and Lauckner (1986) found mortality to increase with parasitic load for *Littorina* and *Hydrobia* in the Baltic Sea. Infection decreased survival of desiccation for *Biomphalaria pfeifferi* (Badger and Oyerinde 1996). In general, most studies showed that mortality is increased due to parasitation (e.g. Huxham et al. 1993; Robson and Williams 1971; Sorensen and Minchella 1998; Webster and Woolhouse 1999), but Hodasi (1972) found increased survival of parasitized *Lymnaea truncatula* in mass laboratory culture. Snails can also be killed by cercaria shed by conspecifics that penetrate into the snails to transform into metacercaria (Campbell 1997).

With exception of an incident in the Small Pond, I found no differences in prevalence between genders. In 1998, infection levels of females but not of males increased dramatically during autumn from an already high level in summer. I can offer no explanation why this sexual bias was observed in autumn 1998/spring 1999. Since the Small Pond population failed to reproduce in 1997, these snails were at least born in 1996. The prevalence with females was around 75%, excluding three out of four older females from reproduction. This emphasises my point that parasites can have a marked negative influence on reproductive capacity and may even pose a threat to whole populations under special circumstances.

In a 2 year survey on *B. tentaculata* in Canada, Ménard and Scott (1987) found no sex-bias for metacercarial infection, but other authors found sexually biased infection levels in molluscs. Males were predominantly parasitized in the snail *Cerithidea californica*, whereas females were preferred by parasites in the bivalve *Anodonta piscinalis* (Lafferty 1993b; Taskinen and Valtonen 1995).

The mechanism by which miracidia find snail hosts are a much debated topic in parasitology but are often more or less speculative so far. Under the proposed mechanisms are random movement of miracidia, orientation along gradients into conditions favourable for the hosts and chemical cues from the host (e.g. Campbell 1997; Kalbe et al. 1996). Under the discussed chemical cues are, among others, sexual hormones from snails. This would account for the observation that often only sexually mature hosts are attacked (e.g. Lauckner 1986; Robson and Williams 1971). But it should be mentioned that at least some trematodes infect also premature snails and it is very feasible that different trematode species (or even strains of trematode species) evolved different strategies for host location and, subsequent, infection.

This point is supported by evidence that different trematodes affect growth patterns of the same snail species differently and that different snail species and even different populations of the same snail species react differently on the same trematode (Gorbushin and Levakin 1999; Mouritsen et al. 1999).

It is also possible that the early trematode stages remain cryptic inside immature hosts after infection until their development is triggered by signals of the sexual maturation of their host. Appropriate selection of snail host species by miracidia and cercaria has frequently been demonstrated in the field and the laboratory (e.g. Campbell 1997; Coy et al. 1982).

The increasing infection levels with increasing age that were exhibited by the Small Pond population after reproductive failure in 1997 point in the direction that infections are acquired over time and accumulate in ageing populations of *B. tentaculata*. I found also a constant increase of infections in young snails in the Small Pond in 1999. They set out near zero per cent infections in spring and reached 20% in August.

That infections accumulate with age was earlier demonstrated for marine snails, freshwater bivalves and metacercarial stages in *B. tentaculata* (e.g. Curtis 1996; Holopainen et al. 1997; Lafferty 1993a,b; Lepitzki and Scott 1994; Ménard and Scott 1987; Sousa 1983). However, Mattison et al. (1995) found that infections were more prevalent in smaller size classes of *B. tentaculata* in Northern India. Selection should therefore favour early reproduction under a high risk of parasitation and increasing infection levels with age. This was demonstrated for a marine and a freshwater snail that matured earlier in habitats where trematodes were abundant (Jokela and Lively 1995; Lafferty 1993a).

Another consequence of increasing infections with age should be that there is no positive selection for snail longevity. In this context I find it remarkable that a substantial amount of *Bithynia* females that reached maturity within a year died after their first reproductive period. However, the longest-lived population inhabited the water body (Small Pond) where parasites were most abundant.

It would be very interesting to study the effect of size (which is closely correlated with age in organisms with indeterminate growth) on the probability of becoming infected. Since the body surface increases with size, this should lead to a higher probability both of a chance encounter with parasites as well as being located by a parasite searching along a gradient of a chemical stimulus originating from the host. Larger animals should be stronger transmitters.

Another way of trematode transmission is the direct ingestion of eggs by hosts. Because larger animals are known to consume larger food quantities, this should also lead to a higher infection probability with increasing size. In combination, this could lead to selection against larger size and for smaller size at maturity even if, in general, size and reproductive output show a strong positive correlation. It could also be one cause of determinate growth and/or semelparity at least in species were the biomass of the parasite is of the same magnitude as the biomass of the host. To my knowledge, no study testing this hypotheses exists so far.

Distribution patterns and number of individuals in groups influence the risk of parasitation. A patchy irregular distribution of animals in their habitat and increasing numbers of individuals in groups decreased the risk of becoming parasitized for a bivalve (Grosholz 1994).

An effect termed reproductive compensation was observed in snails. In this case mature snails freshly infected by trematodes increased their reproductive effort above that of non–infected individuals to compensate for future loss of reproductive capacity (Gérard and Théron 1997; Minchella and Loverde 1981; Minchella 1985; Thornhill et al. 1986), but Sorensen and Minchella (1998) found no reproductive compensation in *Lymnaea elodes*. A shortening of the prereproductive life span was also found in other host-parasite systems

(Agnew et al. 1999; Michalakis and Hochberg 1994). Theoretical models on parasitism and host reproductive effort are presented by Forbes (1993, 1996) and Perrin and Christe (1996).

That sexual reproduction is maintained under severe parasitic pressure was demonstrated with *Potamopyrgus antipodarum*. With this species, clonal strains and sexual populations can coexist. Since parthenogenesis has a twofold advantage over sexual reproduction (since no males are produced), clonal strains should replace sexual populations. But in the presence of castrating parasites, sexually reproducing individuals predominate whereas with decreasing prevalence of trematodes clonal individuals predominate (Jokela and Lively 1995; Jokela et al. 1997). These findings are in favour of the Red Queen hypothesis for the maintenance of sex which states that sexual reproduction is a counteradaption to parasites and is selected for since it produces genetically diverse offspring and rare, resistant genotypes (Fox et al. 1996; Lively and Howard 1994). Interestingly, clonal diversity was also higher in the presence than in the absence of parasites.

Further support for the Red Queen hypothesis came from a study using a bivalve species that demonstrated heritability for resistance to parasites (Grosholz 1994). Resistance to *Schistosoma mansoni* was also heritable in *Biomphalaria glabrata* (Webster and Woolhouse 1999).

Parasites can profoundly alter the behaviour of their hosts (e.g. Thompson 1990). Parasites can, at least in some cases, influence habitat choice of hosts. In the freshwater snail *Potamopyrgus antipodarum*, infection with a trematode species changed the temporal-spatial pattern of habitat use. Infected snails preferred areas where dabbling ducks (the definite hosts of the trematode) were foraging, but left those areas, when a second predator, a snail–eating fish, appeared during the day. Further development of the trematode was only possible in the ducks (Levri 1998; 1999).

The neuropeptide gene expression of *Lymnaea stagnalis* was already changed few hours post infectionem. The parasite influenced host behaviour and inhibited egg laying and accompanying behaviour. The manipulation of the host by the parasite changed according to the parasitic stages inside the host (Hoek et al. 1997). Castration early in infection by chemical factors was also observed in *Lymnaea elodes* (Sorensen and Minchella 1998).

Other factors influencing parasitation were already mentioned above. Habitat size and -structure as well as other abiotic factors attract or repel different types of definite hosts for trematodes and thereby define the species composition of the parasite guild. The composition of the parasite guild within the host is mediated by competition between different trematode species. There are examples for intense competition inside the host that include indirect and direct evidence (Sousa 1983).

In general, multiple infections of hosts are much less often observed during field studies than statistically predicted (Emmel 1942; Fernandez and Esch 1991a; Goater et al. 1989), but Curtis (1997) found high levels of multispecies infections in a marine snail. Direct evidence includes field studies were individual snails changed the species of trematode cercaria they shed and laboratory studies were established infections in snails were substituted by a second infection with eggs or miracidia of another trematode species (Fernandez and Esch 1991b). Cercaria of certain trematode species are even known to be hyperparasites of other trematodes inside the snail hosts (Campbell 1997).

Genetic structure and mating system of host populations and genotypes of parasites introduced by migrating species will also have a profound effect on host-parasite interactions. Temporal fluctuations in species and strains of parasites as well as the structure of the parasitic guild and their interactions affect host-parasite coevolution. Host–parasite coevolution should be impossible when too many trematode species are present.

Immunocompetence is an interesting, but mostly overlooked life history trait. New models of host-parasite coevolution have shown that coevolution must not necessarily lead to decreased virulence of the parasite towards its host, the outcome of host and parasite coevolution proposed by older models (Owens and Wilson 1999; Toft and Karter 1990).

Other studies have found evidence that resistance against parasites is costly (Michalakis and Hochberg 1994). Susceptible *Biomphalaria glabrata* had a higher fertility than resistant snails (Webster and Woolhouse 1999). Counter-intuitively, a reduced immunocompetence may also be adaptive when parasites are virulent and common. If resistance is futile, then potential hosts should withdraw their resources from an immune response and enhance reproduction instead (Baalan and Jukela, cit. in Owens and Wilson 1999).

In my opinion this could explain some of the differences between *Bithynia* species. *B. tentaculata* is infected by too many different trematode species with too many different strategies and high virulence that successful coevolution is impossible and sufficient immunocompetence and resistance is futile. I assume that *B. tentaculata* gave up the combat with the parasites in its evolutionary past and instead relocated its resources to growth and reproduction.

B. leachii is the first host of fewer trematode species belonging to a smaller range of trematode families. This could be the result of successful active parasite resistance by *B. leachii*. *B. leachii* kept on in its battle with the parasites, defeats most and is defeated by few. Since immunocompetence and immune responses are costly, *B. leachii* has fewer resources left for growth and therefore is smaller. This hypothesis would account for the greater range of parasites and their higher prevalence as also the higher susceptibility to fungal diseases in the larger *B. tentaculata*. To test this hypothesis, an assessment of the costs of resistance would be crucial. To explain the observed differences, the costs should be quite high.

-Gigantism

Gigantism (the increased shell growth in response to parasitism) is a topic much debated in molluscan life histories since it has been reported early in the century. Several scientists like Wesenberg-Lund and Rothschild have described gigantism in various snail species in the first half of the last century. Two explanations were formulated: Minchella (1985) saw gigantism as a host adaptation to trematode parasitism, whereas Sousa (1983) explained gigantism as a side effect of parasitic castration or an adaptation of the parasite.

Minchella postulated that due to the increased growth snails enhanced their survival and could thereby outlive parasites and reproduce after infections, but most infections persist in snails during their entire live. There are only very few cases were a loss of trematode infection could be demonstrated (Fernandez and Esch 1991a; Goater et al. 1989). Thereby Sousa's explanation is favoured that gigantism is either a side effect of parasitation because host castration sets free energy for growth otherwise needed for reproduction or gigantism is an adaptation of the parasite to overcome spatial constraints within the host.

Several studies found gigantism in marine and freshwater snails (e.g. Mouritsen and Jensen 1994; Sorensen and Minchella 1998; Wilson and Denison 1980). Other studies failed to demonstrate gigantism or even found "dwarfism" (e.g. Curtis 1997; Fernandez and Esch 1991a; Goater et al. 1989; Huxham et al. 1993; Mouritsen et al. 1999).

Growth rates were enhanced in *Lymnaea truncatula* and *Biomphalaria glabrata* when infected as premature snails and unaltered when infected as adults (Gérard and Théron 1997; Hodasi 1972). Loker (1979) found that infected *Lymnaea catascopium* grew faster the first 2 months post exposure and thereafter more slowly than uninfected controls. Minchella et al. (1985) found the same response for *L. elodes*.

Gorbushin (1997) found that trematode-induced gigantism in *Hydrobia* sp. depended on the trematode species, some trematodes increasing growth rates whereas others had no effect. Alteration of growth rates was also dependent on the origin of host populations. Gorbushin and Levakin (1999) found that infection with *Microphallus* sp. stunted growth in *Littorina obtusata*, had no effect on growth of *L. saxatilis* and enhanced growth in *Onoba aculeus* from the same habitat.

Often growth rates of infected snails were continually below those of uninfected ones (Fernandez and Esch 1991a; Lauckner 1986; Sousa 1983). Mouritsen et al. (1999) and Sousa (1983) assume that gigantism is a phenomenon more likely in short-lived and/or semelparous snails and unlikely in long-lived species due to their differences in life history and resource allocation.

With *B. tentaculata*, evidence is equivocal. Whereas in 2 populations there was no observable size difference, in 3 populations infected snails belonged to a significantly larger subgroup. It should be mentioned that gigantism could not be demonstrated in both populations with the highest number of examined infected snails. Thereby gigantism in *B. tentaculata* may be an artefact due to rather small sample sizes.

On the other hand, Mouritsen et al. (1999) demonstrated that the outcome in regard to changes in growth pattern was not only influenced by the trematode species, but also by the population of *Littorina littorea* observed. Snails from some populations had lower growth rates, whereas other snails did not alter their growth rates when infected with the same trematode. This stresses the necessity of a very regional focus in ecological studies and underlines the difficulties connected with generalizations.

Intra- and interspecific competition and coexisting molluscs

Competition has been a major focus of ecological studies in the past century, but its importance to explain freshwater snail communities has lately been challenged in favour of disturbance and predator-prey interactions (Lodge et al. 1987).

The concept of competition itself poses several difficulties (e.g. Begon et al. 1998; Rohde 1991). Among other reasons, this has to do with the peculiarities of the niche concept in ecology (its unlimited multidimensionality and thereby the implicit impossibility to test it by falsification) and the temporal aspects of competition and evolution ("The ghost of competition past", Connell 1980, cit. in Begon et al. 1998). This means that an apparent lack of competition observed in the present between coexisting species can be a consequence of the extinction of poorer competitors in the past, a consequence of competition in the past that led to coevolution of the species and in the end to the extinction of competition between the coevolving species or that there was never competition at all because the species are simply different. In retrospect it is impossible to decide if competition was or was not involved.

In a study on interspecific competition Fenchel (1975) found character displacement in mudsnails (*Hydrobia* sp.) in sympatric populations compared to allopatric ones. Being of equal size in allopatric populations, in sympatric ones *H. ventrosa* was smaller and *H. ulvae* bigger. Thereby resource overlap and competition should be lessened.

In recent years several studies claimed that the observed patterns are better explained as a consequence of environmental factors acting differently on the species (e.g. Cherrill and James 1987), but Gorbushin (1996) found evidence for intra- and interspecific competition in a field experiment with *Hydrobia*. Most interestingly, the outcome of competition between *Hydrobia* species was influenced by overall snail density. The successfully competing *Hydrobia* species changed when snail density was manipulated in the field experiments.

Barnes and Gandolfi (1998) found evidence for both intra- and interspecific competition in *Hydrobia neglecta.* Increasing numbers of *H. neglecta* decreased egg number per female, but egg production decreased even further when *H. ulvae* was present.

In a field experiment Brönmark et al. (1991) found that food competition by grazing tadpoles had a negative influence on fecundity and growth of 2 pulmonate snail species.

L. stagnalis has a higher grazing efficiency compared to *B. tentaculata* (Nyström et al. 1999). Grazing effects on algae growing on a hard substrate by 5 pulmonate species were identical but a coexisting prosobranch was less effective (Barnese et al. 1990).

Snails of the genus *Lymnaea* are known to forage on spawns of co-occurring snail species (Michelson and DuBois 1974; Vermeij and Covich 1978) as are some other large prosobranchs that also feed on juveniles (Aldridge 1983).

L. emarginata consumed egg masses of *Biomphalaria glabrata* in the laboratory and thereby strongly reduced population growth of the latter species (Michelson and DuBois 1974). Brown (1982) found a negative influence of *L. elodes* on *Physa gyrina* fecundity, but intraspecific competition had a more dramatic effect on growth rates. Since growth rates in *P. gyrina* increased and reproductive success decreased dramatically when kept together with *L. elodes*, I conclude that this was due to intense egg predation overlooked by the authors.

In this study *L. stagnalis* had a strong negative influence on *B. tentaculata* populations in experimental pond communities because snails consumed or damaged spawns and juveniles. In general, interspecific competition should be lessened by increasing the habitat heterogeneity (Lodge et al. 1987). However, increasing the structural diversity of the habitat did not increase juvenile survival in the competiton experiments with *B. tentaculata* and *L. stagnalis*.

In the field, *L. stagnalis* occurred in 3 out of 6 habitats, but was most abundant in the Small Pond. Here lived only few other gastropod species which could be a consequence of long-time competition by *L. stagnalis*. The Small Pond was fairly stable, highly productive and lacked efficient vertebrate predators which should increase the level of competition (Lodge et al. 1987). Its small habitat size was even more reduced by regular oxygen depletion. Thereby the habitats used by *B. tentaculata* and *L. stagnalis* overlapped, increasing the probability that *L. stagnalis* encountered spawns or juveniles of *Bithynia* during foraging.

The reproductive failure observed in 1997 and low numbers of juveniles in 1999 therefore could be caused by predation of *L. stagnalis* on *B. tentaculata*.

Species composition of the Canal and the Ditch demonstrated a clear competitive advantage for pulmonate snails in both habitats. This is a common picture in habitats with low oxygen

(Lodge et al. 1987). *B. tentaculata* dominated clearly in both rivers where also the most prosobranch species existed.

Intraspecific competition was several times demonstrated for gastropods, higher densities leading to reduced growth and/or decreasing fecundity and changes in size at maturity (e.g. Brown 1985; Carter and Ashdown 1984; Cherrill and James 1987; Lazaridou-Dimitriadou et al. 1998). In my opinion intraspecific competition accounts for the pronounced differences in juvenile growth during laboratory culture of *B. tentaculata*, but should not play a major role under densities encountered in the field.

Foraging

Bithynia is able to forage in two different modes, by grazing and via filter-feeding (Meier–Brook and Kim 1977). Filtration of organic matter out of the water leads to a higher energetic net gain than grazing (Brendelberger 1997a; Tashiro 1982). Filtration of green algae or diatoms led to a more rapid growth than grazing on several different food items (Brendelberger 1997a). Food filtration also allows *Bithynia* to remain unmoving for long time periods and to live in fairly large groups that lead to the commonly observed clumped distribution in the field (e.g. Meier-Brook and Kim 1977; Schäfer 1953). By this behaviour both predation and parasitation risks should be lessened.

Bithynia is highly selective and only forages on food of a high energy content in contrast to other freshwater snails (Brendelberger 1995, 1997a). Freshwater snails choose their habitat in accordance to the presence of appropriate food sources (Lodge et al. 1987). Aquatic snails also show different sets of enzymes and enzymatic activities and are thereby differently equipped to use diverse food items (Brendelberger 1997c). Therefore coprophagy can be a food source for some snails, but not for *B. tentaculata* (Brendelberger 1997b). The activity of digestive enzymes in *B. tentaculata* changes with different feeding regimes (Brendelberger 1997c).

2.3. LIFE HISTORY TRAITS

Growth

Growth as a key feature of every life history is affected by gender, age, reproductive investment and other energetic demands (mobility, predator avoidance and phenotypic plasticity, immune responses etc.), climate, food quality and habitat productivity, competition, parasitation, diseases and sex- and size-related mortality.

-Growth pattern

The growth patterns of organisms determine their age at maturity when size at maturity is fixed. Different growth and maturation rates can be an important isolating mechanism in speciation processes in snails (Aldridge 1983). The overall growth pattern of both *Bithynia* species was to some degree different. The growth patterns of the 6 *B. tentaculata* populations showed several differences and some similarities.

The populations also showed different growth patterns in consecutive years. Even individuals within the same population showed differences with regard to growth. The individuals showed no tendency to grow up to equal maximum sizes. Some females grew further after becoming sexually mature, others did not grow any further after starting to reproduce.

However, both in the field and the laboratory, clearly more non-reproductive females grew than reproducing ones. On the other hand, a substantial fraction (approximately 20%) of the females grew after they started to reproduce under both conditions. Likewise, the probability of a given adult female to grow after overwintering did not depend on female size. This means there existed no common pattern like small adult females growing and larger females not growing further.

-Age effects

It is well known that the age of an individual influences its growth pattern. In most cases, growth decreases with age and size. This negative relation between growth rate and size is the most common observation on gastropod growth (e.g. Aldridge 1983; Mouritsen et al. 1999).

Growth was most rapid in newly hatched snails during late summer/autumn. Young *B. tentaculata* had higher weight-specific filtration rates than older snails and young *B. graeca* had the highest daily consumption and assimilation rates (Brendelberger and Jürgens 1993; Eleutheriadis and Lazaridou-Dimitriadou 1996). Caquet (1993) found that shell growth differed between seasons for *Physa fontinalis*, growth being most rapid for juveniles directly after hatching. Growth decreased with size in *Hydrobia ulvae* and *Helisoma anceps* (Fernandez and Esch 1991a; Mouritsen and Jensen 1994).

Bithynia can reach an adult shell size before their first winter. The intensity of growth decreased in all populations for sexually mature snails. In general, most shell growth occurred in the first months of the life span, some after the first overwintering during spring and summer but only few snails grew after their second winter. This was supported by the growth patterns in laboratory culture.

Growth rates of prereproductive *Helisoma anceps* were faster than those of equally sized reproductive snails in summer (Fernandez and Esch 1991a). This is in good agreement with theory that predicts a trade-off between somatic and gonadal demands (Roff 1992; Stearns 1992). However, in *Biomphalaria glabrata* reaching maturity, growth was not reduced after egg laying started in laboratory experiments (Gérard and Théron 1997).

-Gender effects and sexual dimorphism

Growth patterns can be influenced by gender and thereby lead to sexual dimorphic species. This is often the case in prosobranchs (Aldridge 1983). Sex-specific growth rates are common in the genus *Viviparus* with females attaining larger shell heights (e.g. Buckley 1986; Eleutheriadis and Lazaridou-Dimitriadou 1995; Ribi 1999). A more rapid growth of juvenile females has been reported several times for marine prosobranchs (e.g. Sousa 1983).

B. leachii has a pronounced sexual dimorphism, females being on average 20% higher than males. In laboratory experiments, *B. leachii* females grew more rapid than males after hatching. In the field experiments, females grew more often and more rapid than males.
A less pronounced dimorphism (approx. 5%) was found in 4 of the 6 *B. tentaculata* populations. Females were larger in 3 populations, but males were larger in the fourth. The ratio of shell height to shell width was not different between sexes.

B. tentaculata showed no growth differences between males and females in the laboratory. Growth patterns of males and females were mostly the same in field experiments with caged snails with the exception of the Leine in 1999 when an unusual high number of males grew.
There were some differences between sexes in field sample data with regard to growth pattern. Mostly those were differences in the timing of shell growth in the field, but on the whole similarities dominated.

-Shell height at maturity

Size at maturity is one of the key life history traits since it is a central turning point during ontogeny that marks a profound switch in resource allocation.

B. leachii females started to reproduce with approximately 4 mm shell height. Pond and Small Pond females had the largest shell height at maturity with 8 to 9 mm, Leine females were significantly smaller. Laboratory experiments confirmed that river populations mature at smaller shell heights.

Population differences in shell height at maturity did not translate into differences in age at maturity since all females born during summer reached maturity the following year. Shell height at maturity is not known for males, but observations on dissected individuals suggests that males reach maturity at smaller sizes than females.

-Mean shell height

The mean shell height curves showed differences between populations and years. 1997 was a year with homogenous growth curves when only the Small Pond population differed due to its reproductive failure.

On the other hand, differences were pronounced in 1998 and also 1999. The differences had 2 major causes: Populations with low mean shell sizes showed an increased shell growth in spring and the timing of juvenile hatching and subsequent growth differed between populations. In addition, the snails in all populations reached larger shell heights than usual in 1999.

A ranking of the mean shell heights showed clear trends. The river populations contained by far the smallest snails with the Hunte population being even smaller than the one in the Leine. Even large animals seldom reached shell heights above 1 cm. The Ditch population is on average larger than the river populations and the biggest animals can reach 11 mm. By far the largest snails were encountered in the Small Pond where individuals may measure up to 13 mm. Mean shell heights in the Pond and the Canal were the same and lay between the Small Pond and the Ditch.

Reproduction

Life history theory centres on reproduction. All other traits of an organism relate to it in one or the other way. For *Bithynia*, habitat structure and -persistency together with oxygen content of water limit suitable places for spawn deposition. Habitat productivity influences the growth regime, size at maturity and the amount of resources being spent on reproduction. Sex-ratio and population structure influence mating chances and the overall reproductive output of the population. The prevalence of parasites regulates reproductive capability of snails and changes mortality patterns.

Coexisting species like *Lymnaea stagnalis* decrease reproductive success, others may facilitate it. Among others, predation and density-dependent factors modulate the mortality scheme and thereby the number of reproductive seasons per snail. Random events like flood, desiccation, water regulation and pollution also have a severe effect on reproduction.

-Egg number and -size

One of the most fundamental trade-offs is between egg number and egg size. With a limited amount of resources that can be allocated to egg production, a female can produce more smaller eggs or fewer larger eggs. This alternative has a profound effect on type and duration of embryonic development, juvenile size and number etc. (e.g. Roff 1992; Stearns 1992). In general, egg size is positively correlated with developmental time (Chester 1996).

This trade-off was observed twice in this study. *B. tentaculata* females in the Small Pond and the Pond produced larger eggs than the Leine females. As expected, egg number in the Leine lay above the other populations. Egg size therefore explains some of the differences in egg number between the 3 populations.

B. leachii eggs were of the same size as those of the Leine population, but smaller than the eggs of the sympatric *B. tentaculata* population in the Pond. Egg size in the coexisting *Bithynia* populations therefore explains to some degree why the much smaller *B. leachii* laid as many or more eggs than *B. tentaculata* females.

Egg number per female of both *Bithynia* species lay well above those for a semelparous population of *Bithynia graeca* in an artificial lake in northern Greece (109 ± 19,1 eggs; Eleutheriadis and Lazaridou-Dimitriadou 1996).

-Egg development

Bithynia shows direct larval development with suppression of planctonic stages as all other freshwater snails. It is an interesting side effect of the embryonic developmental type that it strongly influences the genotypic diversity of populations. Direct development increases the likelihood for local adaptations (Lafferty 1993a). Hoskin (1997) found that the genotypic diversity of two direct developing prosobranchs was lower than that of a sympatric prosobranch with planktonic development in Australia. He found that even under marine conditions, different populations of direct developing snails were effectively closed and evolved largely without genetic influences from other populations.

If such segregation works even under marine conditions, where habitats are at least connected by a common water body, the effect on freshwater populations should be more dramatic. One may speculate if the invasion capability of *Dreissena polymorpha*, which was able to settle successfully in very diverse habitats in very short time, is at least partially due to a higher genetic diversity maintained by the unique mode of planktonic development in this freshwater species.

A change in developmental type from planktonic to direct development or vice versa has lead to speciation events quite frequently in marine prosobranchs (Oliverio 1996). There are some examples of poecilogony in marine animals. Poecilogenous females produce offspring with different developmental modes, e.g. the polychaete *Streblospio benedicti* (Bridges and Heppel 1996). In an opisthobranch snail species, individual females produce planktonic and also direct developing offspring (Gibson and Chia 1995).

-Spawn number and -size

Another interesting trade-off can be observed between spawn number and spawn size. When at least a substantial part of the resources for egg production is acquired prior to reproduction as is the case with *Bithynia*, a given capital breeder (= investing mostly stored resources) can produce few large or many small spawns. A female producing many small spawns is hedging their bets compared to a female that lays few large spawns. Bet hedging should be advantageous in unstable and unpredictable environments or when predation on eggs is severe.

Again this trade-off was observed twice and in the same combinations as for egg size and -number. The Leine females laid more spawns containing on average fewer eggs than both other *B. tentaculata* populations. *B. leachii* laid the highest number of spawns containing the fewest eggs. *B. leachii* females laid three times more spawns than the sympatric *B. tentaculata* females. Spawns of the latter contained on average a 2,5 fold higher egg number. This is not just an allometrical artefact due to the smaller size of *B. leachii* females since they were able to lay as many eggs per day as *B. tentaculata* females.
The same trade-off between few large and many small clutches was found for a spider (Schneider and Lubin 1998). In *Cepaea nemoralis*, young snails laid fewer and larger clutches than older snails of the same size and origin (Carter and Ashdown 1984). In the land snail *Arianta arbustorum*, clutch size and egg size increased with snails size (Baur 1990).

A surprising constraint on the size of snail egg masses has been shown by several scientists: Embryos within larger egg masses show slower development due to a slowed down gas exchange than embryos from smaller egg masses. Therefore their stage-specific mortality is increased due to the prolonged development (Chaffee and Strathmann 1984; Lee and Strathmann 1998; Marois and Croll 1991). This is a consequence of the increasing diameter of egg masses.
This relationship does not hold true for *Bithynia* since these snails lay their egg masses as long parallel rows of 2 to 4 eggs lacking a common jelly matrix and tertiary egg membrane that is characteristic for pulmonate freshwater snails (Hess 1971; Nekrassow 1929). The gas exchange is not slowed down because with growing egg number only the length of the

spawn increases. Developmental time of spawn is therefore only correlated to temperature and not to spawn size (Richter and Wächtler 1999).

Hatchability of spawn is independent from egg number. Offspring fitness does not decrease with increasing clutch size at least when hatchability is taken as a fitness measure for different sized spawns. Effects of crowding on growth and survival of hatchlings could not be assessed in the field. However, there is circumstantial evidence that crowding is not detrimental to *Bithynia* because adults as well as hatchlings strongly tend towards a patchy distribution under field conditions. A possible benefit of larger clutch size could be a decreased risk of becoming parasitized due to a patchy distribution.

-Mean number of eggs per spawn

The number of eggs per spawn decreased significantly in all three populations and for both species between the onset and the end of the reproductive season. This was observed even for females which did not begin the breeding season with the biggest spawns. A similar decrease in egg number per spawn and also mean egg size during the breeding season was observed by Ito (1997) for individual females of the semelparous opisthobranch snail *Haloa japonica* (Pilsbry) and Carter and Ashdown (1984) for *Cepaea nemoralis*, but Gibson and Chia (1995) found that clutch size increased throughout the breeding season in an opisthobranch snail. Clutch size increased during the first weeks of reproductive activity and decreased afterwards in laboratory cultured *Lymnaea truncatula* and in field populations of the land snail *Arianta arbustorum* (Baur 1990; Hodasi 1972).

Ito (1997) interpreted his findings in the theoretical framework proposed by Begon and Parker (1986) for an optimal allocation of limited resources to reproduction under random mortality. In their model they suggest as ultimate cause of the decline in size and number of offspring during the reproductive period, that females should produce higher numbers of larger eggs at the onset of reproduction because of the reduced probability of surviving to lay further clutches at a later date. This pattern was observed several times for diverse groups like annual plants, lepidoptera and other invertebrates that shared the feature of semelparity (Begon and Parker 1986; Ito 1997).
Even if Parker and Begon (1986) assumed in their model that females do not feed or only feed little as adults, are semelparous and experience random mortality, the general conclusions based on the declining probability of surviving from one reproductive event to the next seems to be of a broader applicability.

It is interesting that in the case of *B. tentaculata*, the trait of declining egg numbers per spawn was observed in a potentially iteroparous species that feeds and, to some extent, even grows during reproduction. The trend to declining egg numbers per spawn is even shown in consecutive breeding seasons by the same females. But it must be emphasised that the linear decrease of clutch size with age (biggest clutch in the beginning followed by a steady decline of egg number) predicted by Begon and Parker's optimality model (1986) was in no case true when spawns were examined on the individual level, where eggs per spawn exhibited wide variation. A large fraction of females started reproduction even with small spawns. The trend toward smaller spawns is therefore an overall tendency when the whole reproductive period is taken into account.

I think this has two causes: First, *Bithynia* seems to be a mixture of capital and income breeder. At the start of the reproductive period, predominantly stored resources are allocated to reproduction and reproductive output is therefore high, but these stores become more and more depleted with time and only newly acquired resources can be allocated to reproduction at the end of the season.
This is supported by laboratory data. It is known that the numerical fecundity of *Bithynia* in laboratory culture is significantly decreased compared to wild populations (Tashiro 1980, this study). In the beginning, the egg laying process in the laboratory is not distinguishable from field observations, but after some weeks there is a steep decline in egg number. So it seems plausible that the costs of reproduction are divided between storage gained in the prebreeding state and acquired resources during the reproductive period, a mixture between capital and income breeding.

Second, an investment early in the season has a higher pay-off in fitness terms than a late investment (Baur 1990). Juveniles from early eggs hatch before the majority of their conspecifics and have the longest time for growth and development before winter. Juveniles from late eggs may be more mortality prone during winter because of their smaller size and limited resources. They also may fail to reach the critical shell size for reproduction the following year. Thereby the pay-off on reproductive investments decreases throughout the season and from a certain time onwards an iteroparous female can expect higher rewards in fitness terms when she stores acquired resources for her own survival and subsequent reproduction the following year (Calow and Sibly 1983; but see also "First spawns").

-Range of egg number per spawn

This parameter illustrates to which extent the egg number of the smallest and the biggest spawn per season differed. *B. leachii* had a low range meaning differences were not pronounced in this species. In contrast, the population in the Small Pond had a high range of eggs per spawn. The differences in egg number between small and large spawns were the most pronounced of all populations. Females in the Small Pond often laid spawns containing more than 100 eggs at the start of reproduction, followed by much smaller spawns for the rest of the season. Pond and Leine females were on a medium level.

-First spawns

A female can start the reproductive season with small or big spawns. When the starting point for reproductive activities marks an especially favourable season for the production of progeny, it should increase the fitness of a female to make large investments.
I therefore expected females to lay their biggest spawns (and hence biggest per cent investment of the reproductive season) directly at the beginning. Approximately 4 out of 5 females in the Small Pond (which also had the heighest range of eggs per spawn) and Pond followed this pattern, their first spawns being also the biggest spawns of the season. In the Leine, 42 females showed this trait, but 29 females laid their biggest spawn later on in the season. Only a few more than half of the *B. leachii* females started with their biggest spawn, the difference being significant compared to the sympatric *B. tentaculata* population.

A lot of variation is therefore maintained in the populations and there should be other factors influencing the increase in fitness through the timing of reproductive investments than those mentioned under "Mean number of eggs per spawn". In this context it is interesting that females differ up to 4 weeks (that translates in 2°-4° Celsius in temperature terms) with regard to the time they start to reproduce. Obviously there is no stable "optimal time" for reproduction that can be selected for (see also "Cumulative egg number").

The egg number of the first spawns had only a weak positive correlation with shell height for the Pond population, but not for the other ones. This signifies that larger females did not start reproduction laying larger spawns than smaller females as proposed by the model of Begon and Parker (1986). Larger females laid larger spawns in an opisthobranch snail (Gibson and Chia 1995).

-Length of reproductive period

As was stated several times by now, reproduction is costly to all organisms. A female with a long reproductive period has therefore fewer time to replenish her storage for overwintering than a female with a short reproductive period. As a consequence, overwintering success should be better for females with a short reproductive period compared to long-time spawners. Although numbers of overwintering snails were too low for statistical analysis, such a tendency was not observed in the field. It seemed again as if good performers survived better even with a long reproductive period (and high reproductive effort).

On other grounds, it is reasonable to assume that selection should shape the length of reproductive periods in such a way that their lengths are congruent with the time frame most appropriate for reproduction in a given habitat. Thereby a long versus a short reproductive period should tell us something about the selective patterns of the habitats.
Leine females had by far the longest reproductive periods, sometimes up to 4 months. Pond females on average had the shortest reproductive periods, but this was mostly due to the rapid die-off after the fungal disease spread. Mean length of reproductive period was 2 months for the Small Pond and *B. leachii*. Obviously a much broader time frame for successful reproduction exists in the river than in the still water populations.

-Hatching rate

The egg number of a given female does not tell us much about its actual reproductive success. This is particularly true for gastropods that often lay extra eggs for nutrition of juveniles and are known to have varying rates of hatching success (Fretter 1984). Other factors may influence hatching rate as well. Hatching rate was on average 86% for *Pomacea canaliculata* (Ampullariidae) and clutch size had no effect on hatching success (Estebenet and Cazzaniga 1993). Hatching rate was negatively influenced by crowding in *Cepaea nemoralis* (Carter and Ashdown 1984). Hatching rate varied greatly with time but was lowest at the end of the reproductive season in a land snail (Baur 1990).

It is interesting that the hatching rate was very high in both *Bithynia* species. With *B. leachii*, almost all eggs that were laid hatched successfully. This is the more interesting when one recalls that eggs are costly in energetic terms and thereby very good food items, but egg predation by invertebrates (invertebrates like leeches, turbellaria and aquatic larvae of insects were able to enter the cages) was not observed in this study.
Hatching rates in the Small Pond and the Pond were also high but lower than for *B. leachii*. Differences between females were most pronounced in the Small Pond. Hatching success was often low for females that laid over proportionally few eggs. As all cages were kept under the same environmental conditions, hatching failure seems more likely due to poorly performing females than to abiotic factors.

Freshwaters are known to carry very large numbers of planktonic organisms including fungal spores, bacteria and viruses (Lampert and Sommer 1993). It is an interesting detail that spawns did not become infected by any of aforementioned pathogens. An analysis of the outer egg membranes for their antibiotic potential seems to me very rewarding. Only mechanically damaged eggs or eggs with dead embryos were successfully attacked by pathogens.

-Correlations

Trade-off theory predicts that several life history traits should be negatively correlated (e.g. Roff 1992; Stearns 1992). Current reproduction should influence both future reproduction and survival negatively (Calow and Sibly 1983). In the same line of reasoning should a higher egg number decrease the viability of the individual egg, but empirical evidence is often contrary.

Lepage et al. (1998) manipulated clutch size in the greater snow goose and found that experimentally enlarged clutch sizes enhanced offspring quality instead of decreasing it like they expected. Crowl and Covich (1990) found that *Physella virgata* individuals that started to reproduce at a younger age and smaller size had a shorter life span than snails with delayed maturity. However, researchers often found positive correlations between the aforementioned traits on the individual level when negative ones are predicted. In short, this means nothing more than the somewhat banal notion that some animals perform better than others and good performers can invest more into conflicting demands (Noordwijk and Jong 1986). Examples include the breeding frequency of the King Penguin *Aptenodytes patagonicus* where current reproduction influences future reproductive success positively and the amphipod *Gammarus minus* where reproductive output and growth were positively correlated (Glazier 2000; Jiguet and Jouventin 1999).

This pattern holds also true for *Bithynia*: A high reproductive investment was associated with a high probability of winter survival and mortality was higher with non-reproductive females or poor reproducers. Likewise, large egg numbers did not influence hatching success negatively, to the contrary, hatching success was inferior for females that laid fewer eggs. Glazier (2000) pointed out that the often overlooked positive correlations should stimulate further research and should be integrated into ecological models. Individual variations in resource acquisition leading to positive correlations have been neglected in favour of the study of resource allocations leading to the predicted negative correlations in theoretical models.

An interesting detail of this study showed that the number of eggs produced by a given female was not positively correlated to the size of the female. A positive correlation between size of parent and number of offspring seems self-evident and has been found throughout the plant and animal kingdoms quite regularly for very diverse organisms and several times for land and freshwater snail species (Aldridge 1982, Begon et al. 1998; *Cepaea nemoralis*: Carter and Ashdown 1984; *Helix aspersa*: Dupont-Nivet et al. 1998; Lazaridou-Dimitriadou et al. 1998; *Semisulcospira libertina* (Prosobranchia): Nakano and Izawa 1996; *Viviparus ater*: Ribi and Gebhardt 1986; *Littorina rudis*: Roberts and Hughes 1980; *Thais* sp.: Spight and

Emlen 1976). However, Ito (1997) found no significant positive correlation between female size and egg number in the opisthobranch snail *Haloa japonica*.
As a consequence, at least in some cases, it is not possible to extrapolate the contribution of a given size class to further generations out of the size class distribution of a population. One possible explanation despite different live history strategies could be the increasing risk of parasitation and host castration with age.

The only strong positive correlation found on the population level for all 4 populations is between length of reproductive period, number of spawns and egg number. In other words, this is the trivial notion that within a longer reproductive period, more spawns are laid leading to a higher egg number.

The most interesting correlation is a weak, but significant correlation between number of spawns and mean number of eggs per spawn. This shows a tendency towards a trade-off between the number of spawns and the eggs per spawn. Females laying more spawns invest less eggs per spawn.

-Cumulative egg numbers

Cumulative egg numbers are a graphical representation of the egg laying process over time. By the slope of the curve one can tell how the egg laying process began, when it was most intense and when intensity started to fade.

The curves were linear in all years for the Pond population. About half of all eggs were laid within the first 3 weeks and about 90% within 6 weeks. Egg laying stopped rapidly because of the spreading fungal disease. It is an interesting detail that the contributions of the first week to total egg number increased from year to year. This is expected when mortality is very high during the reproductive period. Under the observed mortality scheme the highest pay-off in fitness terms should be rewarded to females reproducing early and intensely. Since they will have the most progeny, the trait of early and intense reproduction will become more frequent every year in the population. The fungal disease therefore led to a shift in the life histories of Pond snails within a short time period.

The shape of curves in the Leine was sigmoid. Egg laying began very slowly in all years and was most intense after 3 to 7 weeks and decreased slowly afterwards.

Curves were very different for the Small Pond females. Egg laying started rapidly in 1997 and slowed down continuously afterwards. Half of all eggs were laid after just 2 weeks. In 1998, the curve was more or less linear with a restrained start. In 1999, the curve had a sigmoid shape as in the Leine population. This was partially caused by the younger females starting to reproduce 4 weeks later than older females.

In 1998, the curve for the *B. leachii* females was sigmoid with a restrained start and most intense egg laying between weeks 3 and 6. Egg laying activity decreased only slowly afterwards since some females had a very long reproductive period of up to 20 weeks. In 1999, the curve was linear for the most part of the reproductive season.

Parental effects

Parental effects are phenotypic effects of individuals on the phenotype of their progeny that are unrelated to the genotype of the offspring. They have become a major interest in ecology lately (e.g. Bernardo 1996a, Carrière 1994) and are now also well documented in freshwater snails (Lam 1999). They can be mediated by environmental cues that relate, for example, to season, presence of predators and predation pressure or they can be a direct consequence of the maternal phenotype like the influence of female nutrition on the trajectories of foetal growth in humans (Woods 1989) or on egg size in vertebrates (Reznick et al. 1996) and in invertebrates (Bernardo 1996b).

Significant differences between the egg sizes of females were found in an opisthobranch snail (Gibson and Chia 1995). Food deprived snails produced exclusively offspring with planctonic development whereas snails under normal conditions produced also direct developing offspring. The same observation was made by Chester (1996) in the nudibranch *Tenellia adspersa* where egg size was plastic and related to adult nutrition.

Maternal effects are often mediated through phenotypic plasticity. An example is that good nutritive conditions of mothers lead to a gradual increase of size of progeny over several generations. The evidence for mammals was reviewed by Geist (1989). Another example is reported in an article by Lazaridou-Dimitriadou et al. (1998) on *Helix aspersa* under indoor culture conditions, but the authors failed to recognise the maternal effect.

-Egg size

The size of eggs directly influences juvenile size and fitness and may fluctuate with season or may be fixed. Increasing egg size with season was found for a land snail in alpine populations and a marine polychaete (Baur 1990; Bridges and Heppell 1996). In both cases, larger eggs increased hatchling survival.

In the Leine and Small Pond populations of *B. tentaculata*, where data were collected at the beginning and the end of reproduction, egg size was fixed.

-Oviposition site choice

By choosing the right places for the deposition of eggs or juveniles, a female contributes crucially to successful embryonic development and juvenile survival and thereby to its own fitness. Oviposition site choice has been overlooked traditionally by scientists in favour of "hard" life history components like egg size and egg number (Resetarits 1996). But the ability to detect suitable sites for oviposition should be a major trait of the adaptation of an organism to its environment and therefore is expected to be under strong selection.
For example, *Hyla chrysoscelis* females discriminate between ponds with different degrees of predators and competitors present, avoiding actively predators and conspecific competition (Resetarits and Wilbur 1989). Oviposition site choice is a crucial life history trait in land snails (Baur 1990).

In a choice experiment females of 4 populations of *B. tentaculata* clearly preferred macrophytes for spawn deposition. They discriminated strongly against wood, gravel and, to a lesser extent, dead leaves. This pattern does not reflect foraging preferences of females, since females were found on all 4 substrata and were most often found on dead leaves.

Population structure and sex-ratio

-Population structure

The population structure is influenced by the growth regime, the sex-ratio, the reproductive strategy and the mortality scheme. Mortality schemes have a most profound influence via their size-, age- and sex-related effects. Population density influences the degree of intraspecific competition that has via changes in fitness a feed-back mechanism on population structure. The population structure itself influences reproduction.
The populations in this study were structured differently. This was mainly due to differences in growth regime and maximum shell height, sex-specific mortality and longevity of snails.

-Sex-ratio

The sex-ratio of a population is a consequence of the sex-ratio of the progeny and sex–specific mortality. Although the sex-ratio has far-reaching consequences, its importance is often overlooked in invertebrate studies. Mostly the sex-ratio is assumed to be 1:1.

Sex-ratios in prosobranchs are often female-biased (Hyman 1967). Sex-ratios of adults were female biased in 2 *Viviparus* species but the sex-ratio of juveniles was 1:1, suggesting a sex-specific mortality pattern as in some *Bithynia* populations (Ribi 1999). A Greek population of *Viviparus contectus* had a 1:1 sex-ratio with females being larger than males (Eleutheriadis and Lazaridou-Dimitriadou 1995).

The overall sex-ratio for *Littorina rudis* was 1:1, but the sex-ratio was found to fluctuate erratically in time with no clear seasonal trend (Roberts and Hughes 1980). Robson and Williams (1971) found an overall sex-ratio of 1:1 for *Littorina littorea* in North Yorkshire, but some size classes showed significantly different sex-ratios.

Morton (1991) found different sex-ratios between populations of the same species. He investigated 14 bivalve species in southern China and found several times populations with female-biased sex-ratios and male-biased in others. Sex-ratios also varied with age for some species (and were stable in others), but in contrast to *B. tentaculata*, sex-ratios were biased in younger stages and were 1:1 in older ones.

The sex-ratio of *B. tentaculata* was approximately 1:1 in the Canal, the Hunte and the Small Pond. In the other habitats, males predominated, most pronounced in the Pond and the Leine. With *B. leachii*, females predominated. Since the progeny of both species consisted to equal parts of males and females in the laboratory, a sex-specific mortality is concluded for the populations with differing adult ratios.

Sex-specific mortality schemes are also supported by seasonal fluctuations in gender abundances. There was a general tendency in all populations with exception of the Small Pond that females set out from a level near 50% in spring to a sometimes pronounced low during summer. This points in the direction of sex-specific mortality.

Findings support the hypothesis that reproduction is more costly to females and that these costs are paid earlier in comparison to males (Tashiro 1982). However, there are several examples in the literature where this reasoning is contradicted. In the Viviparidae females are longer lived than males irrespective of their high energetic investment in reproduction (Eleutheriadis and Lazaridou-Dimitriadou 1995; Ribi 1999).

In conclusion, either the proposed trade-off between reproduction and survival is overrated or the methods to measure reproductive effort are not accurate. Personally I'm quite sure that the simple idea of gender investments in reproduction, - eggs costly, sperms cheap -, is inaccurate.

Several other aspects, especially of male reproduction, should bear costs (like increased mobility, less foraging time, structures for mate finding and gender recognition, courtship, cannibalism) that are not easily measured or even observed in invertebrates, but have at least been demonstrated in spiders and freshwater snails (Schneider and Lubin 1998).

Males in *Viviparus* actively searched for mates and could discriminate conspecific over allospecific females before direct contact, whereas females accepted copulations of both con- and allospecific males. Males in *Viviparus* also produce oligopyrene sperm that are absorbed by females and males stopped feeding while copulating (Ribi and Katoh 1998). This demonstrates that males had costs due to mobility, devices for mate recognition and production of different sperm types. Viable models for reproductive effort should try to incorporate those costs.

Mortality

The mortality of organisms is influenced by their age, gender and size. Low food levels, high reproductive investment and higher mobility increase mortality. Biotic interactions like predation, parasitation, diseases and competition have a profound effect on mortality as have abiotic factors like habitat persistency, catastrophes, climate, oxygen depletion etc.

Sex-specific mortality rates are known in diverse invertebrate species. Mortality was higher in male *Hydrobia neglecta* (Barnes and Gandolfi 1998). In the butterfly *Pararge aegeria* mortality rates are sex-specific and the male mortality rates vary between populations due to different patterns in female emergence under varying climates (Gotthard et al. 2000).

There were only slight gender differences observed in *B. tentaculata*. In general, females died somewhat earlier in summer in the field, but mortality curves met again in autumn. Mortality was intensified by parasites and small size in winter. Irrespective of their high parasitic load, the Small Pond snails were clearly the longest-lived in the field, living up to 3 years. On the contrary, Pond snails only lived for approximately 10 months in all years. This potentially iteroparous population was de facto semelparous since a fungal disease killed almost all adults during spring and summer.

Mortality patterns in the Leine showed the largest annual differences. In 1998, no snails survived whereas in 1997 every fourth female lived for a second breeding season. In 1999 more than 80% of all snails lived at overwintering. This is the more remarkable since this was a year with an exceptionally high reproductive effort, an unusual large number of reproducing females and a very long reproductive period. This is contrary to the often proposed trade-off that a higher reproductive effort should increase mortality. This trade–off is so far seldom proven beyond doubt (Stearns 1992).

For *Bithynia* it is known that reproduction is costly in terms of invested protein and overwintering reduces significantly the carbohydrate stores of snails (Tashiro 1980, 1982). It is also known that the numerical fecundity of *Bithynia* in laboratory culture is significantly decreased compared to wild populations (Tashiro 1980, this study). So it seems plausible that the costs of reproduction are divided between storage gained in the prebreeding state and acquired biomass during reproduction. A female with a long reproductive period should therefore have fewer time to replenish her resources for overwintering than a female with a short reproductive period, but the observed trend was opposite to expectations based on life history theory. Good reproductive performers also had better survival.

20% of the *B. leachii* females and 40% of the males lived at overwintering in 1998. Winter mortality was higher for males and 15% of both sexes lived for a second breeding period. In 1999, there was a die-off in June comparable to that of the sympatric *B. tentaculata* population.

Females of all populations lived clearly longer in the laboratory than under field conditions. This shows that mortality is mainly caused by extrinsic factors in the field. Laboratory snails were not exposed to pathogens to the extent of snails in the field and could not aquire new trematode infections. This resulted in a very low level of infected females in the laboratory as was seen for Hunte females.

Spatial and temporal distribution

-Overwintering

Winter survival is positively influenced by snail size and snail nutrition and negatively by length of winter, unusual low temperatures and parasites. Females must replenish their energy stores after reproduction in autumn (Tashiro 1982). Hibernating *Leptoxis carinata* (Prosobranchia) lost 10 - 25 % of their biomass in winter (Aldridge 1982). Winter survival is thereby negatively affected when temperatures start to decrease early in autumn.

It is typical for *Bithynia* to overwinter at the bottom of water bodies (Emmel 1942; Vincent et al. 1981; Young 1975). Due to the density anomaly of water, here the temperatures will not drop below 4°C during winters of normal strength.
Overwintering in the mud at the bottom of the habitat is also displayed by other prosobranchs like *Viviparus* sp. (e.g. Eleutheriadis and Lazaridou-Dimitriadou 1995; Vail 1978).

-Mobility

Snail movement is influenced by temperature, habitat size and the distance between the different habitat parts that are needed for overwintering, foraging, mating etc. In addition, habitat use depends on sex and age of individuals. In general, males are regarded as being more mobile than females because of their more active role in mate searching. In *Bithynia*, the ability for filter feeding and the clumped distribution lessens the need for moving with regard to mating and foraging.

B. tentaculata has been found to move quite large distances during both day and night in artificial ponds (MacRae and Lepitzki 1994). This high mobility seems to be partly an artefact since food sources were rare and unevenly distributed during the experiment. Furthermore, it is in disagreement with observations of the snails' field distributions.

3. A COMPARISON OF THE LIFE HISTORIES OF *B. TENTACULATA* AND *B. LEACHII*

Both species differ in size, *B. leachii* being smaller when reaching maturity and as fully grown adult. Whereas adult *B. tentaculata* reach shell heights of 8 to 12 mm, *B. leachii* females rarely exceed 6 mm and males reach on average only 4 mm. This pronounced sexual dimorphism in *B. leachii* is only detectable to a much lesser extent in 3 of the 6 *B. tentaculata* populations.

Female *B. leachii* show a different growth pattern than *B. tentaculata* females. Females of both species grow during spring and some *B. tentaculata* females continue to grow while reproducing whereas *B. leachii* stops growth when reproducing. Growth stops for all adult *B. tentaculata* by August, but *B. leachii* females surviving reproduction start to grow again in autumn. On the whole, more adult *B. leachii* females grew than *B. tentaculata* females.

B. tentaculata is more often parasitized and has a wider array of trematode parasites than *B. leachii* (for a discussion of possible causes and life history consequences, see last paragraphs of "Parasitation"). Whereas 30 adult *B. leachii* harboured no infections and only 1 out of 56 female *B. leachii* did not reproduce (and was parasitized), the number of non-reproductive *B. tentaculata* females lay much higher (17 out of 77 adult females in the Pond). Several of them were found to be parasitized when dissected after death. Unfortunately this was not possible with most females due to rapid decay of dead snails.
Contrary to *B. tentaculata*, *B. leachii* was also resistant to the fungal disease in 1998, but the following year numbers of both species declined rapidly.

B. leachii egg size is smaller than the egg size of the coexisting *B. tentaculata* population, but *B. leachii* eggs were of equal size to the Leine population of *B. tentaculata*. Consistent with egg size, hatchling size of *B. leachii* is smaller in the Pond. Total egg number per reproducing female showed a trend to higher numbers for *B. leachii* in the coexisting populations. Since more *B. leachii* females reproduced and *B. leachii* had a higher hatching rate than *B. tentaculata*, number of living offspring per adult individual in the Pond is higher for

B. leachii. This becomes even more pronounced since *B. leachii* showed a female-biased population structure whereas *B. tentaculata* was male-biased in the Pond.

B. leachii females laid more spawns containing on average fewer eggs. Therefore both species show different trade-offs with regard to the partitioning of reproductive effort: *B. leachii* produces more and smaller eggs than co-occurring *B. tentaculata*. *B. leachii* lays a lot of spawns with few eggs whereas *B. tentaculata* lays fewer spawns containing higher egg numbers. Since the first spawn of the reproductive period is also less often the biggest spawn for *B. leachii*, the species shows a reproductive strategy that is more in line with bet–hedging than that of the co-occurring *B. tentaculata* population. A negative side-effect of a high spawn number is that females have to find more places suitable for spawn deposition. Therefore they spend more time for searching and more energy on mobility than females with fewer, bigger spawns (Lee and Strathmann 1998). In addition, Aldridge (1983) assumes that small eggs and spawns are an antipredator strategy in freshwater ecosystems.

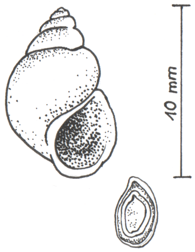
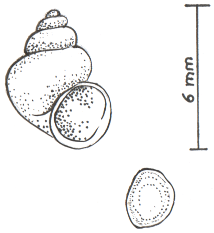
The course of cumulative egg numbers is different in 1998 and equal in 1999. Both curves show a linear increase for nearly the whole reproductive period in 1999. In 1998, the curve was also linear for *B. tentaculata* and of a stretched sigmoid shape for *B. leachii* resembling the curves of the Leine population of *B. tentaculata*.
The different shapes are at least partially explained by the mortality scheme. The *B. tentaculata* population in the Pond suffered from a severe die-off due to a fungal disease during the reproductive period in all years. *B. leachii* showed no such die-off in 1998 and had therefore a long reproductive period with a slow start that lead to a sigmoid curve. In 1999 *B. leachii* snails died in large numbers in early summer and the curve is compressed towards a more linear shape.

On the whole, the reproductive strategy of *B. leachii* in the Pond is clearly different from that of the coexisting *B. tentaculata* population. Surprisingly, *B. leachii* shows several similarities to the Leine population of *B. tentaculata* (egg and juvenile size, the trade-off to produce more spawns with fewer eggs, the shape of the cumulative egg number curves).

The findings do not explain the dominance and broader occurrence of *B. tentaculata*, to the contrary, dominance relations should be rather in favour of *B. leachii*. This point is supported by the successful reproduction of transplanted *B. leachii* snails in the Leine.

Why then do we find a different picture in the field? One point is that this ecological study regards only a short period in time, but the ratio of both species shifted markedly in favour of *B. leachii* between 1997 and 1999. Therefore *B. leachii* may become dominant in the Pond over the next years.

Tab. 53: A comparison of the life histories of the sympatric *Bithynia* populations

 **B. tentaculata**	 **B. leachii**
Adult size 8 - 12 mm	Females: 4 - 6 mm / Males: 2,5 - 4,5 mm
Size at maturity Females: ca 8 mm Males: ?	Females: ca 4 mm Males: ca 2,5 mm (?)
Sexual dimorphism Females slightly bigger than males	Pronounced
Growth pattern Intense during spring, growth continues while reproducing and stops in late summer	Intense during spring, growth stops while reproducing, second growth period afterwards
Parasites Often parasitized	Seldom parasitized
Susceptability to fungal disease High	Medium (?)
Life expectancy 1 - 3 years	1 - 2 years
Egg size Large	Small
Egg number Ø = 180 eggs per reproducing female	Ø = 230 eggs per reproducing female
Hatchability of eggs High (> 85%)	Very high (> 95%)
Spawns Fewer spawns with many eggs	Many spawns with few eggs
First spawn = biggest spawn 42 out of 52 first spawns observed	24 out of 45 first spawns observed

It is also a possibility that the smaller *B. leachii* suffers over proportionally from winter mortality since winter survival is size related. The smaller size may facilitate predation compared to *B. tentaculata,* but direct evidence is missing to support this hypothesis.

A further point could be different migration capabilities. Since migration between habitats is passive, I would expect behavioural causes to change migration probability. When small *B. tentaculata* prefer foraging attached to the water surface and *B. leachii* juveniles do not, chance encounters and transport by waterfowl should favour the spreading of *B. tentaculata*.

4. A COMPARISON OF THE DIFFERENT *B. TENTACULATA* POPULATIONS

DÜMMER POPULATIONS

HUNTE

Hunte snails were the smallest of the 6 populations. They had a balanced sex-ratio and showed no sexual dimorphism. They were numerous and also the dominant snail species in their habitat. The overall parasitation level was 15% with its high in summer when 2 out of 10 adult snails were affected during the reproductive period.

Adult snails were almost completely replaced by juveniles in late summer/autumn, the mean life expectancy therefore being 12-14 months. Juveniles grew slower during summer and autumn than in spring.

Habitat stability was low because of irregular high waters and floods and because the vegetation on the river banks where snails lived died in winter.

CANAL

Canal snails were quite large and of the same mean size as Pond snails. On average, females were larger than males, the sex-ratio was balanced. They were frequently encountered but never common in their habitat.

The overall parasitation level was low. Juveniles replaced adult snails almost completely in the summer of 1997 (data for 1998 are missing). Juveniles grew very fast in autumn reaching adult sizes already in October and grew almost no further after overwintering. Bottom parts of the habitat were frequently anaerobe. There were a lot of sympatric pulmonates.

DITCH

Ditch snails were on average larger than the river but smaller than the other still water populations, but some individuals reached very large sizes. Males predominated but the population showed no sexual dimorphism. Snail abundance was fluctuating irregularly as was juvenile presence. The population structure therefore showed no consistent trends.

Parasitation was normally clearly below 10%, but 25% of the adults were affected in July. The average parasitation level was the same as for the Leine and the lowest observed.

The habitat experienced frequent periods of oxygen depletion and changing water levels. It was clearly suboptimal for *B. tentaculata*. No juveniles hatched in 1998 until August. Pulmonates were by far dominating and no other prosobranchs existed in the Ditch.

POPULATIONS IN HANNOVER

SMALL POND

On average Small Pond snails were by far the largest ones, some individuals reaching a shell height of 13 mm. The sex-ratio was balanced but males were larger than females, this being the only case observed for *B. tentaculata*.

Snails were always common, but sometimes sympatric pulmonates were predominant. *Lymnaea stagnalis* was present in high numbers in later summer. The life expectancy was high with snails living for 2-3 reproductive periods.

The parasitation level lay clearly above all other populations, 4 out of 10 adult snails being parasitized on average. A substantial part of the potentially iteroparous population was therefore functionally semelparous due to parasitic castration. In autumn 1998, 3 out of 4 adults contained parasites.

The population failed almost completely to reproduce in 1997 and also had a poor juvenile recruitment in 1999. Juveniles grew rapidly in autumn and also in spring. They reached maturity at a size well above that for river populations.

Females laid few, big eggs in few, large spawns. The largest spawns were found in this population. The eggs had the lowest hatching success. The length of the reproductive period was intermediate. Deeper habitat parts were anaerobe during the summer season, the vegetation died off in winter.

POND

Pond snails were smaller than Small Pond and larger than Leine snails. Size at maturity was equal to the Small Pond. The population showed a sexual dimorphism with females being larger than males, but the sex-ratio was male biased.

The life expectancy was low and snails were de facto semelparous. The adult snails died almost completely due to a fungal disease in late spring/early summer and were replaced by juveniles in June/July. Juveniles grew rapidly in summer and autumn and again in spring.

Females laid few, big eggs in few, large spawns, the hatching success being very good for most females. The length of the reproductive period was short due to the die-off. On average parasitation levels were low, but could increase in summer.

Snails were clearly less common compared to all other populations. Oxygenation was sufficient throughout the year and the habitat fairly stable. The population was the only one living sympatric with *B. leachii*.

Tab. 54: Life history differences of the 3 *B. tentaculata* populations in Hannover

Mean shell height	Leine < Pond < Small Pond
Shell height at maturity	Leine < Pond = Small Pond
Snail abundance	Leine > Small Pond > Pond
Egg number	Leine > Pond = Small Pond
Size of eggs	Leine < Pond = Small Pond
Spawn number	Leine > Pond = Small Pond
Mean number of eggs per spawn	Leine < Pond = Small Pond
Range of egg number	Leine = Pond < Small Pond
Length of reproductive period	Leine > Small Pond > Pond
Life expectancy	Small Pond > Leine > Pond

LEINE

Leine snails were small on average and also reached maturity at a small size. They had a different height-width-ratio, being slenderer than the other populations. The sex-ratio was male-biased, females being on average larger than males. Life expectancy was intermediate with great variation in number of females taking part in 2 reproductive periods.

In general, most adult snails were replaced by numerous juveniles in late summer. Juveniles were rapidly growing in late summer but not in autumn and again, but somewhat slower, in the following spring. Parasitation was very low but had its high during the reproductive period as in other populations. 2 out of 10 adult snails were parasitized then.

Females laid many, small eggs in many, small spawns. The reproductive period was long, some females even reproducing in autumn.

Snails were more abundant in the Leine than in the 5 other habitats. They were always very common and dominant in all years, the habitat obviously very suitable for *B. tentaculata*. Water velocity fluctuated greatly and floods happened on an irregular basis. Otherwise the habitat was more stable than the others since the snails lived permanently on the underside of stones and vegetation was absent.

Trends and tendencies

In spite of the discussed dissimilarities, some habitats have some trends in common. The river snails are smaller than those from still water, the Leine snails even slenderer than others. I think this is a way to decrease shell resistance to water currents. *B. tentaculata* was most abundant and also the dominant snail species in the rivers, showing that these habitats were very suitable for the species and less suitable for pulmonates. *B. tentaculata* is also the dominant species in the river and estuary section of the St. Lawrence River (Vincent et al. 1981).

It is evident that the Pond and the Small Pond share some common features. Snails from both populations have large sizes at maturity and they grow to large adult sizes. Snails are less abundant than in the rivers. They share several features of their reproductive strategy, namely egg size and -number, mean spawn number and mean number of eggs per spawn.

In most populations the maximum of parasitation is reached during summer when snails are reproducing.

5. THE LIFE HISTORY OF *BITHYNIA* IN CENTRAL EUROPE AND NORTH AMERICA

Early references on the autecology of *B. tentaculata* and *B. leachii* are in general agreement with the description of the life cycle given above (Boycott 1936; Frömming 1956; Wesenberg-Lund 1939).

More detailed work was done on populations in the United States and Canada. Mattice (1971) and Tashiro (1980, 1982) investigated the same population in Lake Oneida, upstate New York. The size at maturity was 7 mm and the general pattern of the reproductive period is similar to my results. Mattice (1971) found great variation in the number of eggs per female. He found values from 60 up to 1000 eggs per female per reproductive period, but he kept his snails in groups and has no data on individuals. He regarded *B. tentaculata* as a semelparous species.

Tashiro (1980, 1982) proofed that the population was iteroparous and snails lived for up to 3 years. He found somewhat lower egg numbers per female, 158 eggs per two-year old female and 175 per three-year old female. Younger females did not reproduce. He used growth marks for age determination, a method that is afflicted with difficulties as I have shown above. Other authors have also challenged the realiability of growth marks for age determination in *Bithynia* (Chung 1983; Young 1975; but see Vincent and Vaillaincourt 1981).

The evidence that one-year old females are not reproducing is based on measurements of nitrogen content of field-sampled snails and not on direct observations. I think it possible that a larger number of females do not reach the critical shell height for reproduction in their first year due to the more continental climate with harder winters in upstate New York. However, I'm sceptical about the notion that all females need 2 years of development. Females can reach sexual maturity within 1 year in a section of the St. Lawrence River 250 km north of Oneida Lake (Vincent and Gaucher 1983). Since a smaller shell size at maturity that would generally allow reproduction in the first year should be adaptive for a mortality–prone organism as a small freshwater snail, it is most interesting that such a trend was not observed in this long established population.

Vincent et al. (1981), Vincent and Gaucher (1983) and Vincent and Harvey (1985) described 2 different life cycles in the St. Lawrence River, Canada. In colder years the hatchlings failed to reach the critical shell height for reproduction before overwintering and had to overwinter a second time until first reproduction. In warmer seasons, hatchlings reached the critical shell height before overwintering and reproduced at an age of approximately 11 months. They reproduced with some delay compared to older females. This delay was also found in the Small Pond population.

In the St. Lawrence River, snails may live up to 4 years and have 2-3 reproductive periods per lifetime. Two-year old females showed the highest reproductive investment. Both life cycles exist simultaneously in German populations, depending on the date of egg laying and hatching.

The general life cycle pattern of the Canadian populations is similar to the populations in this study, but there are also apparent differences. Both the growth and reproductive season in Canada are 1 to 3 months shorter, the differences caused by the colder climate limiting snail activity to a shorter time period.

Vincent and Vaillancourt (1981) found that snail growth was most intense in the second year. On average, snails grew 3,0 mm between hatching and overwintering, 4,0 mm in their second and 0,7 mm in their third season, reaching an average shell height of 8,5 mm (annual growth increment + size at hatching). Shell growth of snails started simultaneously with reproduction in May (Vincent and Harvey 1985).

Shell heights of older snails overlapped broadly and showed great variability. The mean adult size is in good agreement with my river populations, but shell growth after hatching is clearly more intense in Europe as is supported by Frömming (1956).

The age distribution and snail density varied significantly between years in several populations with no clear trend, this being due to changing mortality rates (Vincent et al 1981). I made similar observations for the Leine population. Vincent et al. (1981) found also great variability in juvenile recruitment between years with nearly complete failure in some years, a pattern that I observed only in the Small Pond population.

Vincent and Gaucher (1983) found interpopulation differences in mean shell height of adults, shell height at maturity, sex-ratio, fecundity and mortality that show similar trends to my data. They examined the reproductive period of 3 populations in the St. Lawrence River for one summer season but had data on growth pattern due to aforementioned studies for a period of several years.

The minimal shell size at maturity was 6 mm for 2 populations and 8 mm for the third. Nearly all females larger than 8 mm took part in reproduction in all populations. Parasitation was regarded as being of minor influence, but this was not studied systematically. The mean adult shell size of the population with the largest shell height at maturity lay also above that of the other populations.

The sex-ratio in one population was clearly female-biased for all age classes whereas in the others percentage of females decreased significantly with age. One population had an overall balanced sex-ratio with a trend to male dominance and the third was clearly male-biased. Such clear shifts in female abundance with age were not observed by me and the sex-ratio for *B. tentaculata* was never female biased. Likewise, mortality rates were not sex-specific in my populations as in the Canada.

The populations were sexual dimorphic with males being higher than females in all cases. This is contrary to my observations with exception of the Small Pond.

Growth patterns of hatchlings were also different between populations leading to varying length-frequencies after overwintering.

The findings of Vincent and Gaucher (1983) in regard to fecundity are most interesting in this context. After classifying their populations in age classes by the growth mark method, they found 3 different generations reproducing in all populations. Egg number was generally lowest for females reproducing the first time which had the largest growth increment during the reproductive period. Mean egg numbers of 2 and 3 year old females were the same in 1 population and decreased with age in the others. The population with the largest shell size laid also the most eggs per female. On the other hand, the smallest females laid more eggs than the medium-sized population and had in the 2 year age class the highest mean egg number of all age classes and populations. Due to their abundance and fecundity, the 2 year old females contributed the most offspring in all populations. Mean egg number per spawn was fairly stable within populations but showed differences between populations.

On the whole, data from the St. Lawrence River are in good agreement with interpopulation differences in Northern Germany, but there are also several deviations apparent. I can not discuss the effects of different age classes since I'm sceptical about the growth mark method. Anyway, only Small Pond females lived long enough for some to take part in 3 reproductive periods. Here I found a trend similar to conditions in the St. Lawrence with younger females producing less eggs than older ones.

Contrary to the situation in the St. Lawrence, the biggest females did not have the highest egg number, quite the reverse, the smallest females laid the most eggs. Since Vincent and Gaucher (1983) did not measure egg size, I can not say if the Canadian populations showed different trade-offs as was apparent for populations in Hannover.

The overall egg number per female in the St. Lawrence is in very good agreement with my still water populations, but on average only half as much as in the Leine. The mean egg number per spawn is clearly below the values for populations in Hannover, even below the Leine population. The largest spawns were comparable to the Leine and markedly below still water populations.

This supports a common trade-off in the reproductive strategy of river populations in Europe and America: In running waters *B. tentaculata* produces many spawns with low mean egg numbers. The authors did not offer any furhter data on reproduction or the temporal dynamic of the reproductive period, so these patterns can not be discussed.

Lilly (1953) reports on a broad habitat use of *B. tentaculata* in England. It has a preference for at least slightly flowing waters, but avoids fast flowing parts of rivers where the species withdraws in the weeds lining the river bank.

She found a reproductive period largely similar to Northern Germany with egg laying starting in late April and ending in July. All juveniles had hatched in August. In winter the snails collected in the mud, preferably at places with reduced water flow. Juveniles reached sexual maturity in their first spring at a shell height of roughly 7 mm and could live for more than a year. *B. tentaculata* was coexisting with other prosobranch species as *Potamopyrgus antipodarum*, *Valvata piscinalis* and *Viviparus viviparus .*

Young (1975) gives rough descriptions of the life cycles of several snails in the Worcester–Birmingham Canal, England. His description of the life cycle of *B. tentaculata* is in agreement with my data. He assumes a shell height of 6 mm at maturity. Egg laying started at approximately 12°C water temperature in 2 consecutive years.

In view of the evidence, I regard the general life cycle of *B. tentaculata* as very conservative. This can be seen by the similarities in its life history in different parts of Europe and America. *B. tentaculata* became established in America as a neozoon in the later part of the 19. century, but its life cycle remained mostly unchanged despite the long period of time. This stands in contrast to the pronounced regional life cycle differences of other invasive molluscs like *Dreissena polymorpha* in Europe and America, a species which became established much later than *B. tentaculata* in North America (Nichols 1996).

This general conservatism on a large scale stands in marked contrast to the plasticity on a local level. My data combined with the evidence gathered by Vincent and Gaucher (1983) demonstrate different trade-offs and reproductive strategies between and within populations.

6. LIFE HISTORY DIFFERENCES WITHIN POPULATIONS OF *BITHYNIA*

Marked individual differences with respect to several key live-history traits are apparent even for different individuals within populations that live under exactly the same environmental conditions. Therefore it seems unlikely that these differences are caused solely by enviromental factors and it is supposed that they have at least some genetic basis and should be seen as different life history strategies resulting from microevolutionary adjustments in the populations. However, as in every study in evolutionary biology, it is extremely difficult to separate phenotypic responses to environmental cues from differences caused by different genotypes in the populations under study and to distinguish between phenotypic plasticity, alternative life-history styles due to epigenetic influences on ontogenetic traits via maternal influences and/or environmental cues and microevolutionary genetic adjustments due to natural selection acting on different genotypes (e.g. Bruton 1989; Lam 1999; Stearns 1992).

The variations within populations are a consequence of the reproductive investments a snail makes. In a given year a potentially iteroparous female can reproduce or skip one reproductive period. When reproducing, a female making an investment of, for example, 350 eggs in one reproductive period can do so by rapidly producing a small number of large spawns within a few weeks at the start of the breeding season, by producing a large number of small spawns over several months or by adopting a strategy in between. The female can start reproduction with the biggest spawn or with rather small ones (for data, see Tab. 31).

These alternative strategies have a lasting influence on several key life history features of the females' progeny:

1) the probability of egg hatching (via egg predation, temperature for embryonic development and possible lack of dissolved oxygen in summer, the major cause of egg mortality)

2) juvenile survival and juvenile growth rates

3) time until first reproduction of offspring.

Growth rates are important because they relate crucially to age at first reproduction, are fluctuating in time and are therefore related to the date of hatching (Brendelberger and Jürgens 1993). Growth is also only possible during a limited favourable season and stops with overwintering. Juvenile snails not reaching a critical shell heigth before overwintering fail to reproduce the following spring. This happens to eggs laid in July/August by females with a long reproductive period. For *Viviparus contectus* (Millet) Eleutheriadis and Lazaridou-Dimitriadou (1995) found an increase in time needed to reach maturity from 3 months for spring born to 8 months for autumn born juveniles. As the costs are obvious in both cases, the benefits are not.

One possible benefit for females with long reproductive periods could be the higher probability of their offspring for colonising new habitats through dispersal via waterfowl (Boerger 1975; Brown 1991). For freshwater snails it is a common way to be dispersed as young while attached to the feet or plumage of waterfowl. The chance of such a thing to happen to the offspring of a given female should increase with the length of her reproductive period. Since freshwater snail populations live under, at least in evolutionary terms, a high risk of frequent extinctions, such a trait may enhance individual fitness in the long run.

It would be very interesting to investigate if *B. leachii* is the more conservative species on the local level. If *B. tentaculata* has a higher phenotypic plasticity and/or ability or scope to evolve, this would be a conclusive explanation for its wider and eurytopic distribution, its numerical dominance in comparison to *B. leachii* and its imigration abilities.

7. FURTHER EVIDENCE FOR INTRASPECIFIC LIFE HISTORY DIFFERENCES IN MOLLUSCS

Intraspecific life history differences that include traits as growth, age and/or size at maturity, egg-number, number of spawns and number of eggs per spawn have been found for several mollusc species (e.g. Aldridge 1982, 1983; Brown 1985, Calow 1981; Costil and Daguzan 1995a, Dupont-Nivet et al. 1998; Lam 1994; Lam and Calow 1989a,b; Lassen 1979; Morton 1991; Vincent and Gaucher 1983); other scientists found intrapopulation variation in egg size (Chester 1996; Estebenet and Cazzaniga 1993) and variation in larval developmental type for marine snails (Ito 1997). Gibson and Chia (1995) found even different larval developmental types within the spawns of individuals in an opisthobranch snail. Differences between populations are often attributable to geographic, climatic and/or nutritional differences and habitat productivity (e.g. Bailey and Mackie 1986; Brown et al. 1985; Carter and Ashdown 1984; Lafferty 1993a; Nichols 1996).

Not all molluscs exhibit different reproductive patterns. Uniform reproductive patterns were found for cultured and wild *Mytilus galloprovencalis* in Spain (Cáceres-Martínez and

Figueras 1998), but Bayne et al. (1983) found interpopulation differences with regard to reproduction for *Mytilus edulis* on English coasts.

The evidence for different intraspecific and intrapopulation life cycle strategies (meaning that there is a definite genetic basis for the observed variability) so far is ambiguous. In one of the first thorough studies on this subject, Russel-Hunter (1961) found interpopulation variation in the life cycles of 5 freshwater snails in a Scottish lake: *Planorbis albus* and *Valvata piscinalis* showed differences in growth rates and *Physa fontinalis*, *Lymnaea peregra* and *Ancylus fluviatilis* showed differences in growth rates as well as in reproductive patterns.

Russel-Hunter thought most differences to be environmentally evoked due to the plasticity of snail life cycles, but assumed also a genetic basis in some. He already pointed out that the pecularities of the freshwater environment as there are its small-scale isolation, its transience and rather harsh and fluctuating conditions should lead to a strong selection pressure on adaptive plasticity per se.

Calow (1981) and Lam and Calow (1989b, 1990) interpreted life-history differences for populations of *Lymnea peregra* (Müller) as being microevolutionary adaptations to local selection pressures, meaning they have at least some genetic basis. On the other hand, the number of traits that showed significant interpopulation differences decreased during laboratory culture and a maternal influence was concluded (Lam and Calow 1989b).

In a further study Lam (1994) found differences in several life-history traits for two neighbouring populations of the pulmonate *Radix plicatulus* (Benson) in a Hong Kong stream. Under the influence of a predatory snail almost absent from one habitat, he found differences predicted by general life history theory in regard of age at maturity, length of recruitment period and mean egg number per egg capsule. But during subsequent laboratory culture only the trait mean egg number per capsule was persistently different in the F_1-generation and in the F_2 no differences were apparent. Hence he favours the idea that the observed life history differences are due to maternal influences that diminuish during the course of laboratory culture. The notion that phenotypic plasticity per se may be heritable and therefore adaptive brings no solution to this problem unless the genetic basis can be demonstrated (Lam 1994).

Baur (1990) found profound variations in several life history traits (egg size, clutch size and -number, length of reproductive period, hatching success) between populations of the land snail *Arianta arbustorum* living at different altitudes in the Alps. Most of the variation was an environmental effect caused by the differences in altitude, but transplant experiments showed also a certain level of a population and hence genetic effect.

In *Viviparus ater* , two populations in different alpine lakes showed a different reproductive trade-off, one producing relatively fewer but larger offspring than the other. The lakes differed in their selection regimes but the authors could not attribute life history differences to genetic causes or phenotypic plasticity (Ribi and Gebhardt 1986).

Different life histories exist for *Potamopyrgus antipodarum* (Gray) in New Zealand. In this species there are mixed populations of sexually reproducing and clonal individuals. This is at least partially due to parasitic pressure of the environment, increasing levels of trematode parasitism leading to predominance of sexual reproduction (Jokela and Lively 1995; Jokela et al. 1997). Turner et al. (1999) found interpopulation differences in behavioural reactions to predator presence in *Physella gyrina*.

The coexistence of different mating systems (selfing versus outcrossing) within and among populations was found for the tropical planorbid genus *Bulinus* and the stream limpet *Ancylus fluviatilis* (Städler and Jarne 1997). *Lymnaea* (*Radix*) *peregra* had self-sterile and self-fertile individuals within the same populations. The individual reproductive performances at sexual maturity were heterogenous among self-fertile lineages (Coutellec-Vreto et al. 1998). The authors stressed the necessity to focus on the variation within populations for a better understanding of the evolution of freshwater snail mating systems.
Corbicula fluminea is sexually polymorphic, populations are comprised of males, females and hermaphrodites in some environments whereas males are absent in others (Morton 1991). This is observed quite frequently in freshwater mussels.
Some authors explain the simultaneous existence of separate sexes and hermaphrodites as a passing effect of sex change with increasing size in older mussels. Since sex reversal seems not to be quantitative in mussel populations as is seen by the existence of large males, small females and different-sized hermaphrodites, the observed pattern would be better explained by the existence of different reproductive strategies within populations (a permanent male/female and permanent hermaphrodite strategy and a sex-reversal strategy).
Semelparity and iteroparity are thought not to be stable and mutual exclusive alternative life history strategies in *Pisidium*, but to be plastic responses to the prevailing environment of the bivalves (Holopainen et al. 1997).

Dupont-Nivet et al. (1998), in a study on the quantitative genetics of reproductive traits in *Helix aspersa* (Müller), found low to medium heritabilities of several traits (egg number, mean egg weight, time from hibernating to mating and time from mating to egg laying). They observed a notable variation in all traits (range of eggs in first clutch was 320, range for mating after hibernation was 60 days) that persisted in the first two generations in culture.

Differences in growth patterns between populations were found for *Littorina rudis* and frequently for *Littorina littorea* (e.g. Huxham et al. 1993; Mouritsen et al. 1999; Roberts and Hughes 1980). Mouritsen et al. (1999) found different growth patterns for three

Danish populations, two of them only 3 km apart. The populations showed also significant differences when infected by parasites. The trematode *Renicola* reduced growth in one population but had no effect on another population. Gorbushin (1997) found also a population-specific effect in the alteration of growth rates after trematode infection in *Hydrobia*.

Shell height at maturity differed between 15 mm and 19 mm between 3 *Lymnaea elodes* populations in Indiana depending on habitat permanence and productivity, but transplant experiments revealed that there was also a genetic component involved (Brown 1985). Three river populations of the freshwater prosobranch *Leptoxis carinata*in upstate New York had different sizes at maturity with females maturing at a smaller size laying proportionally more eggs. Eggs showed interpopulation differences in the C:N ratio and developmental time (Aldridge 1982).

Lafferty (1993a,b) found differences in size at maturity between marine snail populations with high and low incidence of parasitic infections, snails maturing at smaller sizes under high parasitic pressure. In a reciprocal transplant experiment, source population had a detectable influence on size at maturity and therefore he assumes a genetic basis in combination with extent phenotypic plasticity, but he can not rule out a maternal effect or an environmentally induced switch in early snail development.

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VI. SUMMARY

The genus *Bithynia* is represented by two species in Central Europe. *Bithynia tentaculata* (L.) is an iteroparous snail common in European inland waters. It is a sexually reproducing dioecious prosobranch that lives up to 4 years showing a broad habitat use (rivers, streams, lakes, permanent and temporary water bodies of diverse quality). *Bithynia leachii* (Sheppard) is somewhat smaller and less common than *B. tentaculata* and is restricted to water bodies with fairly good water quality. *B. leachii* is only found in still waters and seems to occur always sympatric with *B. tentaculata* . In general terms, *B. tentaculata* is eurytopic compared to a stenotopic *B. leachii*.

I studied the life histories of 6 populations of *B. tentaculata* and 1 sympatric population of *B. leachii* for 3 years in Lower Saxonia, Germany. All populations were regularly sampled and males and females out of 4 populations were kept in individual cages in the field during their entire lifespan. Data were collected on the principal life history traits as size and age at maturity, growth pattern and mortality schemes, parasitation and, most important, reproduction. Reproductive traits studied were egg size and - number, spawn size and - number, oviposition site choice, hatching success of eggs and sex ratio of offspring, and the temporal aspects of reproduction. Differences were apparent at 3 levels: between species, between populations and also within populations. Additionally, I found several trade-offs between conflicting demands connected to reproduction that differed in their outcome between species and populations.

Species level: Compared to *B. leachii*, *B. tentaculata* shows some differences in the overall growth pattern, is larger at maturity, attains a larger body size and shows only a slight sexual dimorphism, if any. The females lay fewer but larger spawns containing large eggs. They have a potential longer life span, but are more susceptible to parasitation by trematode larva. *B. leachii* females are approx. 20% larger than males and lay small eggs in many small spawns during a long reproductive period. In direct comparison of the sympatric populations, *B. leachii* laid more eggs per reproducing female that had also a higher hatchability.

Population level: The populations of *B. tentaculata* showed several differences that seem to be local adaptations. Populations differed with regard to mean shell height of populations, shell height at maturity, sexual dimorphism and overall growth patterns. Snail abundance, parasitic infections and life expectancy differed. They also differed in size and number of eggs and spawns produced, egg hatchability and their reproductive pattern over time. In general, river snails were smaller than snails from standing waters and showed a trade-off with regard to egg number and egg size (producing many but smaller eggs and many but smaller spawns) that resembled the trade-off observed for *B. leachii*.

Individual females also showed different life history strategies within populations. Mostly I observed different reproductive patterns in space and time. Some females had a long reproductive period laying many small spawns, others laid few large spawns within short time and had therefore a long postbreeding period.

In conclusion, I compared my data with observations on *B. tentaculata* populations in North America, where the species was introduced during the last century. In general, the life history of *B. tentaculata* seems conservative on a large scale, but shows some plasticity on the local level.

ZUSAMMENFASSUNG

Die Gattung Bithynia ist mit 2 Arten in Mitteleuropa vertreten. *Bithynia tentaculata* (L.) ist ein im Süßwasser häufig vorkommender, sich sexuell vermehrender und getrennt-geschlechtlicher iteroparer Prosobranchier, der bis zu 4 Jahre alt werden kann. Die Art bewohnt ein breites Spektrum unterschiedlicher Habitate auch schlechter Wasserqualität (Flüsse, Bäche, Gräben, Seen, Teiche als auch temporäre Gewässer). *Bithynia leachii* (Sheppard) ist etwas kleiner, ebenfalls getrenntgeschlechtlich und iteropar, weniger weit verbreitet und auf Stillgewässer mit besserer Wasserqualität beschränkt. Interessanterweise scheint die Art stets sympatrisch mit *B. tentaculata* aufzutreten. *B. tentaculata* ist euryök verglichen mit der stenöken *B. leachii*.

Ich habe 6 *B. tentaculata* Populationen und eine sympatrische *B. leachii* Population über einen Zeitraum von 3 Jahren in Niedersachsen, Deutschland, beobachtet. Die Populationen wurden regelmäßig beprobt und Männchen und Weibchen aus 4 Populationen wurden bis zu ihrem Tod individuell in Käfigen am Entnahmestandort gehältert. Ich habe Daten zu den wichtigsten Aspekten des Lebenszyklus der Tiere gesammelt wie Alter und Größe bei der Geschlechtsreife, Wachstumsverlauf, Mortalität, Parasitierung und vor allem zur Reproduktionsbiologie. Aspekte der Reproduktionsbiologie waren u.a. Eigröße und Eizahl, Laichschnurgröße und Laichschnurzahl, Wahl des Eiablageplatzes, Schlupferfolg, Geschlechterverhältnis des Nachwuches und der zeitliche Verlauf der Reproduktionsperiode. Signifikante Unterschiede traten sowohl zwischen den Arten, zwischen den Populationen als auch innerhalb der Populationen auf.

Verglichen mit *B. leachii* hat *B. tentaculata* einen etwas anderen Wachstumsverlauf, ist bei der Geschlechtsreife als auch als Adulttier größer und zeigt in einigen Populationen einen schwach ausgeprägten Geschlechtsdimorphismus. Die Weibchen legen wenige, dafür große Laichschnüre mit großen Eiern. Sie haben eine potentiell höhere Lebenserwartung, sind aber auch häufiger parasitiert. Die Weibchen von *B. leachii* sind ca. 20% größer als die Männchen und legen kleine Eier in Eischnüren, die zumeist nur wenige Eier enthalten. Im Vergleich der beiden sympatrischen Populationen legte *B. leachii* im Verlauf einer längeren Reproduktionsperiode mehr Eier als die größere *B. tentaculata*.

Auch die 6 *B. tentaculata* Populationen zeigten erhebliche Unterschiede. Sie unterschieden sich in der Durchschnittsgröße, der Größe bei Geschlechtsreife, dem Wachstumsverlauf und dem Vorhandensein eines Sexualdimorphismus. Auch Häufigkeit der Art, Parasitierungsgrad und Lebenserwartung waren unterschiedlich. Eizahl und -größe, Laichschnurzahl - und größe, Schlupfraten und zeitlicher Verlauf der Reproduktion waren verschieden. Schnecken aus Fließgewässern waren kleiner und zeigten einen Trade-off, der an *B. leachii* erinnerte, indem sie ihre reproduktive Investition in zahlreichere, aber kleinere Eier in zahlreichen, aber kleinen Laichschnüren aufteilten.

Innerhalb der Populationen zeigten einzelne Weibchen abweichende Reproduktionsverläufe. Zumeist unterschied sich das raumzeitliche Muster der Reproduktion. Es gab Weibchen mit einer langen Laichperiode, in deren Verlauf zahlreiche Laichschnüre mit wenigen Eiern produziert wurden und Weibchen mit kurzer Reproduktionsperiode, in deren Verlauf wenige Laichschnüre mit vielen Eiern gelegt wurden. Dies hatte auch Auswirkungen auf die Dauer der postreproduktiven Phase vor der Überwinterung.

Im Vergleich mit Befunden aus Nordamerika, wo *B. tentaculata* im letzten Jahrhundert eingeschleppt wurde, ergibt sich abschließend, daß der Lebenszyklus der Art weiträumig gesehen sehr konservativ ist, dem aber eine nicht unerhebliche kleinräumige Plastizität entgegensteht.

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