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Size-dependent shell growth and survival in natural populations of the rock-dwelling land snail *Chondrina clienta*

Denes Schmera, Anette Baur and Bruno Baur

D. Schmera[1,2], A. Baur and B. Baur, Section of Conservation Biology, Department of Environmental Sciences, University of Basel, St. Johanns-Vorstadt 10, 4056 Basel, Switzerland.

[1]Corresponding author (e-mail: denes.schmera@unibas.ch).

[2]Present address: Balaton Limnological Institute, Centre for Ecological Research, Hungarian Academy of Sciences, Klebelsberg Kuno 3, 8237 Tihany, Hungary.

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Abstract: Rock-dwelling land snails, feeding on algae and lichens that grow on stone surfaces, may influence the structure and function of these ecosystems. Yet, little is known about the life history of rock-dwelling snails. We performed a 30-month mark-release-resight study in four populations of *Chondrina clienta* (Westerlund, 1883) inhabiting vertical walls of abandoned limestone quarries on the Baltic island of Öland, Sweden, to assess growth rate and survival of juvenile snails and determine age at maturity. We marked 800 individuals ranging in shell height from 1.4 to 4.9 mm, released them in their original habitat, and remeasured their shell height at intervals of 6 months. Shell growth of juvenile *C. clienta* was affected by the site (quarry wall) and the size of the individual, being highest in medium-sized snails. Shell growth occurred both during summer and winter. Annual apparent survival rates of *C. clienta* were size-dependent and ranged from 58.6% to 96.3%. Sexual maturity was reached at an age of 5 years, which is later than in most large-sized snail species. Our study extends current knowledge on life history of land snails to a rarely studied group dwelling on rock surfaces.

Key words: age at maturity, annual survival rate, *Chondrina clienta*, individual growth, life history, rock-dwelling land snail, terrestrial gastropod.

Introduction

Growth is an important life-history process, influencing a range of later fitness-related traits such as age and size at maturity and total reproductive output (Stearns 1992; Charnov 2004; English et al. 2014). Growth of individuals can be variable in space and time, for example as a consequence of variation in food availability, temperature and precipitation, but also due to variation in genotype and phenotype among individuals. Individual growth rate varies also between seasons, years and populations (e.g. in snakes; Forsman 1993). Interindividual variation in growth is a primary determinant of the material on which natural selection acts.

Individual differences in growth rate have been observed in a wide range of species and occur even when animals are housed individually and fed *ad libitum*, suggesting that growth is an intrinsic individual attribute (Arendt 1997; Biro et al. 2014). As an intrinsic trait, individual growth rate is expected to be repeatable across years (i.e. individuals growing rapidly in the first year will also grow fast in the second year). Studies on individual growth have been biased towards large-sized species, whose individuals can easily be tagged and show a high recapture probability in natural populations. Thus, few empirical data are available on individual growth and other life-history traits in many small-sized animal species with a cryptic life. This is also true for terrestrial gastropods. In land snails, knowledge on individual growth, age at maturity and survival in the wild is limited to species with large shells, e.g. *Cepaea nemoralis* (L., 1758), *Arianta arbustorum* (L., 1758), *Rhagada convicta* Cox, 1870, and *Helicella pappi* (Schütt, 1962) (Williamson 1976, Baur and Raboud 1988; Johnson and Black 1991; Lazaridou-Dimitriadou 1995), despite the fact that the majority of snail species have small shells (< 7 mm in shell height or breadth). This can be explained by the notorious difficulties to mark tiny individuals and to recover them in leaf litter or dense vegetation. To circumvent these problems, life-history traits have been examined in snails kept in the laboratory or under semi-natural conditions (e.g. Oosterhoff 1977; Baur 1989; Sulikowska-Drozd and Maltz 2012). This approach provides reliable data on egg size and batch size, but less reliable estimates of individual growth rate, age at maturity, survival and longevity. For example, individuals of *A. arbustorum* from an alpine population needed 186 days from hatching to complete shell growth and reach sexual maturity under laboratory conditions (Baur 1984), while individuals in the wild required 4-5 years (Baur and Raboud 1988). With a few exceptions, empirical data on the life history of small-sized land snail species in their natural habitat are not available (Heller 2001).

In the present study, we investigated growth rate, age at maturity and survival in individuals of the rock-dwelling land snail *Chondrina clienta* (Westerlund, 1883) in their natural habitat. Snails of this small sized-species spend their entire life on rocks, where they graze algae and lichens during periods of optimal temperature and sufficient moisture (Baur 1988; Baur et al. 1994). Attached with their shell opening to the rock surface, the snails rest during unfavorable conditions and manage to survive extreme fluctuations in temperature. The lack of vegetation on rock surfaces and the snails' limited dispersal capacity result in a relatively high recovery rate of marked individuals (Baur and Baur 1995). We traced marked juveniles and periodically recorded their growth on four vertical limestone quarry walls on the Baltic island of Öland, Sweden. This approach allowed an assessment of size-specific, seasonal and annual growth rates and survival rates. Age at maturity was assessed by combining individual growth rates. In a second approach, age at maturity was quantified by analyzing the shell height frequency distribution of a population.

In particular, we addressed the following questions: (1) Do snails from the four rock walls differ in individual growth rate? (2) Do snails also grow during winter, and if so, do individual growth rates differ between summer and winter months? (3) Is the individual growth rate of juvenile *C. clienta* repeatable across years? (4) Does survival of juvenile *C. clienta* depend on individual snail size and differ between seasons? (5) How many years do newly hatched snails need to complete shell growth and achieve sexual maturity?

Materials and methods

The species

Chondrina clienta occurs in open limestone areas of Central and South-eastern Europe and in three isolated areas of Sweden, namely on the Baltic islands of Öland and Gotland and in one small area on the mainland (Kerney and Cameron 1979; Waldén 1984; Baur 1987). The snail has determinate growth. Its cylindro-conical shell is dextral and in adults is 5.5–7 mm high (Baur 1988). Sexual maturity is attained after the completion of shell growth, which is indicated by the building of a reflected lip around the shell aperture and six short folds (teeth) within the aperture. *Chondrina clienta* is ovoviviparous; the shell height of hatchlings is c. 0.8 mm. The animals are well adapted to rocky habitats; they are resistant to drought with activity confined to periods of high air humidity, and their specialized radula enable them to graze algae and epi- and endolithic lichens from rock faces (Schmid 1929; Breure and Gittenberger 1982; Fröberg et al. 1993; Baur et al. 2000). Among other lichen feeding snail species in calcicolous habitats on Öland, *C. clienta* is by far the most abundant species on both horizontal (i.e. limestone pavements, the snails' original habitat) and vertical (e.g. quarry walls) rock surfaces (Fröberg et al. 2011). In a controlled laboratory experiment, juvenile growth rate, time to complete growth, adult shell size and survival were affected by intraspecific competition (Baur and Baur 1990). At the study sites (see below), the land snail *Helicigona lapicida* (L., 1758) lives on adjacent piles of stone. On rainy days, individuals of *H. lapicida* have been observed to graze lichens on vertical quarry walls (Baur and Baur 2006). However, the quarry walls investigated may not differ in density of this potentially competiting species.

Dispersal of marked adult *C. clienta* averaged 96 cm yr^{-1} on vertical rock walls (Baur and Baur 1995).

Study sites and general methods

To assess shell growth and survival of juvenile *C. clienta* we performed a 30-month mark-release-resight study from March 1992 to October 1994 at four sites in the Great Alvar in the southern part of the Baltic island of Öland, Sweden ($56^{\circ}33'$N, $16^{\circ}36'$E). The area is a calcareous grassland grazed by sheep and cattle with several abandoned limestone quarries of small size (50–500 m^{2}; supplementary Figs. S1–S3). The study sites were vertical quarry walls located within an area of 0.5 km^{2}, 1.5 km SSW of Vickleby (for site description see Table 1). The Great Alvar is a UNESCO World Heritage Site since 2000. Vegetation, climate and geomorphology of the Great Alvar have been described by Krahulec et al. (1986).

We searched the quarry walls systematically for juvenile *C. clienta* with a shell height <4.9 mm. To avoid the marking of empty shells, the snails were activated by keeping them in plastic boxes lined with moist paper toweling. We individually marked 200 juveniles from each site by writing tiny numbers (1–200) on their shells with a waterproof ink pen on a minute spot of correction fluid (Tipp-Ex). At the same time we measured the shell height of each individual to the nearest 1/12 mm (shell height: mean = 2.7 mm, range 1.4–4.9 mm; n = 800). Very small individuals (shell height 0.8–1.3 mm) could not be individually marked. Marking and measuring were carried out using a binocular microscope with a stage micrometer. The animals showed no visible reaction to the marking and measuring procedure. We released marked *C. clienta* at their sites of origin within 1–2 days after sampling. To minimize overcrowding at the release point, which may result in increased dispersal, we released the snails in groups of 50 at four points (situated in line with a distance of 50 cm between release points) on each rock wall. All field sampling was done under dry conditions when the snails were at rest attached to the rock surface.

To determine shell growth and survival of *C. clienta*, we searched the entire rock wall at the four sites for marked snails after 6, 12, 18, 24 and 30 months. On each sampling, we measured the shell height of the recovered snails as described above. The resampled snails were released within 2 days at their site of origin following the procedure described above. Very few illegible marks were found. These snails were not considered in the data analyses.

Local population density of *C. clienta* at the four sites A–D was estimated by counting the number of juvenile and adult snails found on the vertical rock surface and in fissures within 3 min. searching time by one of us (B.B.). Density estimates were conducted exclusively under conditions of dry weather, when the snails are at rest (Baur and Baur 1991), because this method reveals reliable density estimates for rock-dwelling land snails

(Armbruster et al. 2007). On each rock wall, density estimates were based on three replicate searches.

Analysing size distributions is the most frequently used approach to estimate growth rates and age at maturity in gastropods. We aimed to compare direct measurements of juvenile growth obtained from individually marked snails (see above) with indirect estimates obtained from a size distribution. We used a representative subset of a population of *C. clienta* to assess the time required to complete shell growth and thus to reach sexual maturity. We sampled all snails found within an area of 6 m^2 on a rock wall located 50 m from sites A–D on 23 October 1990. The sampling area of 6 m^2 corresponded to the area of the rock walls at site B and C. Using a magnifying glass we could also find tiny individuals in small fissures. The shell height of each snail was measured as described above.

Data on temperature and precipitation were obtained from the Meteorological Station in Kalmar, 15 km NW of the study sites. The annual mean temperature in Kalmar is 7.5 ^{o}C (July mean: 17.5 ^{o}C; January mean: –0.9 ^{o}C) and the annual mean precipitation is 543 mm (mean values from 1978–2013; SMHI 2014). The mean temperature in the first 12 months of our study was 0.7 ^{o}C higher than the annual mean temperature, while the amount of precipitation was 21% less than the annual mean precipitation. The following 12 months were 0.3 ^{o}C colder than the annual mean temperature and the amount of precipitation exceeded the annual mean precipitation by 10%.

Data analyses

Preliminary analysis showed that individual shell growth differs among snails of different size. We therefore assigned individuals of *C. clienta* to ten size classes for the analyses on size-dependent growth rate and survival. Size class 1 consisted of individuals with shell height ≤ 2.0 mm, size class 2 of individuals with shell height 2.1–2.5 mm, size class 3 of individuals with shell height 2.6–3.0 mm, and so on. Size class 10 consisted of individuals with a shell height > 6 mm.

Individual shell growth was assessed in two ways. Absolute growth was expressed as shell height increase of an individual between t_0 and t_1. The relative shell growth of an individual in percent was calculated as 100 x (h_{t1}– h_{t0})/h_{t0} where h_{t0} is the shell height of an individual at t_0 and h_{t1} its shell height at t_1. Absolute and relative shell growth was determined over 6 months (growth during winter and summer, respectively) and over 1 year (annual growth). To quantify individual shell growth within a year, we only considered individuals belonging to the size classes 1 to 5 at the beginning of the experiment and which were recovered both after 12 and 24 months. We fitted a linear model with the factors site and size class and the interaction of the two factors and selected the minimal adequate model explaining relative shell growth using the Akaike Information Criterion (AIC). Data were checked for homoscedasticity prior to the analyses.

To examine whether individual growth rate of juvenile *C. clienta* is repeatable between years, we calculated the Pearson correlation between the shell height increase in the first year and that in the second year for all individuals of a size class, using separate analyses for the size classes 1–5. Juveniles belonging to the size class 6 at the beginning of the study were not considered because they attained adult size in the second year.

We applied Cormark-Jolly-Seber (CJS) modeling with the effects time and size class to estimate survival from mark-release-resight data (Kéry and Schaub 2012). This analysis uses a Bayesian approach (Kéry 2010) and quantifies the *recapture probability* (probability of resighting a marked individual at time *t* that is alive in the sampling population at *t*) and the *survival probability* (probability that an individual that is alive and in the population at time *t* is still alive and in the population at time *t+1*; Kéry and Schaub 2012). An important biological issue is that only apparent survival can be estimated with CJS modeling; that is "*1–survival*" represents both animals that died and animals that left the population or study area (emigration). In the first analysis, we examined the potential effect of the site on apparent survival, in the second analysis the effect of size class on apparent survival. For the survival analyses we used *WINBUGS 14* (Lunn et al. 2000) and the package *r2WinBUGS* (Sturtz et al. 2005) in the R environment (R Core Team 2013).

The frequency distribution of shell height represents a cross section of a population at a specific time. We fitted finite mixture distribution models to the data by using a maximum likelihood method with a combination of Newton-type algorithms and the expectation-maximization algorithms (Macdonald and Pitcher 1979; Macdonald and Green 1988). This approach allows estimates of size and age at maturity. The package *mixdist* (Macdonald and Du 2012) in the R environment (R Core Team 2013) was used for this analysis.

Results

Recovery of marked snails

The percentage of marked snails resighted decreased with time from 61.5 ± 2.1% (mean ± SE, n = 4 sites) after 6 months to 49.9 ± 2.7% after 12 months, 42.9 ± 3.6% after 18 months, 31.9 ± 1.0 after 24 months, and 4.9 ± 1.0% after 30 months. Due to the steep decline in recovery rate between 24 and 30 months we considered only data obtained within 24 months for the growth and survival analyses. Considering snails belonging to different size classes, recovery rate of marked individuals was slightly higher in larger juveniles than in smaller ones after 6, 12 and 18 months (supplementary Table S1). After 24 months, the recovery rate of marked individuals was very similar in all size classes (supplementary Table S1).

Shell growth

Individually-marked *C. clienta* differed considerably in shell growth (supplementary Fig. S4). In the first year, the relative shell growth was affected by the site (quarry wall) and the size class to which the individual belonged (Table 2). Snails at site C grew faster (mean relative shell increase = 48.2%) than individuals at site A (32.8%; linear model, estimate = 0.512, s.e. = 0.122, t = 4.197, P < 0.001). The significant interaction between site and size class indicates that snails of different size classes showed different relative growth rates on the four rock walls in that year. In the second year, relative shell growth was again affected by the site and tended to be influenced by the size class (Table 2). Snails at site D showed the largest relative growth (mean relative shell increase = 69.0%), while snails at site B showed the smallest relative growth (mean = 47.7%).

Snails from the four sites may represent the variation in shell growth of *C. clienta* inhabiting limestone quarries. We therefore pooled data of snails from the four sites for further growth analyses. Considering different size classes, annual shell increase showed a hump-shaped pattern (Fig. 1). It was highest in medium-sized individuals (shell height 2.5–4.5 mm) and relatively low in small and large (but not yet fully-grown) individuals. Relative shell growth showed a similar hump-shaped, size-dependent pattern (not shown).

The two measurements taken per year allow an assessment of shell growth during the summer and winter months. Interestingly, the growth rate of individually marked *C. clienta* did not differ between summer and winter, whatever the size classes (Fig. 2; paired *t* test, $t = 0.926$, df = 9, $P = 0.379$).

Comparing the shell height increase of individual snails in the first and second year revealed two different patterns (supplementary Fig. S5). The shell height increases of juvenile *C. clienta* belonging to the size classes 1 and 2 at the beginning of the study were not correlated between the two years. In contrast, the shell height increase in the first year was negatively correlated with that of the second year in snails belonging to the size classes 3–5, indicating a trade-off in shell growth (supplementary Fig. S5). Individuals growing rapidly in the first year were growing slowly in the second year and vice versa.

Survival

The recapture probability varied with the size of the marked individuals. Recapture probability was highest in snails belonging to the size classes 2–6 (see methods) ranging from 65.9% to 79.1%, but lower in the smallest snails (size class 1: 46.2%) and the largest ones (size class 7: 51.0%). Bayesian analysis revealed that apparent survival of *C. clienta* over 6 months followed a similar pattern at the four sites, ranging from 74.0% to 80.6% (supplementary Fig. S6). Considering the different seasons, apparent survival of juveniles was generally lower during winter (mean 76.9% and 73.2% after 6 and 18 months, respectively) than during summer (mean 86.9% and 83.1% after 12 and 24 months). Apparent survival over 6 months was higher at site A than at site B (range of creditable interval -0.666 – -0.082), but did not differ among the other sites (supplementary Fig. S6).

Bayesian analysis revealed annual apparent survival rates of *C. clienta* individuals ranging from 58.6% to 96.3%. Annual apparent survival depended on the size of the individuals (supplementary Fig. S7). The smallest snails (size class 1) had an annual apparent survival rate of 92.1% and 90.2% in the two consecutive years. In size class 2, annual apparent survival was 64.8% and 58.6%. In snails belonging to the size classes 3–7, annual apparent survival increased with the size of the individuals, being highest in the largest snails (96.3% and 95.4% in the two successive years; supplementary Fig. S7).

Age at sexual maturity

The time to complete shell growth and thus the age at sexual maturity can be deduced by combining data of marked individuals that were recovered on all occasions (Fig. 3). Snails of size class 1 (shell height > 2 mm) needed 1 year to reach the shell height of size class 2 (2.01–2.50 mm). Snails of size class 2 reached either size class 3 (2.51–3.00 mm), size class 4 (3.01–3.50 mm) or size class 5 (3.51–4.00 mm) within 1 year. Snails of size class 4 needed 1 year to attain size class 6 (4.05–4.50 mm) and snails of size class 6 required another year to complete shell growth. Assuming that individuals belonging to size class 1 were already 1-year old, then based on the average annual shell increase a snail requires 5 years to attain adult size and sexual maturity (Fig. 3). However, the huge interindividual variation in shell growth may allow a few individuals to reach adult size within 4 years, while others may need 6 or 7 years.

Size (shell heigth frequency) distribution

Individuals of *C. clienta* sampled on a quarry wall on 23 October 1990 ranged in shell height from 0.83 to 6.25 mm (n = 375; Fig. 4). The frequency distribution of shell height shows four peaks among the juveniles and one distinct large peak of fully-grown (adult) snails indicating that there are four year cohorts of juveniles and – assuming that the first peak represents 1-year-old snails – that adult size is attained at an age of 5 years. The frequency of juvenile individuals decreased with increasing shell height, indicating mortality between year cohorts. Snails with a reflected shell lip measured at least 5 mm, an exception was one individual with a shell height of 4.83 mm (Fig. 4). The frequency of fully-grown snails in the size distribution suggests that this size class consists of several year cohorts, and consequently that adult snails may live for several years.

Discussion

The present study showed that individual shell growth rate of juvenile *C. clienta* differed among quarry walls and that growth rate depended on the size of the snails. Similarly, the survival rate was size-dependent in juvenile *C. clienta*. Most interestingly, shell growth occurred not only during summer, but also during the winter half year.

In terrestrial gastropods, climate and weather are an important source of variation in growth rate because their activity is constrained by humidity and temperature conditions (Oosterhoff 1977; Riddle 1983). Activity of rock-dwelling snails is restricted to periods of optimal temperature and sufficient moisture (Neuckel 1981). The clausilid *Cristataria genezarethana* (Tristram, 1865) is active only during 1.2–3.3% of the time of a year on karstic rocks in Israel (Heller and Dolev 1994), and *Chondrina avenacea* (Bruguière, 1792) 11–14% of the time of a year on limestone cliffs near Basel, Switzerland (Neuckel 1981). During summer heat or during winter frosts, the snails must cope with extreme temperatures. *Chondrina avenacea* enters estivation very rapidly whenever the snails experience drying out of their environment. The snails rapidly suppress their metabolism and minimize water loss using a discontinuous gas exchange pattern (Kostal et al. 2013). Hibernating snails rely on a supercooling strategy which allows them to survive when air temperature drops to as low as –21 ^{o}C (Kostal et al. 2013). Winter dormancy in *C. clienta* is, however, not deep. Schlesch (1937) observed individuals of *C. clienta* grazing lichens under mild conditions in January on Öland. This may explain the surprising finding that the shell growth rate during the winter half year did not differ from that of the summer half year. In the populations studied, *C. clienta* may become active throughout the year whenever the environmental conditions are favorable. The yearly variation in shell growth might be a result of the prevailing weather conditions, in particular of the amount of precipitation and its temporal distribution within the year.

Individuals of *C. clienta* feed on cyanobacteria, algae and various species of lichens (Baur et al. 1992; Fröberg et al. 1993; Baur et al. 1994). Lichens are protected against herbivores by a number of mechanisms. The presence of different secondary compounds, the lichens' nutrient content, surface toughness, type of photobiont, and their growth form (epilithic, endolithic, foliose) may account for differential preferences shown by grazing snails (Fröberg et al. 1993; Hesbacher et al. 1995; 1996; Baur et al. 2000). The small-scale spatial distribution of cyanobacteria and lichen species varies considerably on rock surfaces, resulting in a spatial heterogeneous distribution of food resources for the snails (Baur et al. 1995; Baur and Baur 1997; Fröberg et al. 2011). Considering the relatively short periods of time favorable for grazing and the snails' limited dispersal capacity, individuals may encounter more or less favorable food patches, which may result in more or less shell growth (Fröberg et al. 2011).Thus, differences in food availability and in microclimate (the aspect of the rock wall may influence the length of snail activity) in combination with intraspecific competition could explain the differences in growth rate found among sites. However, the number of replicates (n = 4 rocks walls) does not allow to test this hypothesis.

The hump-shaped growth rate distribution of *C. clienta* belonging to different size classes indicates that individual growth curves have a sigmoid shape with the fastest shell increase in juveniles of medium size, a growth pattern found in other land snail species as well (Baur 1984; Kuznik-Kowalska 2006). The slower growth in the final juvenile stage could be explained by the investment of energy to build the shell armature as has been reported in clausiliid species (Maltz and Sulikowska-Drozd 2011). Interestingly, we did not find repeatable individual shell growth between two successive years. On the contrary, individuals of three size classes growing rapidly in the first year grew slowly in the second year and vice-versa. The underlying cause for this intraindividual trade-off between current and future shell growth remains to be investigated.

Our study showed that apparent survival in *C. clienta* is size-dependent. Larger individuals had a higher survival rate than smaller ones, an exception being individuals of the smallest size class. The actual survival rate might even be higher, because in the estimate of apparent survival snails that died and snails that left the study area were considered the same (see Statistical analyses). On vertical rock walls, the distances moved by juvenile *C. clienta* increased with the shell size of the individuals (Baur and Baur 1995). In the present study, a few individuals might have left the quarry walls, which represented the study areas. However, the size class-specific recovery rate of marked individuals was not lower in larger juveniles than in smaller ones (supplementary Table S1), as expected by the snails' dispersal capacity. This indicates that not only the apparent survival rate but also the actual survival rate is size-dependent in *C. clienta*.

Unfavorable weather is known to act as a density-independent mortality factor in many invertebrate species (Begon et al. 2006). Winter mortality is assumed to be one of the crucial factors in the life cycle of land snails (Wolda 1963; Wolda and Kreulen 1973; Cain 1983). Extreme temperatures (cold and heat) may cause a substantial part of the total mortality in land snails (Williamson et al. 1977). Land snails overwintering at or near the soil surface in temperate regions are potentially exposed to low temperatures, being readily killed by ice formation in the tissue (Ansart et al. 2014). Consequently, behavioral adaptations (e.g., searching for favorable hibernation positions) and physiological acclimatization, such as the development of cold-hardiness in autumn and the maintenance of sufficient cold resistance during winter, may be essential in such species (Riddle and Miller 1988; Kostal et al. 2013; Ansart et al. 2014).

Winter mortalities ranging from 2.4% to 19.0% have been reported for *Allogona ptychophora* (Brown, 1870), *A. profunda* (Say, 1821), *Mesodon thyroidus* (Say, 1816), *C. nemoralis* and *A. arbustorum* (Blinn 1963; Carney 1966; Williamson et al. 1977; Terhivuo 1978; Andreassen 1981). All these species have relatively large shells (shell breadth >15 mm) and hibernate buried into the soil or under leaf litter. In contrast, winter mortality of *C. clienta* inhabiting exposed stone walls on Öland averaged 13.9% in juveniles and 10.5% in adults during mild winters but increased to 64.3% in juveniles and 67.9% in adults during an extremely cold winter (Baur and Baur 1991). In all four winters, mortality was not influenced by the local population density (Baur and Baur 1991). In the present study, the winters were relatively mild (mean minimum temperatures in January of –2.5 ^{o}C in 1993 and –2.0 ^{o}C in 1994), and did not cause any increased snail mortality.

In life-history theory, age at maturity in animals is defined as age at first reproduction. *C. clienta* reproduces for the first time in the autumn after having attained adult size. In our study, the results of two different approaches (combination of individual shell growth data and the analysis of the shell size distribution of a population) revealed that most individuals of *C.*

clienta completed shell growth at an age of 5 years, even though a few individuals reach adult size within 4 years, while others need 6 or 7 years, indicating a relatively late maturity in this small-sized land snail species. The size (shell height frequency) distribution data were obtained 1.5 years before the start of the growth experiment. Considering individual growth rates (5 years to attain adult size), a large proportion of the individually marked snails were already alive when the sample for the size distribution was collected. It is very unlikely that the time elapsed between the two studies affects the results. A similar age at maturity was reported in the small-sized rock-dwelling land snail *Cristataria genezarethana* (Tristram, 1865) (Heller and Dolev 1994), whereas most large-sized snail species (e.g., *C. nemoralis*) reach sexual maturity at an age of 2–3 years (Oosterhoff 1977; Heller 2001).

Life-history theory predicts later maturity if there is further growth and if fecundity increases with size leading to a higher initial fecundity (Stearns 1992). Furthermore, maturity will be delayed if it improves the instantaneous juvenile survival rate, e.g., by giving birth to larger offspring. In the majority of land snails, female fecundity (number of eggs or hatchlings produced) increases with the size of the individual (Baur 1994). With a delayed maturity individuals of *C. clienta* attain a larger adult size and thus have a higher fecundity. A further delay in maturity might be counteracted by the cumulated juvenile mortality. The balancing selection pressures of attaining a large shell size through delayed maturity versus the cumulated higher juvenile mortality varies among localities, indicated by a considerable variation in mean age at maturity among land snail populations within species (Heller 2001). For examples, age at maturity in *A. arbustorum* increased along an elevational gradient from 2 years at 1220 m to 5 years at 2600 m in the European Alps (Baur and Raboud 1988). Some of these interpopulational differences in age at maturity are genetically determined, while others are environmentally induced (Baur 1984).

Conclusions

Previous studies have been concerned mainly with large-sized gastropods. The work presented here fills a gap in land snail ecology and thus leads to a better understanding of the population dynamics of small-sized rock-dwelling land snails. Our results show that individual growth and juvenile survival are size-dependent in *C. clienta*, and vary slightly among populations, most probably due to habitat-related differences in microclimate. The mean age at maturity of 5 years found in *C. clienta* is higher than those reported in most large-sized snail species. Our work also underlines the notion that winter is not a time of constant hibernation for this rock-dwelling snail species in natural populations in southern Scandinavia, indicated by shell growth in juveniles during the colder season.

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References

Andreassen, E.M. 1981. Population dynamics of *Arianta arbustorum* and *Cepaea nemoralis* in western Norway. Fauna Nor. A, **2**: 1–13.

Ansart, A., Guiller, A., Moine, O., Martin, M.-C., and Madec, L. 2014. Is cold hardiness size-constrained? A comparative approach in land snails. Evol. Ecol. **28**: 471–493. doi:10.1007/s10682-013-9680-9.

Arendt, J.D. 1997. Adaptive intrinsic growth rates: an integration across taxa. Rev. Biol. **72**: 149–177. doi:10.1086/419764.

Armbruster, G.F.J., Hofer, M., and Baur, B. 2007. Effect of cliff connectivity on the genetic population structure of a rock-dwelling land snail species with frequent self-fertilization. Biochem. Syst. Ecol. **35**: 325–333. doi:10.1016/j.bse.2006.12.005.

Baur, A., and Baur, B. 1991. The effect of hibernation position on winter survival of the rock-dwelling land snails *Chondrina clienta* and *Balea perversa* on Öland, Sweden. J. Mollusc. Stud. **57**: 331–336. doi:10.1093/mollus/57.3.331.

Baur, A., Baur, B., and Fröberg, L. 1992. The effect of lichen diet on growth-rate in the rock-dwelling land snails *Chondrina clienta* (Westerlund) and *Balea perversa* (Linnaeus). J. Mollusc. Stud. **58**: 345–347. doi:10.1093/mollus/58.3.345.

Baur, A., Baur, B., and Fröberg, L. 1994. Herbivory on calcicolous lichens – different food preferences and growth rates in two coexisting land snails. Oecologia, **98**: 313–319. doi:10.1007/bf00324219.

Baur, B. 1984. Shell size and growth rate differences for alpine populations of *Arianta arbustorum* (L.) (Pulmonata: Helicidae). Rev. Suisse Zool. **91**: 37–46.

Baur, B. 1987. Richness of land snail species under isolated stones in a karst area on Öland, Sweden. Basteria, **51**: 129–133.

Baur, B. 1988. Microgeographical variation in shell size of the land snail *Chondrina clienta*. Biol. J. Linn. Soc. **35**: 247–259. doi:10.1111/j.10958312.1988tb00469.x.

Baur, B. 1989. Growth and reproduction of the minute land snail *Punctum pygmaeum* (Draparnaud). J. Mollusc. Stud. **55**: 383–387. doi:10.1093/mollus/55.3.383.

Baur, B. 1994. Parental care in terrestrial gastropods. Experientia, **50**: 5–14. doi:10.1007/BF01992042.

Baur, B., and Baur, A. 1990. Experimental evidence for intra- and interspecific competition in two species of rock-dwelling land snails. J. Anim. Ecol. **59**: 301–315. doi:10.2307/5174.

Baur, B., and Baur, A. 1995. Habitat-related dispersal in the rock-dwelling land snail *Chondrina clienta*. Ecography, **18**: 123–130. doi:10.1111/j.1600-0587.1995.tb00332.x.

Baur, B., and Baur, A. 1997. *Xanthoria parietina* as food resource and shelter for the land snail *Balea perversa*. Lichenologist **29:** 99–102. doi:10.1017/S0024282997000145.

Baur, B., and Baur, A. 2006. Dispersal of the land snail *Helicigona lapicida* in an abandoned limestone quarry. Malakol. Abh. **24:** 135–139.

Baur, B., and Raboud, C. 1988. Life history of the land snail *Arianta arbustorum* along an altitudinal gradient. J. Anim. Ecol. **57**: 71–87. doi:10.2307/4764.

Baur, B., Fröberg, L., and Baur, A. 1995. Species diversity and grazing damage in a calcicolous lichen community on top of stone walls in Öland, Sweden. Ann. Bot. Fenn. **32**: 239–250.

Baur, B., Fröberg, L., Baur, A., Guggenheim, R., and Haase, M. 2000. Ultrastructure of snail grazing damage to calcicolous lichens. Nord. J. Bot. **20**: 119–128. doi:10.1111/j.1756-1051.2000.tb00741.x.

Begon, M., Harper, J.L., and Townsend, C.R. 2006. Ecology – From Individuals to

Populations. 4th ed. Blackwell Science, Oxford.

Biro, P.A., Adriaenssens, B., and Sampson, P. 2014. Individual and sex-specific differences in intrinsic growth rate covary with consistent individual differences in behaviour. J. Anim. Ecol. **83**: 1186–1195. doi:10.1111/1365-2656.12210.

Blinn, W.C. 1963. Ecology of the land snails *Mesodon thyroidus* and *Allogona profunda*. Ecology, **44**: 498–505. doi:10.2307/1932528.

Breure, A.S.H., and Gittenberger, E. 1982. The rock-scraping radula, a striking case of convergence (Mollusca). Neth. J. Zool. **32**: 307–312. doi:10.1163/002829681X00347.

Cain, A.J. 1983. Ecology and ecogenetics of terrestrial molluscan populations. *In* The Mollusca, **6**: Ecology. *Edited by* W.D. Russell-Hunter. Academic Press, London. pp. 597–647.

Carney, W.P. 1966. Mortality and aperture orientation in *Allogona ptychophora* during winter hibernation in Montana. Nautilus, **79**: 134–136.

Charnov, E. 2004. The optimal balance between growth rate and survival in mammals. Evol. Ecol. Res. **6**: 307–313.

English, S., Bateman, A.W., Mares, R., Ozgul, A., and Clutton-Brock, T.H. 2014. Maternal, social and abiotic environmental effects on growth vary across life stages in a cooperative mammal. J. Anim. Ecol. **83**: 332–342. doi:10.1111/1365-2656.12149.

Forsman, A. 1993. Growth rate in different colour morphs of the adder, *Vipera berus*, in relation to yearly weather variation. Oikos, **66**: 279–285. doi:10.2307/3544815.

Fröberg, L., Baur, A., and Baur, B. 1993. Differential herbivore damage to calcicolous lichens by snails. Lichenologist, **25**: 83–95. doi:10.1006/lich.1993.1015.

Fröberg, L., Stoll, P., Baur, A., and Baur, B. 2011. Snail herbivory decreases cyanobacterial abundance and lichen diversity along cracks of limestone pavements. Ecosphere, **2**(3): article 38. doi:10.1890/ES10-00197.1.

Heller. J. 2001. Life history strategies. *In* The Biology of Terrestrial Molluscs. *Edited by* G.M. Barker. CABI Publishing, Oxon. pp. 413–447.

Heller, J., and Dolev, A. 1994. Biology and population dynamics of a crevice-dwelling land snail, *Cristataria genezarethana* (Clausiliidae). J. Mollusc. Stud. **60**: 33–46.

Hesbacher, S., Baur, B., Baur, A., and Proksch, P. 1995. Sequestration of lichen compounds by three species of terrestrial snails. J. Chem. Ecol. **21**: 233–246. doi:10.1007/BF02036654.

Hesbacher, S., Fröberg, L., Baur, A., Baur, B., and Proksch, P. 1996. Chemical variation within and between individuals of the lichenized ascomycete *Tephromela atra*. Biochem. Syst. Ecol. **24**:603–609. doi:10.1016/S0305-1978(96)000804.

Johnson, M., and Black, R. 1991. Growth survivorship, and population size in the land snail *Rhagada convicta* Cox, 1870 (Pulmonata: Camaenidae) from a semiarid environment in Western Australia. J. Mollusc. Stud. **57**: 367–374. doi:10.1093/mollus/57.3.367.

Kerney, M.P., and Cameron, R.A.D. 1979. A Field Guide to the Land Snails of Britain and Northwest Europe. Collins, London.

Kéry, M. 2010. Introduction to WinBUGS for Ecologists. A Bayesian Approach to Regression, ANOVA, Mixed Models and Related Analyses. Academic Press, New York.

Kéry, M., and Schaub, M. 2012. Bayesian Population Analysis Using WinBUGS. A Hierarchical Perspective. Academic Press, New York.

Kostal, V., Rozsypal, J., Pech, P., Zahradnickova, H., and Simek, P. 2013. Physiological and biochemical responses to cold and drought in the rock-dwelling pulmonate snail, *Chondrina avenacea*. J. Comp. Physiol. B **183**: 749–761. doi:10.1007/s00360-013-0749-0.

Krahulec, F., Rosén, E., and van der Maarel. E. 1986. Preliminary classification and ecology of dry grassland communities on Ölands Stora Alvar (Sweden). Nordic J. Bot. **6**: 797–809. doi:10.1111/j.1756-1051.1986.tb00483.x.

Kuznik-Kowalska, E. 2006. Life cycle of *Discus ruderatus* (Férussac, 1821) (Gastropoda: Pulmonata: Endodontidae). Folia Malacol. **14**: 35–46.

Lazaridou-Dimitriadou, M. 1995. The life cycle, demographic analysis, growth and secondary production of the snail *Helicella (Xerothracia) pappi* (Schütt, 1962) (Gastropoda, Pulmonata) in E. Macedonia (Greece). Malacologia, **37**: 1–11.

Lunn, D. J., Thomas, A., Best, N., and Spiegelhalter, D. 2000. Win-BUGS – a Bayesian modelling framework: concepts, structure, and extensibility. Stat. Comput. **10**: 325–337.

Macdonald, P. and Du, J. 2012. mixdist: Finite Mixture Distribution Models. R package version 0.5-4. http://CRAN.R-project.org/package=mixdist

MacDonald, P.D.M., and Green, P.E. 1988. User's guide to program MIX: An interactive program for fitting mixtures of distributions. Ichthus Data Systems.

MacDonald, P.D.M., and Pitcher, T.J. 1979. Age-groups from size-frequency data: a versatile and efficient method of analyzing distribution mixtures. J. Fish. Res. Board Can. **36**: 987–1001. doi:10.1139/f79-137.

Maltz, T.K., and Sulikowska-Drozd, A. 2011. Delayed maturation in the genus *Vestia* P. Hesse (Gastropoda: Pulmonata: Clausiliidae): a model for clausiliid lifecycle strategy. J. Mollusc. Stud. **77:** 41–53. doi:10.1093/mollus/eyq040.

Neuckel, W. 1981. Zu Aktivitätsregelung und Wasserhaushalt von *Chondrina avenacea* (Bruguière 1792), einer Felsen bewohnenden Landlungenschnecke. PhD-Thesis, University of Basel.

Oosterhoff, L.M. 1977. Variation in growth rate as an ecological factor in the landsnail *Cepaea nemoralis* (L.). Neth. J. Zool. **27**: 1–132. doi:10.1163/002829677X00072.

R Core Team. 2013. R: A language and environment for statistical computing. Foundation for Statistical Computing, Vienna, Austria.

Riddle, W.A. 1983. Physiological ecology of land snails and slugs. *In* The Mollusca, 6: Ecology. *Edited by* W.E. Russell-Hunter. Academic Press, New York. pp. 431–461.

Riddle, W.A., and Miller, V.J. 1988. Cold-hardiness in several species of land snails. J. therm. Biol. **13**: 163–167. doi:10.1016/0306-4565(88)90028-9.

Schlesch, H. 1937. Beitrag zur Molluskenfauna Öland's. Arch. Molluskenk. **69**: 19–34.

Schmid, G. 1929. Endolithische Kalkflechten und Schneckenfrass. Biol. Zentralbl., **49**: 28–35.

SMHI. 2014. Annual temperature and precipitation. Swedish Meteorological and Hydrological Institute. Available from http://www.smhi.se/klimatdata [accessed on 3 October 2014]

Sulikowska-Drozd, A., and Maltz, T.K. 2012. Reproduction of *Balea (Pseudalinda) fallax* (Rossmässler, 1836) (Gastropoda: Pulmonata: Clausiliidae) kept under laboratory conditions. Folia Malacol. **20**: 27–34.

Stearns, S. 1992. The Evolution of Life Histories. Oxford University Press, Oxford.

Sturtz, S., Ligges, U., and Gelman, A. 2005. R2WinBUGS: A Package for Running WinBUGS from R. J. Statistical Software, **12**: 1–16.

Terhivuo, J. 1978. Growth, reproduction and hibernation of *Arianta arbustorum* (L.) (Gastropoda, Helicidae) in southern Finland, Ann. Zool. Fenn. **15**: 8–16.

Waldén, H.W. 1984. Sveriges landmollusker – en artlista med kommentarer. Fauna och flora, **79**: 29–43.

Williamson, P. 1976. Size-weight relationships and field growth rates of the landsnail *Cepaea nemoralis* L. J. Anim. Ecol. **45**: 875–885. doi:10.2307/3586.

Williamson, P., Cameron, R.A., and Carter, M.A. 1977. Population dynamics of the land snail *Cepaea nemoralis* (L.): a six year study. J. Anim. Ecol. **46**: 181–194.

Wolda, H. 1963. Natural populations of the polymorphic land snail *Cepaea nemoralis* (L.). Arch. Néerl. Zool. **15**: 381–471.

Wolda, H., and Kreulen, D.A. 1973. Ecology of some experimental populations of the landsnail *Cepaea nemoralis* (L.). II. Production and survival of eggs and juveniles. Neth. J. Zool. **23**:168–188.

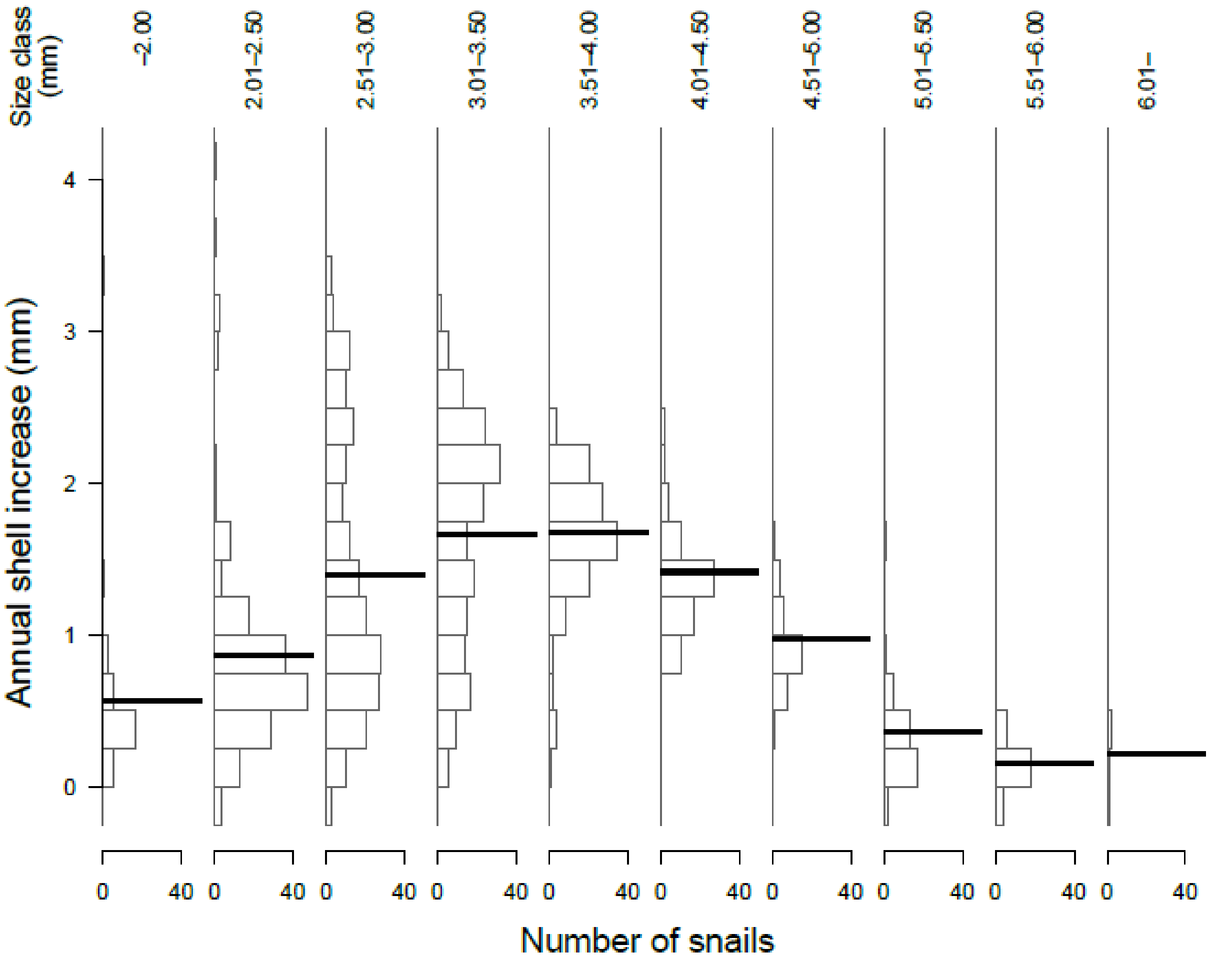


Fig. 1. Distribution of annual shell increase in individually marked *C. clienta* belonging to different size classes. Bold horizontal lines indicate median values for each size class.

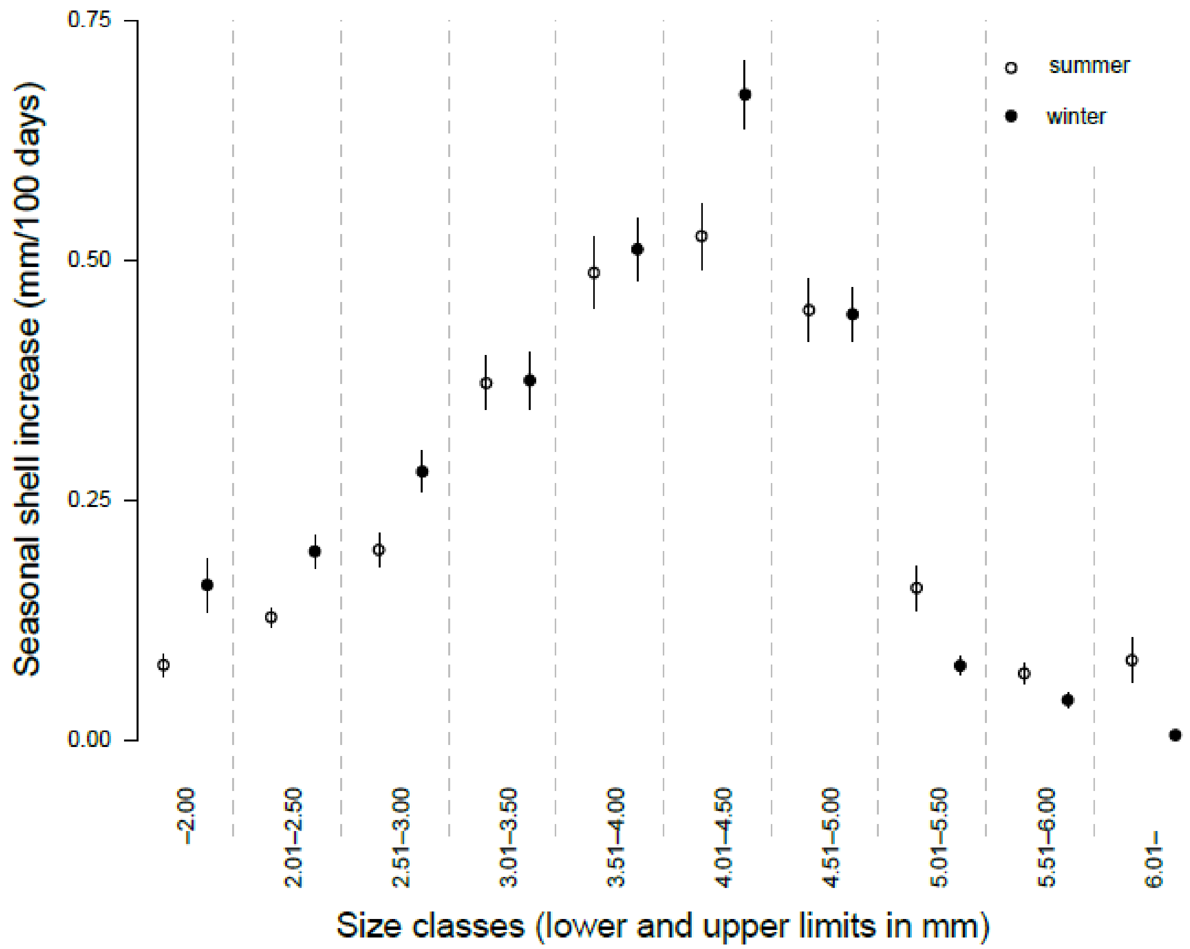
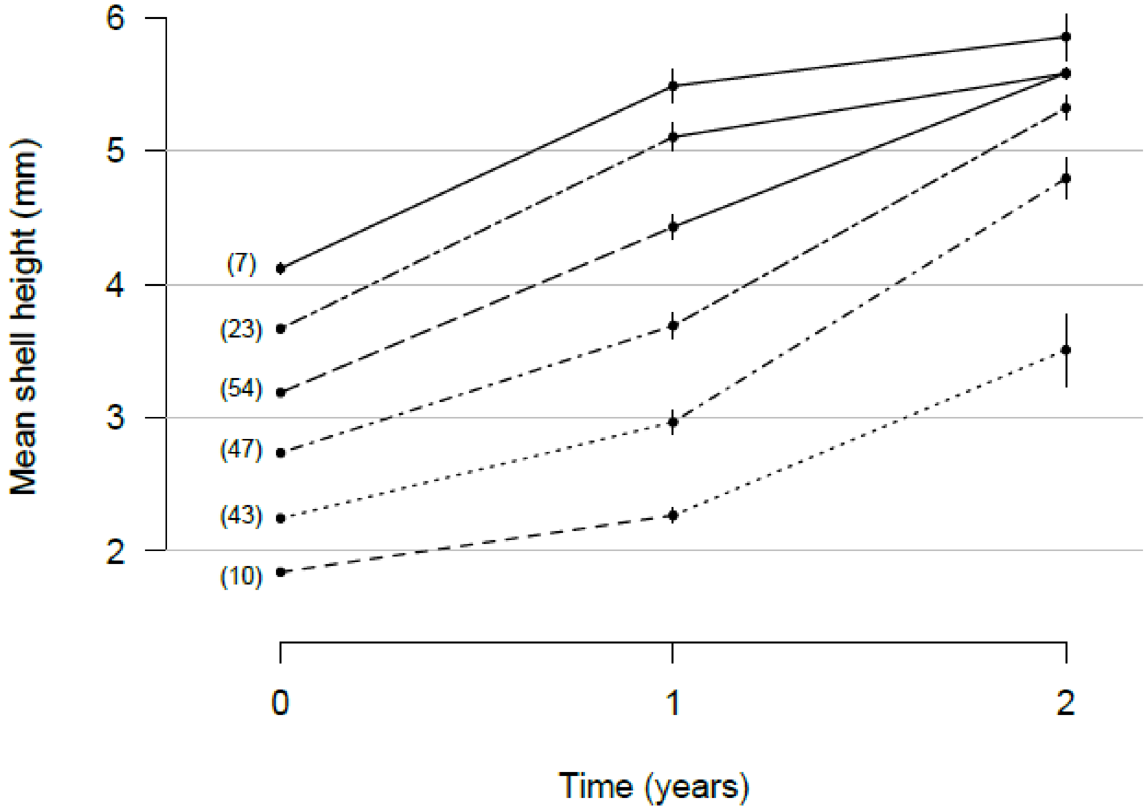


Fig. 2. Shell increase in individually marked *C. clienta* belonging to different size classes during summer (open dots) and winter (full dots). Shell growth is expressed as shell height increase within 100 days.



596

597 **Fig. 3.** Change in the mean shell height of *C. clienta* (± SE) over two years. Individually

598 marked snails were assigned to six size classes at the beginning of the study. Sample size for

599 each size class is given in parenthesis.

600

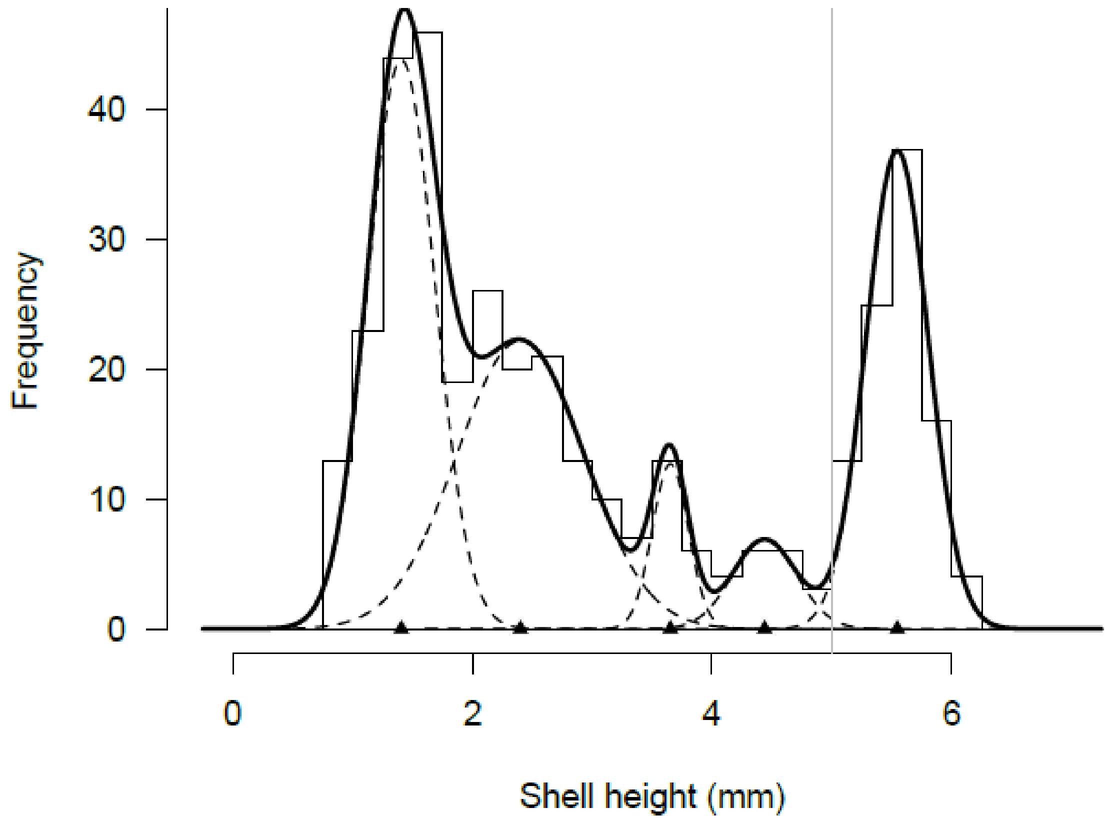


Fig. 4. Frequency distribution of shell height of *C. clienta* in a population sampled on 23 September 1990. Idealized curves of year cohorts are shown with triangles indicating the mean shell height of the corresponding cohort. The group of adult snails consists of individuals from several cohorts.

Table 1. Size and aspect of the four vertical quarry walls (sites) on which growth and survival of snails were assessed together with local snail density and shell size.

Site	Wall area (height x breadth, in m)	Aspect	Snail density* Mean ± SE	Adult shell height (mm)¶ Mean ± SE
A	1.15 x 20.0	NE	36.7 ± 3.4	5.6 ± 0.04
B	0.95 x 7.5	NW	33.0 ± 5.7	5.8 ± 0.08
C	0.65 x 7.0	NW	37.0 ± 11.0	5.9 ± 0.06
D	1.40 x 8.0	NE	32.0 ± 6.6	5.9 ± 0.06

* Number of fully-grown snails collected in 3 minutes (*n* = 3 replicates).

¶ Based on 25 fully-grown individuals from each site.

Table 2. Summary of ANOVA table examining the effect of site and snail size class on the relative growth rate per year in individuals of *C. clienta*.

Year	Predictor	df	SS	*F*	*P*
1991/1992	Site	3	2.404	20.197	< 0.001
	Size class	4	0.687	4.331	0.002
	Site x size class	12	0.907	1.905	0.033
	Residuals	362	14.362		
1992/1993	Site	3	0.795	7.178	< 0.001
	Size class	3	0.269	2.427	0.070
	Residuals	94	3.472		

Analyses were run separately for each year. The minimal adequate model was selected using the Akaike Information Criterion. Only snails belonging to the size classes 1–5 were considered in the analyses.