normally burrow. The most likely forcing factor for the retention of mobility in this case is disturbance of the bottom by iceberg scour, which is known to occur regularly in the shallow waters where *L. elliptica* are abundant[4,8]. Fitness is clearly increased by having a capacity for surface movement, following dislodgement from the sediment, combined with the ability to re-burrow, which would allow some individuals from any population disturbed by ice scour to regain the protection of their normal habitat. What is clearly a secondary development of a mode of locomotion that exploits morphological features primarily associated with the deep-burrowing habit, emphasises yet again the plasticity of function in the adaptive radiation of bivalve molluscs, especially in the Anomalodesmata, a group that Yonge and Morton[9] described as 'the culmination of evolution—although very far from the peak of success— within the Bivalvia'.

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Phally status and size in Niger populations of *Bulinus truncatus* (Gastropoda: Planorbidae)

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Phally polymorphism is characterized by the co-occurrence in natural populations of hermaphroditic animals of individuals deprived of the male copulatory organ (aphallic) and regular euphallic individuals.[1] It has been recorded in Pulmonates only,[2] and actually studied in *Bulinus truncatus* (Audouin, 1827) only.[1,3,4] The percentage of aphallic individuals, hereafter referred to as the aphally ratio, is highly variable among populations though generally higher than one-half.[5] Phally polymorphism has been shown to have both an environmental and a genetic basis.[1,6,7] Populations of *B. truncatus* have a high selfing rate, whatever their aphally ratio.[8] An important question is how a mutation leading to aphally can invade an originally euphallic population and rise to the high frequencies observed. Both stochastic and selective factors have been suggested.[4,5] Given the selfing rates observed in natural populations, even a limited selective advantage to aphallic individuals will favour the spread of an aphallic

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mutation. In terms of the theory of sex allocation,[9] such an advantage may result from a reallocation of resources from the lost male function to other functions, such as reproduction as female, growth or survival. Tests of this idea produced inconsistent results.[3,10,11,12] However these studies were performed in the laboratory, and may therefore have missed some factors acting in natural populations. Previous surveys have shown that aphallic individuals are smaller than euphallic individuals in a land snail,[13] though the reverse was found in *B. truncatus*.[14] If variations in life-history traits such as growth or survival have an impact on body size, size difference may constitute a valuable and synthetic estimator when testing for resource reallocation. This was the basis for undertaking an analysis of size distribution in 15 populations from Niger of *B. truncatus* and comparing size between aphallic and euphallic individuals. Individuals were collected on three occasions separated by three-week intervals early 1995. We also tested for a relationship between the aphally ratio and population density, and provide

some information on the population biology of *B. truncatus* in southern Niger.

General information on the population biology and ecology of *B. truncatus* is given in Brown.[15] Snails were collected from 15 sites in Niger early 1995. Populations were sampled three times at three-week intervals (sample I: January 11–18; II: February 1–8; III: February 20–24). The geographic situation of populations is given elsewhere.[16] Snails were hand-collected by looking at vegetation (mainly water lilies), branches, sticks and plastic bags. Main supports were water lilies (populations NamagaPM, B and W, MariS and N, Kotaki and Bala), dead branches (TeraR and D, Kotaki, Ligido, Doubalma, Boyze I and II), plastic bags (Niumpalma) and a dead tree trunk (Taka). The overall searching time per site was up to two hours, conducted by either two persons (second sampling; up to one hour per person) or four persons (first and third sampling; up to 30 min per person). All snails over about three mm in length were collected, irrespective of size. A size of three mm was chosen since this is the lowest size at which phally status can be determined. Density was estimated per unit time of searching. Snails were brought back alive to the laboratory in Niamey. Individual size was measured at the nearest 0.1 mm as the distance from the apex to the base of the aperture using a caliper. Phally status was scored at the same time observing narcotized individuals under a binocular microscope. Time between sampling and measurement was less than five days, except for the second sampling for which it was about two weeks. Limited mortality was recorded over this period.

We first compared the size of aphallic and euphallic individuals using a t-test. Residuals turned out to strongly depart from normality despite appropriate data transformation. We then used non-parametric analyses (Kruskall-Wallis one-way analysis of variance) for size comparison between aphallic and euphallic individuals, and between individuals among sampling dates within each population. Rank-correlation was estimated between density and aphally ratio for each sampling date on one side, and on densities between sampling dates on the other side. Statistical analyses were performed following Sokal & Rohlf.[17]

A total of 7080 individuals were measured and their sexual status checked. Aphally ratios per sampling date and per population[ee 16] ranged from 0.19 in Niumpalma (third sampling) to 1.00 in Taka (first sampling). We note though that most values are above 0.5, and also that the aphally ratio tended to decrease over the course of the study. Mean size values per population per sampling date and per sexual status and their standard deviation are given in Table 1, together with the number of individuals studied and the associated probabilities for rejecting the null hypothesis of size equality. As we did not collect individuals smaller than three mm, our dataset was not suited for a proper cohort analysis. However at least two differentiated cohorts occur in some populations. On the other hand the full range

of sizes with no obvious modes was represented in most samples more or less regularly, meaning that reproduction is approximately continuous in the populations studied (see examples in Fig. 1). Mean size decreased over time (Table 1). A significant decrease over the three sampling dates appeared in seven populations, whereas no significant increase was detected. In some populations this decrease coincided with the disappearance of large individuals (e.g. Nagama B in Fig. 1) or the occurrence of small individuals (e.g. Doubalma; not shown) due to a more active reproduction. However, the evolution of size distributions in time may, in other less clear-cut examples, be due either to mortality, or to very limited growth.

Densities correlated relatively well between sampling dates (I–II: $r = 0.676$, p < 0.001; II–III: $r = 0.147$, non-significant; I–III: $r = 0.582$, p < 0.005). However we did not detect any correlation between density (data not shown) and aphally ratio (I: $r = -0.125$, non-significant; II, $r = -0.314$, non-significant; III, $r = -0.006$, non-significant). We also found that aphallic individuals are larger than euphallic individuals. This is quite significant when all samples were pooled (p $< 10^{-4}$); however the situation varies with populations (Table 1) with significant larger size of aphallic individuals in TeraR I, Kotaki II, Bala III, Niumpalma I, II and III and Doubalma III. Exceptions to this trend are Tera D and Boyze I, where euphallics are larger (Table 1).

A first and qualitative assessment from our sampling is the aggregative distribution of snails within ponds when available supports are scarcely distributed. This distribution is much more continuous when for example water lilies cover the whole sampled area. That the distribution seems aggregative may mainly be due to two reasons. First sampling may be biased because it is easier to collect snails on supports than on muddy bottoms. As our sampling design is neither exhaustive, nor regular, this may lead to the false impression of aggregation. Alternatively our sampling may truly represent the snail distribution, and supports may constitute kind of refuges. A highly aggregated distribution has also been observed in southern Africa for *Bulinus tropicus* in muddy seasonally drying pools, where snails were associated with scattered refuges such as logs of rotting wood.[18] We also showed that density across the area studied varies quite similarly with time among populations, and that density is a poor indicator of the aphally ratio, confirming previous results obtained in Northern Nigeria[4]. On density estimates, as well as size distributions, a more detailed analysis would be required[ee 19,20] for distinguishing between the various hypotheses.

The tendency to a decrease of the aphally ratio in time[16] may be related to the fact that aphally is partly under the influence of temperature[6], and temperature at the stage in the snails' ontogeny when phally was determined here decreased in time. A decrease of mean temperature is indeed expected to correlate with a decrease of the aphally ratio. Temperature data obtained in this study (not shown) and by

Table 1. Mean size for each population per morph (A and E refer to aphallic and euphallic snails respectively) and per sampling date (I, II and III refer to the first, second and third sampling respectively). The number of individuals analysed and the standard deviation on the mean are given in parentheses. p and 'significance' are the probabilities associated with the comparisons between morphs and among sampling dates respectively. Probabilities lower than 5% are given in bold characters. — = no data.

Population		Sampling I	II	III	Significance
NamagaPM	A	9.16 (34; 4.81)	7.41 (20; 3.46)	9.06 (34; 4.01)	0.393
	E	7.63 (10; 3.40)	5.77 (32; 1.22)	7.50 (26; 2.57)	**0.041**
	p	0.441	0.056	0.184	
NamagaB	A	8.18 (65; 1.72)	5.62 (60; 1.50)	4.10 (174; 0.95)	$<10^{-4}$
	E	8.42 (11; 1.60)	6.77 (6; 1.41)	3.94 (56; 0.45)	$<10^{-4}$
	p	0.434	0.086	0.274	
NamagaW	A	—	6.96 (43; 1.42)	6.63 (94; 3.05)	0.200
	E	—	6.79 (22; 1.28)	6.48 (13; 49)	0.811
	p	—	0.814	0.913	
TeraR	A	6.55 (86; 2.11)	6.22 (72; 1.76)	5.98 (88; 2.73)	0.069
	E	5.21 (14; 1.40)	6.30 (19; 1.22)	6.68 (8; 2.76)	0.073
	p	**0.017**	0.767	0.330	
TeraD	A	5.30 (7; 2.00)	5.28 (157; 1.29)	5.60 (147; 1.69)	0.259
	E	5.87 (3; 0.60)	5.98 (36; 1.39)	5.90 (57; 1.65)	0.846
	p	0.424	**0.003**	0.210	
Taka	A	6.58 (136; 2.11)	5.71 (127; 1.26)	5.84 (310; 2.05)	$<10^{-4}$
	E	—	5.70 (7; 0.48)	6.38 (8; 3.17)	0.451
	p	Irrelevant	0.502	0.793	
MariS	A	5.08 (169; 0.91)	5.51 (82; 0.99)	4.74 (333; 1.31)	$<10^{-4}$
	E	4.94 (55; 0.94)	5.64 (43; 0.73)	4.70 (139; 1.31)	$<10^{-4}$
	p	0.341	0.446	0.610	
MariN	A	5.39 (199; 1.02)	4.94 (144; 1.07)	3.80 (268; 0.63)	$<10^{-4}$
	E	5.11 (38; 0.84)	5.23 (36; 0.93)	3.92 (59; 0.83)	$<10^{-4}$
	p	0.112	0.120	0.694	
Kotaki	A	5.17 (158; 1.82)	4.45 (280; 1.44)	4.53 (234; 1.86)	$<10^{-4}$
	E	5.01 (70; 1.11)	3.91 (290; 0.63)	4.02 (238; 1.01)	$<10^{-4}$
	p	0.641	$<10^{-4}$	**0.006**	
Bala	A	5.43 (35; 0.93)	4.80 (29; 1.18)	5.61 (50; 1.28)	**0.008**
	E	5.11 (34; 1.05)	4.71 (72; 0.94)	5.19 (147; 1.29)	**0.018**
	p	0.161	0.934	**0.045**	
Niumpalma	A	5.56 (229; 1.59)	4.07 (87; 1.05)	4.09 (31; 1.43)	$<10^{-4}$
	E	4.74 (89; 1.22)	3.65 (121; 0.63)	3.61 (141; 0.57)	$<10^{-4}$
	p	$<10^{-4}$	**0.004**	**0.038**	
Ligido	A	5.96 (260; 1.46)	5.54 (42; 1.26)	4.66 (40; 1.56)	$<10^{-4}$
	E	6.22 (66; 1.21)	5.33 (9; 0.82)	4.09 (12; 2.03)	$<10^{-4}$
	p	0.099	0.711	0.103	
Doubalma	A	7.93 (131; 2.28)	6.45 (98; 2.02)	5.78 (140; 2.33)	$<10^{-4}$
	E	7.48 (45; 2.43)	6.17 (46; 1.60)	4.31 (81; 1.79)	$<10^{-4}$
	p	0.257	0.695	$<10^{-4}$	
Boyze I	A	5.32 (56; 1.27)	5.04 (16; 0.77)	4.68 (46; 1.22)	**0.023**
	E	6.10 (14; 0.45)	6.14 (7; 1.46)	5.10 (6; 1.51)	0.417
	p	**0.032**	0.076	0.510	
Boyze II	A	5.94 (54; 1.39)	5.63 (27; 0.90)	—	0.249
	E	5.00 (1; 0.00)	5.80 (1; 0.00)		irrelevant
	p	0.394	0.620		

Namaga B   Namaga PM
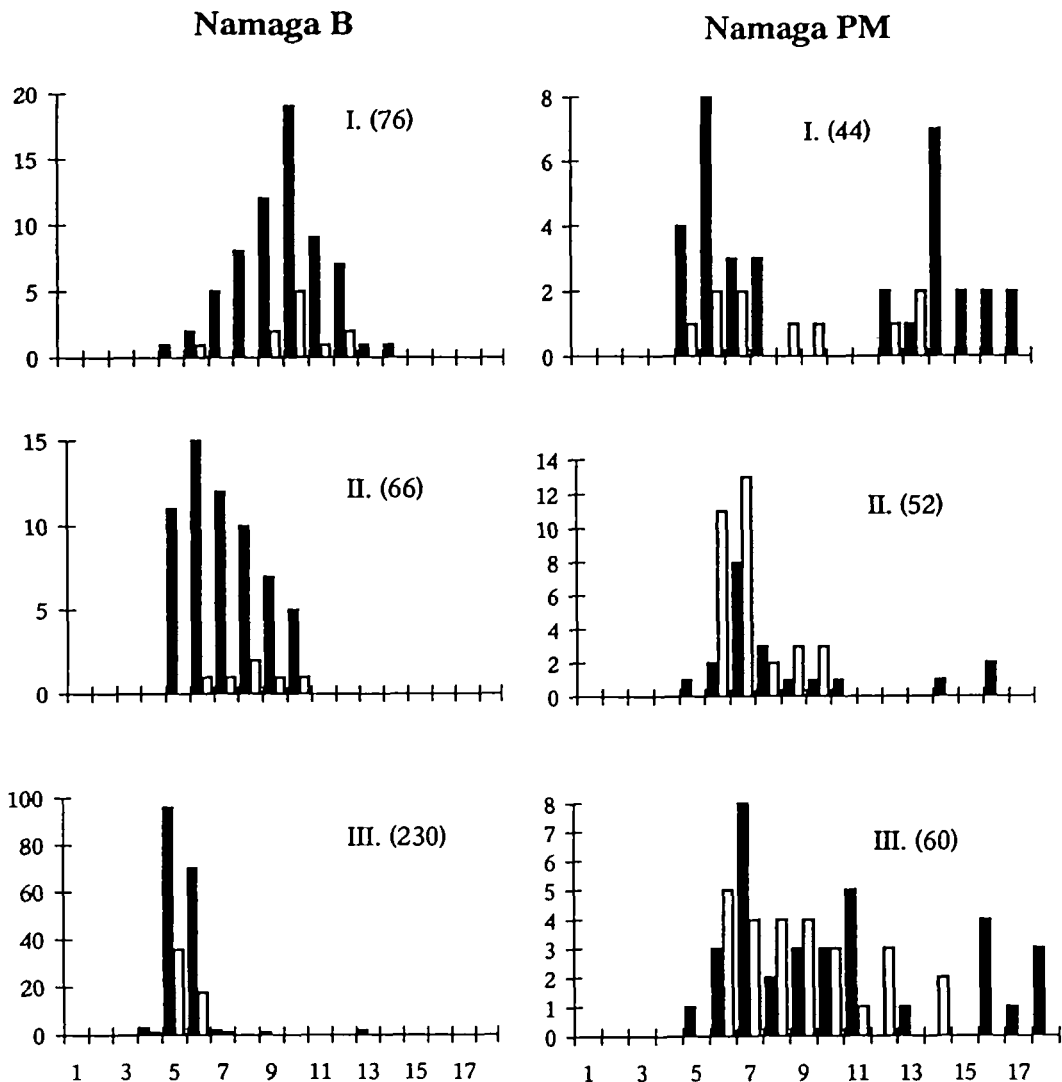
Figure 1. Size distributions per sampling date for two of the populations studied. I, II and III refer to the first, second and third sampling date respectively, and the value in parentheses is the number of individuals measured. Size is in mm, and size classes include all individual within one mm. Black bars refer to aphallic individuals.

others[19,21] in the same area are indicative of a trend towards lower values over the period during which the phally status of the snails studied here was determined.

The most interesting result of our work is the larger mean size of aphallic individuals when compared to euphallic individuals. This confirms results from a survey of populations of *B. truncatus* in Northern Nigeria.[14] This difference may have three origins: (i) aphallic and euphallic individuals have the same mean age, though aphallics grow faster,

(ii) aphallic individuals are on average older than euphallic individuals because of a better survival and (iii) aphallic individuals are on average older than euphallic, as a result of the decrease of the aphally ratio in time noted above. (i) and (ii) are consistent with the reallocation theory presented above. Such a size difference has never been found in laboratory conditions. Indeed any difference observed concerned reproduction.[3,10] However it may be that the harsher conditions of natural populations allow such a difference to develop, since

differences in fitness may appear under stressful conditions where no differences are detected under milder conditions.[22] Hypothesis (iii) would be consistent with temperature determination of aphally[14,16] and the actual decrease of the aphally ratio in time shown here. That the populations for which the largest decrease of the aphally ratio was recorded (Doubalma, Kotaki and Niumpalma[16]) also exhibited the largest size differences between the two morphs is a further argument in favour of this hypothesis.

Confounding age and growth effect is a common problem in population biology.[x,23] Evaluating hypothesis (i) is in principle possible provided that individual age is known. On the other hand, (ii) and (iii) are both based on aphallic individuals being on average older than euphallic individuals. Assuming equal growth between aphallic and euphallic individuals, (ii) and (iii) can be distinguished within each population by fitting a linear model where phally status (as a binary variable) is a combination of size and sampling date. If (ii) holds, the size effect only is expected to be significant whereas under (iii) the effect of both size and sampling date must be significant. This test was performed using the software GLIM[24] in the populations in which a marked decrease in aphally ratio was noted (Doubalma, Kotaki and Niumpalma). The effect of size was significant in the three populations ($p < 10^{-4}$) while the sampling date effect was significant in the last two populations only ($p = 0.004$ and $p < 10^{-4}$ respectively). This suggests that (ii) may not be rejected in Niumpalma and Kotaki while the size difference in Doubalma is rather explained by growth or survival. Another possible test distinguishing between (ii) and (iii) would be to sample eggs or juveniles in the field and estimate the aphally ratio as soon as possible so as to maintain mortality at its lowest.

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