3

4

5

6 **Size-dependent shell growth and survival in natural populations of the**

7 **rock-dwelling land snail *Chondrina clienta***

8

9

10 **Denes Schmera, Anette Baur and Bruno Baur**

11

12

13

14

15 **D. Schmera[1,2], A. Baur and B. Baur,** Section of Conservation Biology, Department of

16 Environmental Sciences, University of Basel, St. Johanns-Vorstadt 10, 4056 Basel,

17 Switzerland.

18 [1]Corresponding author (e-mail: denes.schmera@unibas.ch).

19 [2]Present address: Balaton Limnological Institute, Centre for Ecological Research,

20 Hungarian Academy of Sciences, Klebelsberg Kuno 3, 8237 Tihany, Hungary.

21

22

23   **Size-dependent shell growth and survival in natural populations of the rock-dwelling**

24   **land snail *Chondrina clienta***

25

26   **Denes Schmera, Anette Baur and Bruno Baur**

27

28   **Abstract:** Rock-dwelling land snails, feeding on algae and lichens that grow on stone

29   surfaces, may influence the structure and function of these ecosystems. Yet, little is known

30   about the life history of rock-dwelling snails. We performed a 30-month mark-release-

31   resight study in four populations of *Chondrina clienta* (Westerlund, 1883) inhabiting

32   vertical walls of abandoned limestone quarries on the Baltic island of Öland, Sweden, to

33   assess growth rate and survival of juvenile snails and determine age at maturity. We

34   marked 800 individuals ranging in shell height from 1.4 to 4.9 mm, released them in their

35   original habitat, and remeasured their shell height at intervals of 6 months. Shell growth of

36   juvenile *C. clienta* was affected by the site (quarry wall) and the size of the individual,

37   being highest in medium-sized snails. Shell growth occurred both during summer and

38   winter. Annual apparent survival rates of *C. clienta* were size-dependent and ranged from

39   58.6% to 96.3%. Sexual maturity was reached at an age of 5 years, which is later than in

40   most large-sized snail species. Our study extends current knowledge on life history of land

41   snails to a rarely studied group dwelling on rock surfaces.

42

45

46

Introduction

47

48   Growth is an important life-history process, influencing a range of later fitness-related

49   traits such as age and size at maturity and total reproductive output (Stearns 1992;

50   Charnov 2004; English et al. 2014). Growth of individuals can be variable in space and

51   time, for example as a consequence of variation in food availability, temperature and

52   precipitation, but also due to variation in genotype and phenotype among individuals.

53   Individual growth rate varies also between seasons, years and populations (e.g. in snakes;

54   Forsman 1993). Interindividual variation in growth is a primary determinant of the

55   material on which natural selection acts.

56   Individual differences in growth rate have been observed in a wide range of species

57   and occur even when animals are housed individually and fed *ad libitum*, suggesting that

58   growth is an intrinsic individual attribute (Arendt 1997; Biro et al. 2014). As an intrinsic

59   trait, individual growth rate is expected to be repeatable across years (i.e. individuals

60   growing rapidly in the first year will also grow fast in the second year). Studies on

61   individual growth have been biased towards large-sized species, whose individuals can

62   easily be tagged and show a high recapture probability in natural populations. Thus, few

63   empirical data are available on individual growth and other life-history traits in many

64   small-sized animal species with a cryptic life. This is also true for terrestrial gastropods. In

65   land snails, knowledge on individual growth, age at maturity and survival in the wild is

66   limited to species with large shells, e.g. *Cepaea nemoralis* (L., 1758), *Arianta arbustorum*

67   (L., 1758), *Rhagada convicta* Cox, 1870, and *Helicella pappi* (Schütt, 1962) (Williamson

68   1976, Baur and Raboud 1988; Johnson and Black 1991; Lazaridou-Dimitriadou 1995),

69   despite the fact that the majority of snail species have small shells (< 7 mm in shell height

70   or breadth). This can be explained by the notorious difficulties to mark tiny individuals

71   and to recover them in leaf litter or dense vegetation. To circumvent these problems, life-

72   history traits have been examined in snails kept in the laboratory or under semi-natural

73   conditions (e.g. Oosterhoff 1977; Baur 1989; Sulikowska-Drozd and Maltz 2012). This

74   approach provides reliable data on egg size and batch size, but less reliable estimates of

75   individual growth rate, age at maturity, survival and longevity. For example, individuals

76 of *A. arbustorum* from an alpine population needed 186 days from hatching to complete

77 shell growth and reach sexual maturity under laboratory conditions (Baur 1984), while

78 individuals in the wild required 4-5 years (Baur and Raboud 1988). With a few

79 exceptions, empirical data on the life history of small-sized land snail species in their

80 natural habitat are not available (Heller 2001).

81   In the present study, we investigated growth rate, age at maturity and survival in

82 individuals of the rock-dwelling land snail *Chondrina clienta* (Westerlund, 1883) in their

83 natural habitat. Snails of this small sized-species spend their entire life on rocks, where

84 they graze algae and lichens during periods of optimal temperature and sufficient moisture

85 (Baur 1988; Baur et al. 1994). Attached with their shell opening to the rock surface, the

86 snails rest during unfavorable conditions and manage to survive extreme fluctuations in

87 temperature. The lack of vegetation on rock surfaces and the snails' limited dispersal

88 capacity result in a relatively high recovery rate of marked individuals (Baur and Baur

89 1995). We traced marked juveniles and periodically recorded their growth on four vertical

90 limestone quarry walls on the Baltic island of Öland, Sweden. This approach allowed an

91 assessment of size-specific, seasonal and annual growth rates and survival rates. Age at

92 maturity was assessed by combining individual growth rates. In a second approach, age at

93 maturity was quantified by analyzing the shell height frequency distribution of a

94 population.

95   In particular, we addressed the following questions: (1) Do snails from the four rock

96 walls differ in individual growth rate? (2) Do snails also grow during winter, and if so, do

97 individual growth rates differ between summer and winter months? (3) Is the individual

98 growth rate of juvenile *C. clienta* repeatable across years? (4) Does survival of juvenile *C.*

99 *clienta* depend on individual snail size and differ between seasons? (5) How many years

100 do newly hatched snails need to complete shell growth and achieve sexual maturity?

101

102 **Materials and methods**

103 **The species**

104   *Chondrina clienta* occurs in open limestone areas of Central and South-eastern Europe

105 and in three isolated areas of Sweden, namely on the Baltic islands of Öland and Gotland

106 and in one small area on the mainland (Kerney and Cameron 1979; Waldén 1984; Baur

107 1987). The snail has determinate growth. Its cylindro-conical shell is dextral and in adults

108 is 5.5–7 mm high (Baur 1988). Sexual maturity is attained after the completion of shell

109 growth, which is indicated by the building of a reflected lip around the shell aperture and

110 six short folds (teeth) within the aperture. *Chondrina clienta* is ovoviviparous; the shell

111 height of hatchlings is c. 0.8 mm. The animals are well adapted to rocky habitats; they are

112 resistant to drought with activity confined to periods of high air humidity, and their

113 specialized radula enable them to graze algae and epi- and endolithic lichens from rock

114 faces (Schmid 1929; Breure and Gittenberger 1982; Fröberg et al. 1993; Baur et al. 2000).

115 Among other lichen feeding snail species in calcicolous habitats on Öland, *C. clienta* is by

116 far the most abundant species on both horizontal (i.e. limestone pavements, the snails'

117 original habitat) and vertical (e.g. quarry walls) rock surfaces (Fröberg et al. 2011). In a

118 controlled laboratory experiment, juvenile growth rate, time to complete growth, adult

119 shell size and survival were affected by intraspecific competition (Baur and Baur 1990).

120 At the study sites (see below), the land snail *Helicigona lapicida* (L., 1758) lives on

121 adjacent piles of stone. On rainy days, individuals of *H. lapicida* have been observed to

122 graze lichens on vertical quarry walls (Baur and Baur 2006). However, the quarry walls

123 investigated may not differ in density of this potentially competing species.

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

125 and Baur 1995).

126

127 **Study sites and general methods**

128   To assess shell growth and survival of juvenile *C. clienta* we performed a 30-month

129 mark-release-resight study from March 1992 to October 1994 at four sites in the Great

130 Alvar in the southern part of the Baltic island of Öland, Sweden (56°33'N, 16°36'E). The

131 area is a calcareous grassland grazed by sheep and cattle with several abandoned limestone

132 quarries of small size (50–500 m^2; supplementary Figs. S1–S3). The study sites were

133 vertical quarry walls located within an area of 0.5 km^2, 1.5 km SSW of Vickleby (for site

134   description see Table 1). The Great Alvar is a UNESCO World Heritage Site since 2000.

135   Vegetation, climate and geomorphology of the Great Alvar have been described by

136   Krahulec et al. (1986).

137   We searched the quarry walls systematically for juvenile *C. clienta* with a shell height

138   <4.9 mm. To avoid the marking of empty shells, the snails were activated by keeping them

139   in plastic boxes lined with moist paper toweling. We individually marked 200 juveniles

140   from each site by writing tiny numbers (1–200) on their shells with a waterproof ink pen

141   on a minute spot of correction fluid (Tipp-Ex). At the same time we measured the shell

142   height of each individual to the nearest 1/12 mm (shell height: mean = 2.7 mm, range 1.4–

143   4.9 mm; n = 800). Very small individuals (shell height 0.8–1.3 mm) could not be

144   individually marked. Marking and measuring were carried out using a binocular

145   microscope with a stage micrometer. The animals showed no visible reaction to the

146   marking and measuring procedure. We released marked *C. clienta* at their sites of origin

147   within 1–2 days after sampling. To minimize overcrowding at the release point, which

148   may result in increased dispersal, we released the snails in groups of 50 at four points

149   (situated in line with a distance of 50 cm between release points) on each rock wall. All

150   field sampling was done under dry conditions when the snails were at rest attached to the

151   rock surface.

152   To determine shell growth and survival of *C. clienta*, we searched the entire rock wall

153   at the four sites for marked snails after 6, 12, 18, 24 and 30 months. On each sampling, we

154   measured the shell height of the recovered snails as described above. The resampled snails

155   were released within 2 days at their site of origin following the procedure described above.

156   Very few illegible marks were found. These snails were not considered in the data

157   analyses.

158   Local population density of *C. clienta* at the four sites A–D was estimated by counting

159   the number of juvenile and adult snails found on the vertical rock surface and in fissures

160   within 3 min. searching time by one of us (B.B.). Density estimates were conducted

161   exclusively under conditions of dry weather, when the snails are at rest (Baur and Baur

162   1991), because this method reveals reliable density estimates for rock-dwelling land snails

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

164   replicate searches.

165   Analysing size distributions is the most frequently used approach to estimate growth

166   rates and age at maturity in gastropods. We aimed to compare direct measurements of

167   juvenile growth obtained from individually marked snails (see above) with indirect

168   estimates obtained from a size distribution. We used a representative subset of a

169   population of *C. clienta* to assess the time required to complete shell growth and thus to

170   reach sexual maturity. We sampled all snails found within an area of 6 m^2 on a rock wall

171   located 50 m from sites A–D on 23 October 1990. The sampling area of 6 m^2

172   corresponded to the area of the rock walls at site B and C. Using a magnifying glass we

173   could also find tiny individuals in small fissures. The shell height of each snail was

174   measured as described above.

175   Data on temperature and precipitation were obtained from the Meteorological Station

176   in Kalmar, 15 km NW of the study sites. The annual mean temperature in Kalmar is 7.5 $^{\circ}$C

177   (July mean: 17.5 $^{\circ}$C; January mean: –0.9 $^{\circ}$C) and the annual mean precipitation is 543 mm

178   (mean values from 1978–2013; SMHI 2014). The mean temperature in the first 12 months

179   of our study was 0.7 $^{\circ}$C higher than the annual mean temperature, while the amount of

180   precipitation was 21% less than the annual mean precipitation. The following 12 months

181   were 0.3 $^{\circ}$C colder than the annual mean temperature and the amount of precipitation

182   exceeded the annual mean precipitation by 10%.

183

184   **Data analyses**

185   Preliminary analysis showed that individual shell growth differs among snails of different

186   size. We therefore assigned individuals of *C. clienta* to ten size classes for the analyses on

187   size-dependent growth rate and survival. Size class 1 consisted of individuals with shell height

188   ≤ 2.0 mm, size class 2 of individuals with shell height 2.1–2.5 mm, size class 3 of individuals

189   with shell height 2.6–3.0 mm, and so on. Size class 10 consisted of individuals with a shell

190   height > 6 mm.

191   Individual shell growth was assessed in two ways. Absolute growth was expressed as shell

192   height increase of an individual between t_0 and t_1. The relative shell growth of an individual in

193   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

194   and h_{t1} its shell height at t_1. Absolute and relative shell growth was determined over 6 months

195   (growth during winter and summer, respectively) and over 1 year (annual growth). To quantify

196   individual shell growth within a year, we only considered individuals belonging to the size

197   classes 1 to 5 at the beginning of the experiment and which were recovered both after 12 and

198   24 months. We fitted a linear model with the factors site and size class and the interaction of

199   the two factors and selected the minimal adequate model explaining relative shell growth

200   using the Akaike Information Criterion (AIC). Data were checked for homoscedasticity prior

201   to the analyses.

202   To examine whether individual growth rate of juvenile *C. clienta* is repeatable between

203   years, we calculated the Pearson correlation between the shell height increase in the first year

204   and that in the second year for all individuals of a size class, using separate analyses for the

205   size classes 1–5. Juveniles belonging to the size class 6 at the beginning of the study were not

206   considered because they attained adult size in the second year.

207   We applied Cormark-Jolly-Seber (CJS) modeling with the effects time and size class to

208   estimate survival from mark-release-resight data (Kéry and Schaub 2012). This analysis uses a

209   Bayesian approach (Kéry 2010) and quantifies the *recapture probability* (probability of

210   resighting a marked individual at time *t* that is alive in the sampling population at *t*) and the

211   *survival probability* (probability that an individual that is alive and in the population at time *t*

212   is still alive and in the population at time *t+1*; Kéry and Schaub 2012). An important

213   biological issue is that only apparent survival can be estimated with CJS modeling; that is "*1−*

214   *survival*" represents both animals that died and animals that left the population or study area

215   (emigration). In the first analysis, we examined the potential effect of the site on apparent

216   survival, in the second analysis the effect of size class on apparent survival. For the survival

217   analyses we used *WINBUGS 14* (Lunn et al. 2000) and the package *r2WinBUGS* (Sturtz et al.

218   2005) in the R environment (R Core Team 2013).

219   The frequency distribution of shell height represents a cross section of a population at a

220   specific time. We fitted finite mixture distribution models to the data by using a maximum

221 likelihood method with a combination of Newton-type algorithms and the expectation-

222 maximization algorithms (Macdonald and Pitcher 1979; Macdonald and Green 1988). This

223 approach allows estimates of size and age at maturity. The package *mixdist* (Macdonald and

224 Du 2012) in the R environment (R Core Team 2013) was used for this analysis.

225

226 **Results**

227 **Recovery of marked snails**

228   The percentage of marked snails resighted decreased with time from 61.5 ± 2.1% (mean ±

229 SE, *n* = 4 sites) after 6 months to 49.9 ± 2.7% after 12 months, 42.9 ± 3.6% after 18 months,

230 31.9 ± 1.0 after 24 months, and 4.9 ± 1.0% after 30 months. Due to the steep decline in

231 recovery rate between 24 and 30 months we considered only data obtained within 24 months

232 for the growth and survival analyses. Considering snails belonging to different size classes,

233 recovery rate of marked individuals was slightly higher in larger juveniles than in smaller ones

234 after 6, 12 and 18 months (supplementary Table S1). After 24 months, the recovery rate of

235 marked individuals was very similar in all size classes (supplementary Table S1).

236

237 **Shell growth**

238   Individually-marked *C. clienta* differed considerably in shell growth (supplementary Fig.

239 S4). In the first year, the relative shell growth was affected by the site (quarry wall) and the

240 size class to which the individual belonged (Table 2). Snails at site C grew faster (mean

241 relative shell increase = 48.2%) than individuals at site A (32.8%; linear model, estimate =

242 0.512, s.e. = 0.122, *t* = 4.197, *P* < 0.001). The significant interaction between site and size class

243 indicates that snails of different size classes showed different relative growth rates on the four

244 rock walls in that year. In the second year, relative shell growth was again affected by the site

245 and tended to be influenced by the size class (Table 2). Snails at site D showed the largest

246 relative growth (mean relative shell increase = 69.0%), while snails at site B showed the

247 smallest relative growth (mean = 47.7%).

248   Snails from the four sites may represent the variation in shell growth of *C. clienta* inhabiting

249 limestone quarries. We therefore pooled data of snails from the four sites for further growth

250 analyses. Considering different size classes, annual shell increase showed a hump-shaped

251 pattern (Fig. 1). It was highest in medium-sized individuals (shell height 2.5–4.5 mm) and

252 relatively low in small and large (but not yet fully-grown) individuals. Relative shell growth

253 showed a similar hump-shaped, size-dependent pattern (not shown).

254   The two measurements taken per year allow an assessment of shell growth during the

255 summer and winter months. Interestingly, the growth rate of individually marked *C. clienta* did

256 not differ between summer and winter, whatever the size classes (Fig. 2; paired t test, $t = 0.926$,

257 df $= 9$, $P = 0.379$).

258   Comparing the shell height increase of individual snails in the first and second year revealed

259 two different patterns (supplementary Fig. S5). The shell height increases of juvenile *C. clienta*

260 belonging to the size classes 1 and 2 at the beginning of the study were not correlated between

261 the two years. In contrast, the shell height increase in the first year was negatively correlated

262 with that of the second year in snails belonging to the size classes 3–5, indicating a trade-off in

263 shell growth (supplementary Fig. S5). Individuals growing rapidly in the first year were

264 growing slowly in the second year and vice versa.

265

266 **Survival**

267   The recapture probability varied with the size of the marked individuals. Recapture

268 probability was highest in snails belonging to the size classes 2–6 (see methods) ranging from

269 65.9% to 79.1%, but lower in the smallest snails (size class 1: 46.2%) and the largest ones (size

270 class 7: 51.0%). Bayesian analysis revealed that apparent survival of *C. clienta* over 6 months

271 followed a similar pattern at the four sites, ranging from 74.0% to 80.6% (supplementary Fig.

272 S6). Considering the different seasons, apparent survival of juveniles was generally lower

273 during winter (mean 76.9% and 73.2% after 6 and 18 months, respectively) than during

274 summer (mean 86.9% and 83.1% after 12 and 24 months). Apparent survival over 6 months

275 was higher at site A than at site B (range of creditable interval -0.666 – -0.082), but did not

276 differ among the other sites (supplementary Fig. S6).

277   Bayesian analysis revealed annual apparent survival rates of *C. clienta* individuals ranging

278 from 58.6% to 96.3%. Annual apparent survival depended on the size of the individuals

279   (supplementary Fig. S7). The smallest snails (size class 1) had an annual apparent survival rate

280   of 92.1% and 90.2% in the two consecutive years. In size class 2, annual apparent survival was

281   64.8% and 58.6%. In snails belonging to the size classes 3–7, annual apparent survival

282   increased with the size of the individuals, being highest in the largest snails (96.3% and 95.4%

283   in the two successive years; supplementary Fig. S7).

284

285   **Age at sexual maturity**

286   The time to complete shell growth and thus the age at sexual maturity can be deduced by

287   combining data of marked individuals that were recovered on all occasions (Fig. 3). Snails of

288   size class 1 (shell height > 2 mm) needed 1 year to reach the shell height of size class 2 (2.01–

289   2.50 mm). Snails of size class 2 reached either size class 3 (2.51–3.00 mm), size class 4 (3.01–

290   3.50 mm) or size class 5 (3.51–4.00 mm) within 1 year. Snails of size class 4 needed 1 year to

291   attain size class 6 (4.05–4.50 mm) and snails of size class 6 required another year to complete

292   shell growth. Assuming that individuals belonging to size class 1 were already 1-year old, then

293   based on the average annual shell increase a snail requires 5 years to attain adult size and

294   sexual maturity (Fig. 3). However, the huge interindividual variation in shell growth may allow

295   a few individuals to reach adult size within 4 years, while others may need 6 or 7 years.

296

297   **Size (shell heigth frequency) distribution**

298   Individuals of *C. clienta* sampled on a quarry wall on 23 October 1990 ranged in shell

299   height from 0.83 to 6.25 mm ($n = 375$; Fig. 4). The frequency distribution of shell height

300   shows four peaks among the juveniles and one distinct large peak of fully-grown (adult) snails

301   indicating that there are four year cohorts of juveniles and – assuming that the first peak

302   represents 1-year-old snails – that adult size is attained at an age of 5 years. The frequency of

303   juvenile individuals decreased with increasing shell height, indicating mortality between year

304   cohorts. Snails with a reflected shell lip measured at least 5 mm, an exception was one

305   individual with a shell height of 4.83 mm (Fig. 4). The frequency of fully-grown snails in the

306   size distribution suggests that this size class consists of several year cohorts, and consequently

307   that adult snails may live for several years.

308

309   **Discussion**

310   The present study showed that individual shell growth rate of juvenile *C. clienta*

311   differed among quarry walls and that growth rate depended on the size of the snails.

312   Similarly, the survival rate was size-dependent in juvenile *C. clienta*. Most interestingly,

313   shell growth occurred not only during summer, but also during the winter half year.

314   In terrestrial gastropods, climate and weather are an important source of variation in growth

315   rate because their activity is constrained by humidity and temperature conditions (Oosterhoff

316   1977; Riddle 1983). Activity of rock-dwelling snails is restricted to periods of optimal

317   temperature and sufficient moisture (Neuckel 1981). The clausilid *Cristataria genezarethana*

318   (Tristram, 1865) is active only during 1.2–3.3% of the time of a year on karstic rocks in Israel

319   (Heller and Dolev 1994), and *Chondrina avenacea* (Bruguière, 1792) 11–14% of the time of a

320   year on limestone cliffs near Basel, Switzerland (Neuckel 1981). During summer heat or

321   during winter frosts, the snails must cope with extreme temperatures. *Chondrina avenacea*

322   enters estivation very rapidly whenever the snails experience drying out of their environment.

323   The snails rapidly suppress their metabolism and minimize water loss using a discontinuous

324   gas exchange pattern (Kostal et al. 2013). Hibernating snails rely on a supercooling strategy

325   which allows them to survive when air temperature drops to as low as -21 ^{o}C (Kostal et al.

326   2013). Winter dormancy in *C. clienta* is, however, not deep. Schlesch (1937) observed

327   individuals of *C. clienta* grazing lichens under mild conditions in January on Öland. This may

328   explain the surprising finding that the shell growth rate during the winter half year did not

329   differ from that of the summer half year. In the populations studied, *C. clienta* may become

330   active throughout the year whenever the environmental conditions are favorable. The yearly

331   variation in shell growth might be a result of the prevailing weather conditions, in particular of

332   the amount of precipitation and its temporal distribution within the year.

333   Individuals of *C. clienta* feed on cyanobacteria, algae and various species of lichens (Baur et

334   al. 1992; Fröberg et al. 1993; Baur et al. 1994). Lichens are protected against herbivores by a

335   number of mechanisms. The presence of different secondary compounds, the lichens' nutrient

336   content, surface toughness, type of photobiont, and their growth form (epilithic, endolithic,

337   foliose) may account for differential preferences shown by grazing snails (Fröberg et al. 1993;

338   Hesbacher et al. 1995; 1996; Baur et al. 2000). The small-scale spatial distribution of

339   cyanobacteria and lichen species varies considerably on rock surfaces, resulting in a spatial

340   heterogeneous distribution of food resources for the snails (Baur et al. 1995; Baur and Baur

341   1997; Fröberg et al. 2011). Considering the relatively short periods of time favorable for

342   grazing and the snails' limited dispersal capacity, individuals may encounter more or less

343   favorable food patches, which may result in more or less shell growth (Fröberg et al.

344   2011).Thus, differences in food availability and in microclimate (the aspect of the rock wall

345   may influence the length of snail activity) in combination with intraspecific competition could

346   explain the differences in growth rate found among sites. However, the number of replicates (n

347   = 4 rocks walls) does not allow to test this hypothesis.

348   The hump-shaped growth rate distribution of *C. clienta* belonging to different size classes

349   indicates that individual growth curves have a sigmoid shape with the fastest shell increase in

350   juveniles of medium size, a growth pattern found in other land snail species as well (Baur

351   1984; Kuznik-Kowalska 2006). The slower growth in the final juvenile stage could be

352   explained by the investment of energy to build the shell armature as has been reported in

353   clausiliid species (Maltz and Sulikowska-Drozd 2011). Interestingly, we did not find

354   repeatable individual shell growth between two successive years. On the contrary, individuals

355   of three size classes growing rapidly in the first year grew slowly in the second year and vice-

356   versa. The underlying cause for this intraindividual trade-off between current and future shell

357   growth remains to be investigated.

358   Our study showed that apparent survival in *C. clienta* is size-dependent. Larger individuals

359   had a higher survival rate than smaller ones, an exception being individuals of the smallest size

360   class. The actual survival rate might even be higher, because in the estimate of apparent

361   survival snails that died and snails that left the study area were considered the same (see

362   Statistical analyses). On vertical rock walls, the distances moved by juvenile *C. clienta*

363   increased with the shell size of the individuals (Baur and Baur 1995). In the present study, a

364   few individuals might have left the quarry walls, which represented the study areas. However,

365   the size class-specific recovery rate of marked individuals was not lower in larger juveniles

366 than in smaller ones (supplementary Table S1), as expected by the snails' dispersal capacity.

367 This indicates that not only the apparent survival rate but also the actual survival rate is size-

368 dependent in *C. clienta*.

369   Unfavorable weather is known to act as a density-independent mortality factor in many

370 invertebrate species (Begon et al. 2006). Winter mortality is assumed to be one of the crucial

371 factors in the life cycle of land snails (Wolda 1963; Wolda and Kreulen 1973; Cain 1983).

372 Extreme temperatures (cold and heat) may cause a substantial part of the total mortality in land

373 snails (Williamson et al. 1977). Land snails overwintering at or near the soil surface in

374 temperate regions are potentially exposed to low temperatures, being readily killed by ice

375 formation in the tissue (Ansart et al. 2014). Consequently, behavioral adaptations (e.g.,

376 searching for favorable hibernation positions) and physiological acclimatization, such as the

377 development of cold-hardiness in autumn and the maintenance of sufficient cold resistance

378 during winter, may be essential in such species (Riddle and Miller 1988; Kostal et al. 2013;

379 Ansart et al. 2014).

380   Winter mortalities ranging from 2.4% to 19.0% have been reported for *Allogona*

381 *ptychophora* (Brown, 1870), *A. profunda* (Say, 1821), *Mesodon thyroidus* (Say, 1816), *C.*

382 *nemoralis* and *A. arbustorum* (Blinn 1963; Carney 1966; Williamson et al. 1977; Terhivuo

383 1978; Andreassen 1981). All these species have relatively large shells (shell breadth >15 mm)

384 and hibernate buried into the soil or under leaf litter. In contrast, winter mortality of *C. clienta*

385 inhabiting exposed stone walls on Öland averaged 13.9% in juveniles and 10.5% in adults

386 during mild winters but increased to 64.3% in juveniles and 67.9% in adults during an

387 extremely cold winter (Baur and Baur 1991). In all four winters, mortality was not influenced

388 by the local population density (Baur and Baur 1991). In the present study, the winters were

389 relatively mild (mean minimum temperatures in January of –2.5 $^{\circ}$C in 1993 and –2.0 $^{\circ}$C in

390 1994), and did not cause any increased snail mortality.

391   In life-history theory, age at maturity in animals is defined as age at first reproduction. *C.*

392 *clienta* reproduces for the first time in the autumn after having attained adult size. In our study,

393 the results of two different approaches (combination of individual shell growth data and the

394 analysis of the shell size distribution of a population) revealed that most individuals of *C.*

395 *clienta* completed shell growth at an age of 5 years, even though a few individuals reach adult

396 size within 4 years, while others need 6 or 7 years, indicating a relatively late maturity in this

397 small-sized land snail species. The size (shell height frequency) distribution data were obtained

398 1.5 years before the start of the growth experiment. Considering individual growth rates (5

399 years to attain adult size), a large proportion of the individually marked snails were already

400 alive when the sample for the size distribution was collected. It is very unlikely that the time

401 elapsed between the two studies affects the results. A similar age at maturity was reported in

402 the small-sized rock-dwelling land snail *Cristataria genezarethana* (Tristram, 1865) (Heller

403 and Dolev 1994), whereas most large-sized snail species (e.g., *C. nemoralis*) reach sexual

404 maturity at an age of 2–3 years (Oosterhoff 1977; Heller 2001).

405   Life-history theory predicts later maturity if there is further growth and if fecundity

406 increases with size leading to a higher initial fecundity (Stearns 1992). Furthermore, maturity

407 will be delayed if it improves the instantaneous juvenile survival rate, e.g., by giving birth to

408 larger offspring. In the majority of land snails, female fecundity (number of eggs or hatchlings

409 produced) increases with the size of the individual (Baur 1994). With a delayed maturity

410 individuals of *C. clienta* attain a larger adult size and thus have a higher fecundity. A further

411 delay in maturity might be counteracted by the cumulated juvenile mortality. The balancing

412 selection pressures of attaining a large shell size through delayed maturity versus the

413 cumulated higher juvenile mortality varies among localities, indicated by a considerable

414 variation in mean age at maturity among land snail populations within species (Heller 2001).

415 For examples, age at maturity in *A. arbustorum* increased along an elevational gradient from 2

416 years at 1220 m to 5 years at 2600 m in the European Alps (Baur and Raboud 1988). Some of

417 these interpopulational differences in age at maturity are genetically determined, while others

418 are environmentally induced (Baur 1984).

419

420 **Conclusions**

421   Previous studies have been concerned mainly with large-sized gastropods. The work

422 presented here fills a gap in land snail ecology and thus leads to a better understanding of the

423 population dynamics of small-sized rock-dwelling land snails. Our results show that individual

424 growth and juvenile survival are size-dependent in *C. clienta*, and vary slightly among

425 populations, most probably due to habitat-related differences in microclimate. The mean age at

426 maturity of 5 years found in *C. clienta* is higher than those reported in most large-sized snail

427 species. Our work also underlines the notion that winter is not a time of constant hibernation

428 for this rock-dwelling snail species in natural populations in southern Scandinavia, indicated

429 by shell growth in juveniles during the colder season.

430

431 **Acknowledgements**

432 We thank B. Braschler, H.-P. Rusterholz and two anonymous reviewers for valuable

433 comments on the manuscript.

434

435 **References**

436 Andreassen, E.M. 1981. Population dynamics of *Arianta arbustorum* and *Cepaea nemoralis* in

437 western Norway. Fauna Nor. A, **2**: 1–13.

438 Ansart, A., Guiller, A., Moine, O., Martin, M.-C., and Madec, L. 2014. Is cold hardiness size-

439 constrained? A comparative approach in land snails. Evol. Ecol. **28**: 471–493.

440 doi:10.1007/s10682-013-9680-9.

441 Arendt, J.D. 1997. Adaptive intrinsic growth rates: an integration across taxa. Rev. Biol. **72**:

442 149–177. doi:10.1086/419764.

443 Armbruster, G.F.J., Hofer, M., and Baur, B. 2007. Effect of cliff connectivity on the genetic

444 population structure of a rock-dwelling land snail species with frequent self-fertilization.

445 Biochem. Syst. Ecol. **35**: 325–333. doi:10.1016/j.bse.2006.12.005.

446 Baur, A., and Baur, B. 1991. The effect of hibernation position on winter survival of the rock-

447 dwelling land snails *Chondrina clienta* and *Balea perversa* on Öland, Sweden. J. Mollusc.

448 Stud. **57**: 331–336. doi:10.1093/mollus/57.3.331.

449 Baur, A., Baur, B., and Fröberg, L. 1992. The effect of lichen diet on growth-rate in the rock-

450 dwelling land snails *Chondrina clienta* (Westerlund) and *Balea perversa* (Linnaeus). J.

451 Mollusc. Stud. **58**: 345–347. doi:10.1093/mollus/58.3.345.

452 Baur, A., Baur, B., and Fröberg, L. 1994. Herbivory on calcicolous lichens – different food

453   preferences and growth rates in two coexisting land snails. Oecologia, **98**: 313–319.

454   doi:10.1007/bf00324219.

455 Baur, B. 1984. Shell size and growth rate differences for alpine populations of *Arianta*

456   *arbustorum* (L.) (Pulmonata: Helicidae). Rev. Suisse Zool. **91**: 37–46.

457 Baur, B. 1987. Richness of land snail species under isolated stones in a karst area on Öland,

458   Sweden. Basteria, **51**: 129–133.

459 Baur, B. 1988. Microgeographical variation in shell size of the land snail *Chondrina clienta*.

460   Biol. J. Linn. Soc. **35**: 247–259. doi:10.1111/j.10958312.1988tb00469.x.

461 Baur, B. 1989. Growth and reproduction of the minute land snail *Punctum pygmaeum*

462   (Draparnaud). J. Mollusc. Stud. **55**: 383–387. doi:10.1093/mollus/55.3.383.

463 Baur, B. 1994. Parental care in terrestrial gastropods. Experientia, **50**: 5–14.

464   doi:10.1007/BF01992042.

465 Baur, B., and Baur, A. 1990. Experimental evidence for intra- and interspecific competition in

466   two species of rock-dwelling land snails. J. Anim. Ecol. **59**: 301–315. doi:10.2307/5174.

467 Baur, B., and Baur, A. 1995. Habitat-related dispersal in the rock-dwelling land snail

468   *Chondrina clienta*. Ecography, **18**: 123–130. doi:10.1111/j.1600-0587.1995.tb00332.x.

469 Baur, B., and Baur, A. 1997. *Xanthoria parietina* as food resource and shelter for the land

470   snail *Balea perversa*. Lichenologist **29:** 99–102. doi:10.1017/S0024282997000145.

471 Baur, B., and Baur, A. 2006. Dispersal of the land snail *Helicigona lapicida* in an abandoned

472   limestone quarry. Malakol. Abh. **24:** 135–139.

473 Baur, B., and Raboud, C. 1988. Life history of the land snail *Arianta arbustorum* along an

474   altitudinal gradient. J. Anim. Ecol. **57**: 71–87. doi:10.2307/4764.

475 Baur, B., Fröberg, L., and Baur, A. 1995. Species diversity and grazing damage in a

476   calcicolous lichen community on top of stone walls in Öland, Sweden. Ann. Bot. Fenn.

477   **32**: 239–250.

478 Baur, B., Fröberg, L., Baur, A., Guggenheim, R., and Haase, M. 2000. Ultrastructure of snail

479   grazing damage to calcicolous lichens. Nord. J. Bot. **20**: 119–128. doi:10.1111/j.1756-

480   1051.2000.tb00741.x.

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

482   Populations. 4th ed. Blackwell Science, Oxford.

483   Biro, P.A., Adriaenssens, B., and Sampson, P. 2014. Individual and sex-specific differences in

484   intrinsic growth rate covary with consistent individual differences in behaviour. J. Anim.

485   Ecol. **83**: 1186–1195. doi:10.1111/1365-2656.12210.

486   Blinn, W.C. 1963. Ecology of the land snails *Mesodon thyroidus* and *Allogona profunda*.

487   Ecology, **44**: 498–505. doi:10.2307/1932528.

488   Breure, A.S.H., and Gittenberger, E. 1982. The rock-scraping radula, a striking case of

489   convergence (Mollusca). Neth. J. Zool. **32**: 307–312. doi:10.1163/002829681X00347.

490   Cain, A.J. 1983. Ecology and ecogenetics of terrestrial molluscan populations. *In* The

491   Mollusca, **6**: Ecology. *Edited by* W.D. Russell-Hunter. Academic Press, London. pp. 597–

492   647.

493   Carney, W.P. 1966. Mortality and aperture orientation in *Allogona ptychophora* during winter

494   hibernation in Montana. Nautilus, **79**: 134–136.

495   Charnov, E. 2004. The optimal balance between growth rate and survival in mammals. Evol.

496   Ecol. Res. **6**: 307–313.

497   English, S., Bateman, A.W., Mares, R., Ozgul, A., and Clutton-Brock, T.H. 2014. Maternal,

498   social and abiotic environmental effects on growth vary across life stages in a cooperative

499   mammal. J. Anim. Ecol. **83**: 332–342. doi:10.1111/1365-2656.12149.

500   Forsman, A. 1993. Growth rate in different colour morphs of the adder, *Vipera berus*, in

501   relation to yearly weather variation. Oikos, **66**: 279–285. doi:10.2307/3544815.

502   Fröberg, L., Baur, A., and Baur, B. 1993. Differential herbivore damage to calcicolous lichens

503   by snails. Lichenologist, **25**: 83–95. doi:10.1006/lich.1993.1015.

504   Fröberg, L., Stoll, P., Baur, A., and Baur, B. 2011. Snail herbivory decreases cyanobacterial

505   abundance and lichen diversity along cracks of limestone pavements. Ecosphere, **2**(3):

506   article 38. doi:10.1890/ES10-00197.1.

507   Heller. J. 2001. Life history strategies. *In* The Biology of Terrestrial Molluscs. *Edited by* G.M.

508   Barker. CABI Publishing, Oxon. pp. 413–447.

509   Heller, J., and Dolev, A. 1994. Biology and population dynamics of a crevice-dwelling land

510   snail, *Cristataria genezarethana* (Clausiliidae). J. Mollusc. Stud. **60**: 33–46.

511   Hesbacher, S., Baur, B., Baur, A., and Proksch, P. 1995. Sequestration of lichen compounds

512   by three species of terrestrial snails. J. Chem. Ecol. **21**: 233–246.

513   doi:10.1007/BF02036654.

514   Hesbacher, S., Fröberg, L., Baur, A., Baur, B., and Proksch, P. 1996. Chemical variation

515   within and between individuals of the lichenized ascomycete *Tephromela atra*. Biochem.

516   Syst. Ecol. **24**:603–609. doi:10.1016/S0305-1978(96)000804.

517   Johnson, M., and Black, R. 1991. Growth survivorship, and population size in the land snail

518   *Rhagada convicta* Cox, 1870 (Pulmonata: Camaenidae) from a semiarid environment in

519   Western Australia. J. Mollusc. Stud. **57**: 367–374. doi:10.1093/mollus/57.3.367.

520   Kerney, M.P., and Cameron, R.A.D. 1979. A Field Guide to the Land Snails of Britain and

521   Northwest Europe. Collins, London.

522   Kéry, M. 2010. Introduction to WinBUGS for Ecologists. A Bayesian Approach to

523   Regression, ANOVA, Mixed Models and Related Analyses. Academic Press, New

524   York.

525   Kéry, M., and Schaub, M. 2012. Bayesian Population Analysis Using WinBUGS. A

526   Hierarchical Perspective. Academic Press, New York.

527   Kostal, V., Rozsypal, J., Pech, P., Zahradnickova, H., and Simek, P. 2013. Physiological and

528   biochemical responses to cold and drought in the rock-dwelling pulmonate snail,

529   *Chondrina avenacea*. J. Comp. Physiol. B **183**: 749–761. doi:10.1007/s00360-013-

530   0749-0.

531   Krahulec, F., Rosén, E., and van der Maarel. E. 1986. Preliminary classification and ecology

532   of dry grassland communities on Ölands Stora Alvar (Sweden). Nordic J. Bot. **6**: 797–

533   809. doi:10.1111/j.1756-1051.1986.tb00483.x.

534   Kuznik-Kowalska, E. 2006. Life cycle of *Discus ruderatus* (Férussac, 1821) (Gastropoda:

535   Pulmonata: Endodontidae). Folia Malacol. **14**: 35–46.

536   Lazaridou-Dimitriadou, M. 1995. The life cycle, demographic analysis, growth and secondary

537   production of the snail *Helicella (Xerothracia) pappi* (Schütt, 1962) (Gastropoda,

538   Pulmonata) in E. Macedonia (Greece). Malacologia, **37**: 1–11.

539   Lunn, D. J., Thomas, A., Best, N., and Spiegelhalter, D. 2000. Win-BUGS – a Bayesian

540   modelling framework: concepts, structure, and extensibility. Stat. Comput. **10**: 325–337.

541   Macdonald, P. and Du, J. 2012. mixdist: Finite Mixture Distribution Models. R package

542   version 0.5-4. http://CRAN.R-project.org/package=mixdist

543   MacDonald, P.D.M., and Green, P.E. 1988. User's guide to program MIX: An interactive

544   program for fitting mixtures of distributions. Ichthus Data Systems.

545   MacDonald, P.D.M., and Pitcher, T.J. 1979. Age-groups from size-frequency data: a versatile

546   and efficient method of analyzing distribution mixtures. J. Fish. Res. Board Can. **36**:

547   987–1001. doi:10.1139/f79-137.

548   Maltz, T.K., and Sulikowska-Drozd, A. 2011. Delayed maturation in the genus *Vestia* P.

549   Hesse (Gastropoda: Pulmonata: Clausiliidae): a model for clausiliid lifecycle strategy. J.

550   Mollusc. Stud. **77:** 41–53. doi:10.1093/mollus/eyq040.

551   Neuckel, W. 1981. Zu Aktivitätsregelung und Wasserhaushalt von *Chondrina avenacea*

552   (Bruguière 1792), einer Felsen bewohnenden Landlungenschnecke. PhD-Thesis,

553   University of Basel.

554   Oosterhoff, L.M. 1977. Variation in growth rate as an ecological factor in the landsnail

555   *Cepaea nemoralis* (L.). Neth. J. Zool. **27**: 1–132. doi:10.1163/002829677X00072.

556   R Core Team. 2013. R: A language and environment for statistical computing. Foundation for

557   Statistical Computing, Vienna, Austria.

558   Riddle, W.A. 1983. Physiological ecology of land snails and slugs. *In* The Mollusca, 6:

559   Ecology. *Edited by* W.E. Russell-Hunter. Academic Press, New York. pp. 431–461.

560   Riddle, W.A., and Miller, V.J. 1988. Cold-hardiness in several species of land snails. J. therm.

561   Biol. **13**: 163–167. doi:10.1016/0306-4565(88)90028-9.

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

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

564   SMHI. 2014. Annual temperature and precipitation. Swedish Meteorological and Hydrological

565   Institute. Available from http://www.smhi.se/klimatdata [accessed on 3 October 2014]

566   Sulikowska-Drozd, A., and Maltz, T.K. 2012. Reproduction of *Balea (Pseudalinda) fallax*

567   (Rossmässler, 1836) (Gastropoda: Pulmonata: Clausiliidae) kept under laboratory

568   conditions. Folia Malacol. **20**: 27–34.

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

570   Sturtz, S., Ligges, U., and Gelman, A. 2005. R2WinBUGS: A Package for Running

571   WinBUGS from R. J. Statistical Software, **12**: 1–16.

572   Terhivuo, J. 1978. Growth, reproduction and hibernation of *Arianta arbustorum* (L.)

573   (Gastropoda, Helicidae) in southern Finland, Ann. Zool. Fenn. **15**: 8–16.

574   Waldén, H.W. 1984. Sveriges landmollusker – en artlista med kommentarer. Fauna och flora,

575   **79**: 29–43.

576   Williamson, P. 1976. Size-weight relationships and field growth rates of the landsnail *Cepaea*

577   *nemoralis* L. J. Anim. Ecol. **45**: 875–885. doi:10.2307/3586.

578   Williamson, P., Cameron, R.A., and Carter, M.A. 1977. Population dynamics of the land snail

579   *Cepaea nemoralis* (L.): a six year study. J. Anim. Ecol. **46**: 181–194.

580   Wolda, H. 1963. Natural populations of the polymorphic land snail *Cepaea nemoralis* (L.).

581   Arch. Néerl. Zool. **15**: 381–471.

582   Wolda, H., and Kreulen, D.A. 1973. Ecology of some experimental populations of the

583   landsnail *Cepaea nemoralis* (L.). II. Production and survival of eggs and juveniles. Neth.
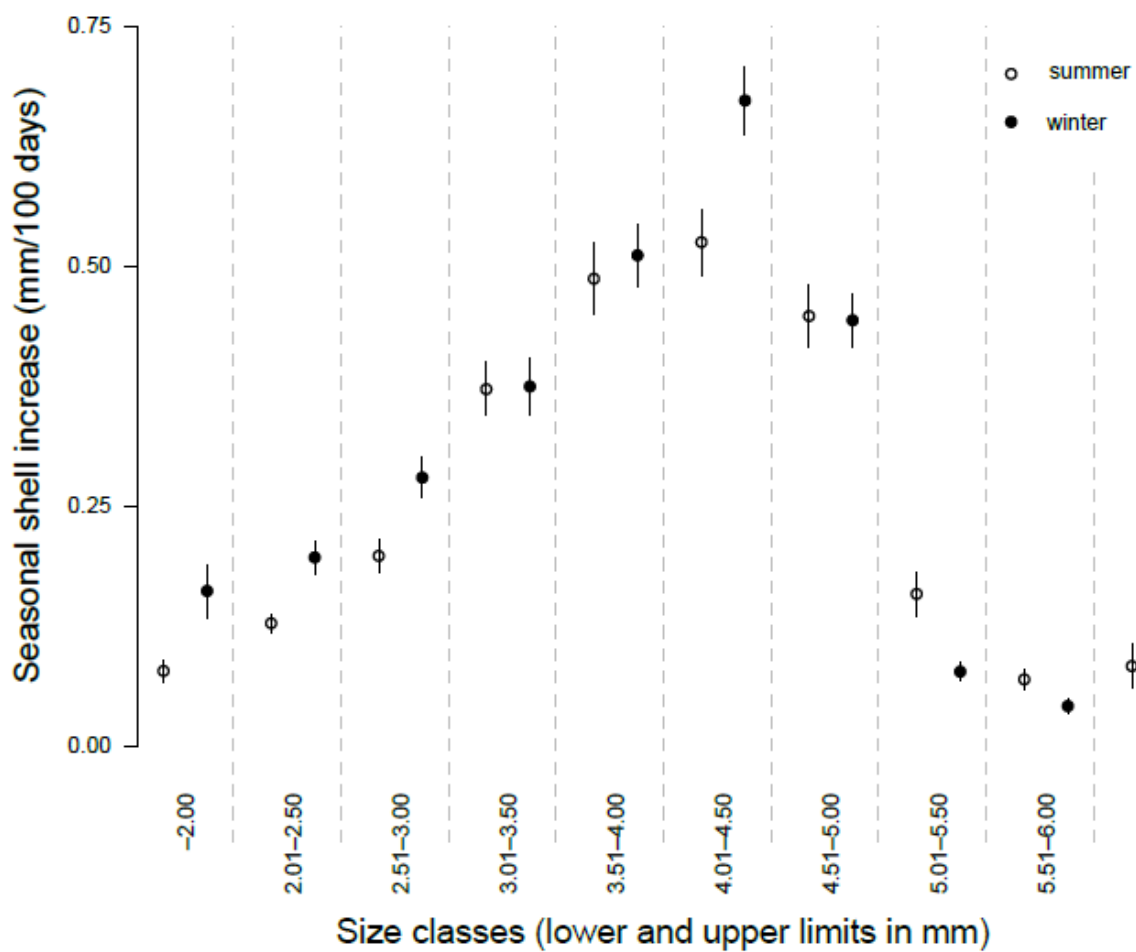
584   J. Zool. **23**:168–188.

585

586

587
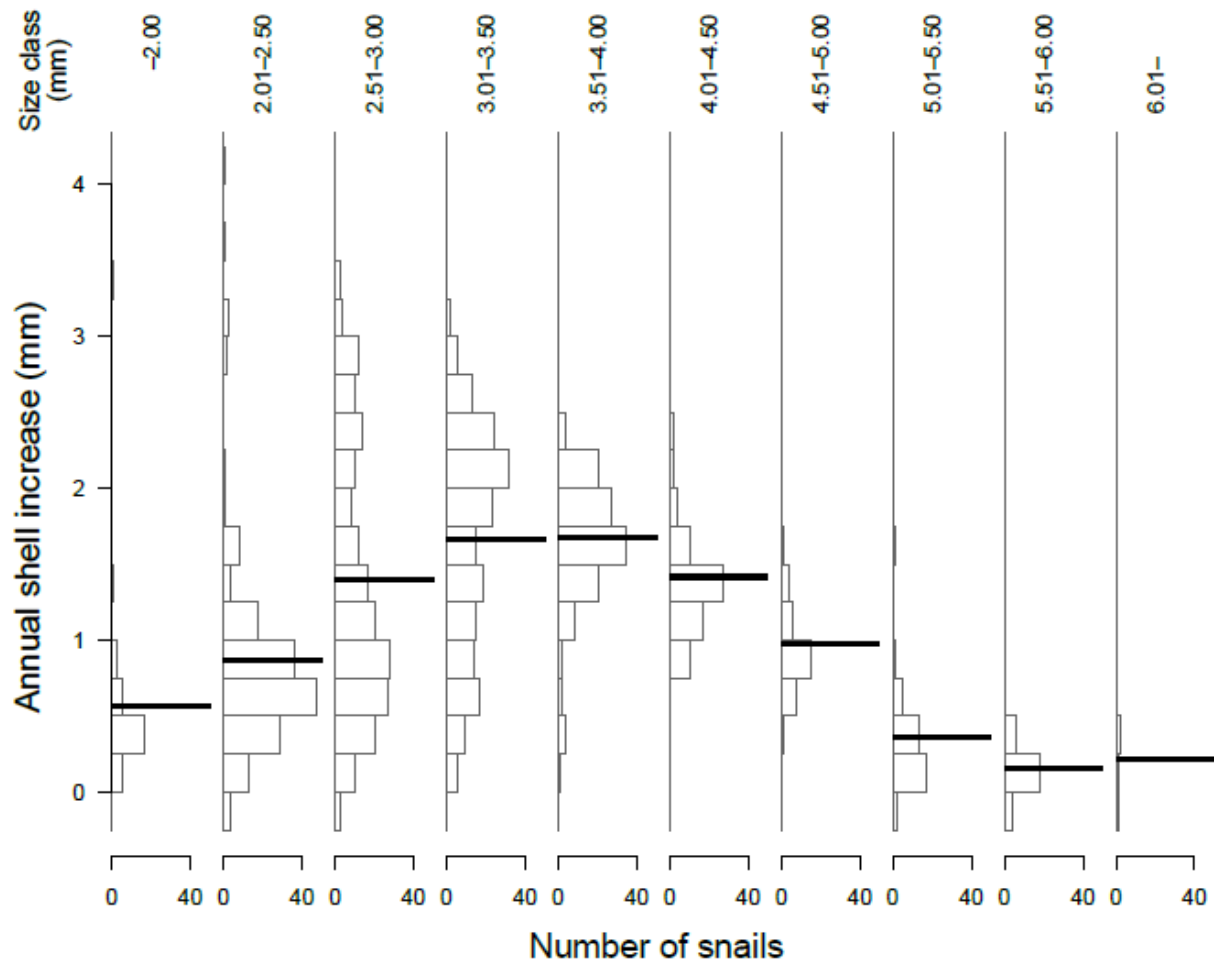
Fig. 1. Distribution of annual shell increase in individually marked *C. clienta* belonging to

different size classes. Bold horizontal lines indicate median values for each size class.

590

591

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.

595
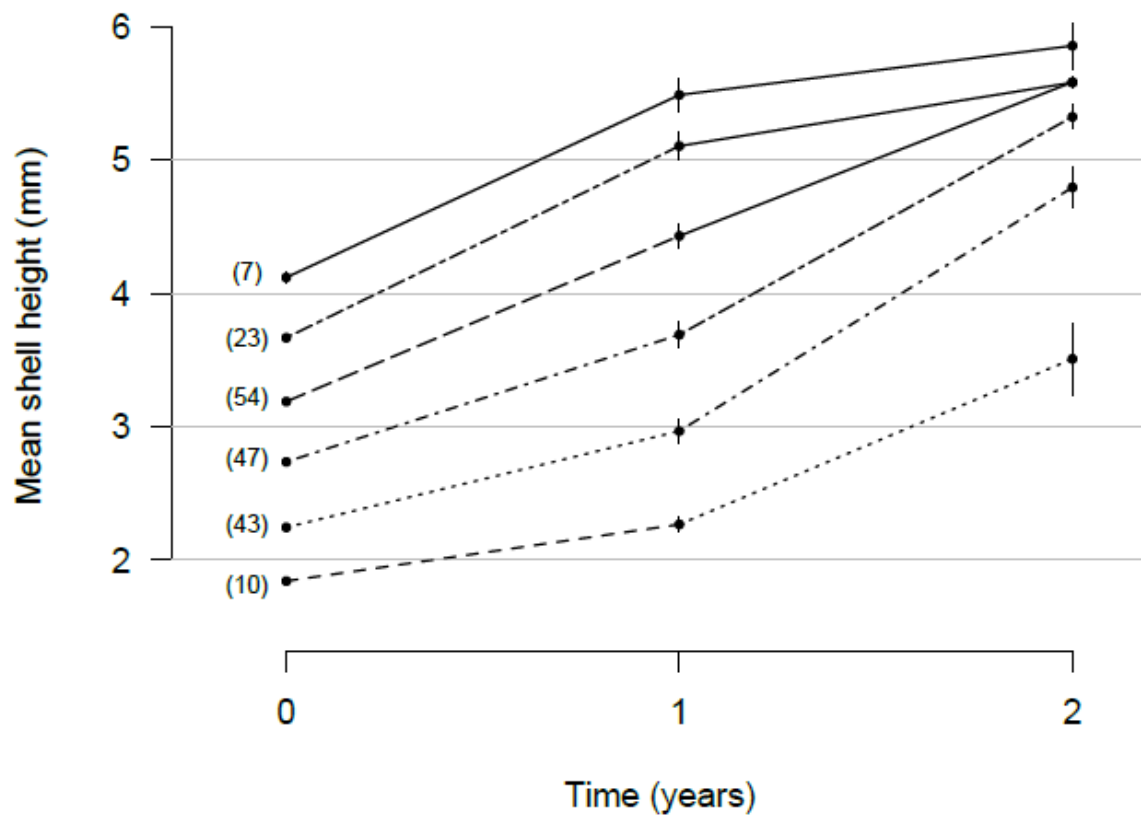
596

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
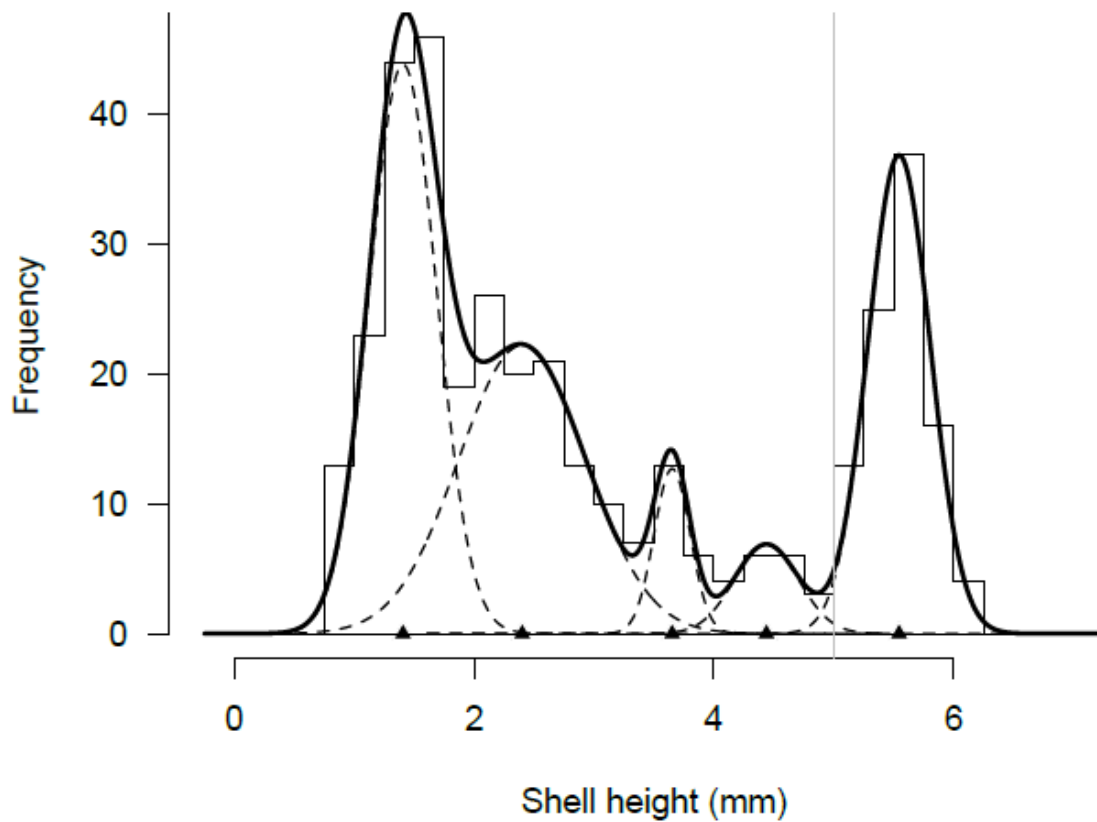
601

602 **Fig. 4.** Frequency distribution of shell height of *C. clienta* in a population sampled on 23

603 September 1990. Idealized curves of year cohorts are shown with triangles indicating the mean

604 shell height of the corresponding cohort. The group of adult snails consists of individuals from

605 several cohorts.

606

607 **Table 1.** Size and aspect of the four vertical quarry walls (sites) on which growth and

608 survival of snails were assessed together with local snail density and shell size.

609

610

611

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

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

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

623 **Table 2.** Summary of ANOVA table examining the effect of site and snail size class on

624 the relative growth rate per year in individuals of *C. clienta*.
625

626
627

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		

640 Analyses were run separately for each year. The minimal adequate model was selected using

641 the Akaike Information Criterion. Only snails belonging to the size classes 1–5 were

642 considered in the analyses.