Variation in desiccation tolerance in freshwater snails and its consequences for invasion ability

B. Facon[1,*], E. Machline[1], J.P. Pointier[2] & P. David[1]
[1]*Centre d'Ecologie Fonctionnelle et Evolutive, Centre National de la Recherche Scientifique, 1919 route de Mende, 34293 Montpellier Cedex, France;* [2]*Laboratoire de Biologie Marine et Malacologie, Centre de Biologie et d'Ecologie Tropicale et Méditerranéenne, Perpignan, France; *Author for correspondence (e-mail: facon@cefe.cnrs-mop.fr)*

Abstract

The freshwaters of Martinique (French West Indies) have recently been invaded by snails belonging to the Thiaridae family (Gastropoda; Prosobranchia). Eight distinct Thiarid lines have been successively introduced in Martinique, and are still in the process of sequentially replacing one another within local habitats, revealing a range of increasing invasive abilities. Our aim was to test whether the variation in invasive ability can be partly explained by a specific life-history trait, desiccation tolerance, which might be important in view of the typical instability of tropical freshwater habitats. We therefore tested desiccation tolerance in both juveniles and adults under laboratory conditions. Our data show that, although all Thiarid lines resist desiccation quite well, they exhibit extreme variation in the degree of tolerance. These differences are mostly mediated by individual size, but are definitely of genetic origin given that our individuals were of similar ages and were raised under standardized laboratory conditions. The overall invasive success of a line in Martinique, deduced from field surveys, does not correlate with its desiccation tolerance. However, desiccation tolerance does seem to be a limiting factor for the invasion of the small fraction of habitats that are most exposed to drought. More generally, our study exemplifies the possibility that the invasion differential among habitats, rather than a general invasion ability, be predicted according to a particular life-history trait, within a set of closely related invasive taxa.

Introduction

Biological invasions facilitated by human activities have become a worldwide environmental problem in the last century (Everett 2000). Humans have caused an unprecedented redistribution of numerous organisms, plants as well as animals. Indeed, human activities (such as agriculture, trade exchange...) have often broken down natural dispersal barriers (Kolar and Lodge 2001). As an example, the rate of species introductions in freshwaters is continuously increasing throughout the world (Welcomme 1992). The most spectacular cases include the homogenization of fish faunas across the United States (Rahel 2000), and the recent mass invasion of the North American Great Lakes by Ponto-Caspian species (Ricciardi and MacIsaac 2000).

The case of invasive freshwater molluscs has been extensively studied, especially because of their conflicting consequences for human health (Pointier 1999). Indeed some freshwater gastropods can play the role of intermediate hosts for numerous parasites infecting domestic animals and humans. Introduced exotic molluscs can be responsible for the new establishment or the increased rate of parasite transmission to humans (see, for example, the transmission of the liver fluke in

Andean countries by *Lymnaea truncatula* introduced from Europe, Jabbour-Zahab et al. 1997). On the other hand, recent studies have shown that other invading species may have a positive influence on human health by displacing local molluscan vectors (Pointier and McCullough 1989; Pointier 1993).

The present study focuses on the recent invasion of the freshwaters of Martinique Island (French West Indies) by several snails belonging to the Thiaridae family (Gastropoda; Prosobranchia). The invasion sequence is well documented. Indeed, after 1979, time of the first introduction of Thiarids, annual surveys have been conducted in Martinique (Pointier et al. 1993; Pointier 2001). These surveys have revealed that introductions repeatedly occurred in Martinique. Various Thiarid lines seem to successively replace one another within local habitats (Pointier 2001).

Many studies have tried to identify the traits that characterize a good invader (Hill et al. 1993; Williamson and Fitter 1996a). Although some life-history traits can explain some successful invasions (Hill et al. 1993; Williamson and Fitter 1996a), a high diversity in the life-history traits of successfully introduced species is observed throughout the world (Lockwood 1999; Sakai et al. 2001), and it seems very difficult to make general predictions (Williamson and Fitter 1996b). Moreover, some studies (Moyle and Light 1996; Rosecchi et al. 2001; Hacker et al. 2001) suggest that abiotic factors can also determine invasive success.

This study forms part of a research program with the general aim to test whether the variability in invasive abilities among the different Thiarid lines occurring in Martinique can be explained by differences in life-history-traits. We will here focus on desiccation tolerance that might constitute an important life-history trait in freshwater molluscs. Drought and flood are indeed prominent factors shaping freshwater environments in the tropics, and thus may influence the distribution and life cycles of freshwater molluscs (Appleton 1978; Jarne and Städler 1995; Brown 1994). The ability to invade tropical freshwater environments could therefore be related to desiccation tolerance. Survival under drying conditions is expected to play a key role in two components of the invasive process: (i) it could influence the ability to spread from a water body (or a watershed) to another, as migrant individuals must spend some time out of water during this process, whatever migration vector is involved. (ii) It could increase colonization capacity and/or resistance to local population

extinction in environments characterized by large fluctuations in water levels, such as temporary ponds and river margins. On such bases, it could also be expected that molluscs exhibit differential invasive ability according to habitat types: isolated, unstable habitats, such as temporary ponds, should be more sensitive to invasion by desiccation-tolerant taxa or genotypes, than more connected and stable habitats, such as permanent rivers.

Using our annual survey of the Martinique freshwater habitats and an experimental design in laboratory, we attempt to answer the following questions:

1. Are there differences in desiccation tolerance between the different Thiarid lines which have invaded Martinique Island? Which part of this variation is due to differences in individual size? These questions have been asked for two age classes, adults and juveniles.
2. Did Thiarid lines differentially invade temporary and permanent habitats according to their desiccation tolerance?

Materials and methods

Biological material

Melanoides tuberculata and *Tarebia granifera* are tropical freshwater prosobranch gastropods belonging to the Thiaridae family which recently invaded the whole intertropical belt (Pointier 1999). Before 1940, the two species were found in various regions of Asia and Africa. Since then, Neotropical waters (from Argentinia to Florida) have been quickly invaded by one species or the other. The third species, *Melanoides amabilis*, originates from Sulawesi, Indonesia (Reeve 1860). Its discovery in Martinique in 1997 constitutes its first report out of its origin area (Pointier 2001). These three species are classically considered to be parthenogenetic (Abbott 1952; Jacob 1958; Stoddart 1985), although there is evidence that sexual reproduction occurs at low frequency in natural populations for *M. tuberculata* (Samadi et al. 1999). Surveys in recently invaded areas, especially in the French West Indies (Pointier 1989; Samadi et al. 1999), have shown that *M. tuberculata* exhibits an important variation in shell ornamentation, that allows the definition of discrete morphs. Microsatellite surveys have revealed that each morph corresponds to a genetically homogeneous, clonally-propagated

parthenogenetic line. Unlike *M. tuberculata*, the two other species (*M. amabilis* and *T. granifera*) consist in single clonal lines essentially devoid of morphological variation. Up to now, in Martinique, a total of eight different lines of invasive Thiarids have been observed: *M. amabilis* (MA), *T. granifera* (TG) and six morphs of *M. tuberculata* (PAP, FAL, PDC, CPF, FDF, MAD) (Pointier 1999). We can notice here that *T. granifera*, which is the most taxonomically distant line, exhibits a distinctive morphology compared to all *Melanoides* lines, with a proportionally larger aperture. For five lines (PAP, FAL, PDC, MAD and MA), seven individuals were collected in two populations in the field and transferred to the laboratory. Given the decline of FAL in Martinique, we had to collect one of the two populations of FAL in Marie Galante, another island of the French West Indies in which the FAL morph arrived approximately at the same time in the 1970s. For two lines (CPF and TG), three populations were sampled, and for FDF, the only population known in Martinique was sampled. Figure 1 shows the location of these populations and abbreviations used in this study. The individuals collected in the field constitute the first generation (G0). Offspring (G1) laid by these snails (6–7 newborn per G0 individual) were isolated in individual boxes and fed *ad libitum* with boiled lettuce until they were adults. They were maintained under a 12 : 12 L : D photoperiod in 75-ml plastic boxes filled with water originating from the Lez spring (near Montpellier). Water and food were changed once a week and the position of rearing boxes was randomly changed once a week. These snails were used to test the desiccation tolerance of adult snails using the drying protocol explained below. Because all G1 offspring were collected over a relatively short period, our protocol ensures that all G1 snails had approximately the same age (13 $\pm$ 1 months), and had been raised under standardized conditions throughout their lives, when the experiment started. Any line effect observed is therefore entirely due to genetic differences. Offspring (G2) produced by these individuals (before they were submitted to desiccation tests) was used to test the desiccation tolerance of juvenile snails.

Drying protocol

Juveniles

Thiarids are viviparous snails and directly produce juveniles. A total of 1234 G2 juveniles from all populations and morphs was collected (maximum age: 7 days) and placed under drying conditions (exposed to air at a temperature of 25 °C and a relative humidity of 80%) during a 3-h period. They were then put back into water to detect the surviving individuals. The survivors were counted and the mean survival rate was calculated per population. The same protocol was repeated with other
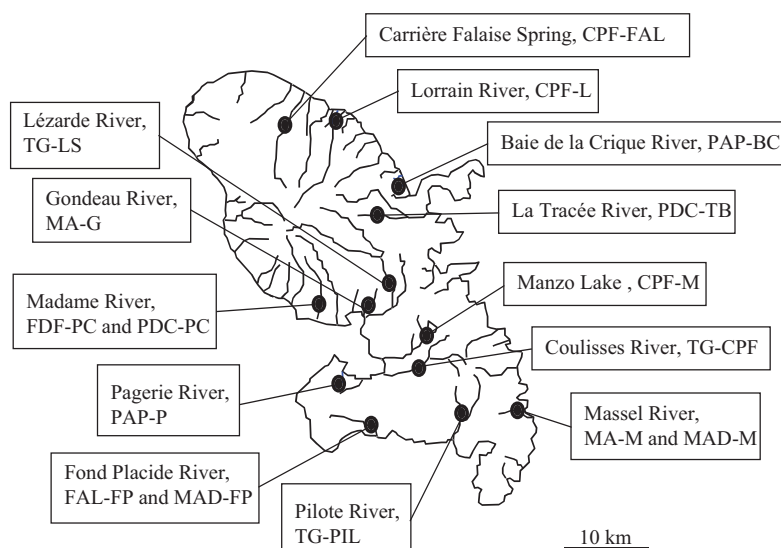

Figure 1. Map of Martinique Island showing the locations of populations collected in this study. The code used is as following: the first two or three letters correspond to the name of the Thiarid lines (for instance, PAP, FAL or TG), and the last letters correspond to an abbreviation of the sampled populations (for instance, FP for Fond Placide river, or PIL for Pilote river). The second population of FAL (FAL-N) was collected in Nesmond Pond (Marie Galante Island).

G2 juveniles for a drying time of 15 h ($N = 1369$). Dead and surviving juveniles were separately transferred into alcohol immediately after the experiment. All shells were later digitized and their lengths automatically measured to the nearest 0.1 mm using the morphometric software Optimas 6.5$^{©}$.

Adults

G1 adults ($N = 746$) were first put individually in drying conditions for a period of 24 h. Then they were put back into water during 48 h, which allowed us to detect the surviving individuals. These surviving individuals were then submitted to drying conditions for 48 h, then brought back into water during 48 h. This process was repeated with increasing drying periods (1, 2, 3, 4, 5, 6, 7, 8, 10, 12, 14, 16, 18, 20, 24, 28 days) up to a point where all the snails died. Hence a maximum survival time in drying conditions could be estimated for each individual. Adult shell length was measured for each individual using a binocular microscope.

Statistical analysis

Juveniles

For each drying period (3 and 15 h, respectively) survival was a binomial variable and the mean survival probability (and 95% CI) was estimated for each population and line. The effects of explanatory variables (line, population and shell length) on logit-transformed survival probabilities were analyzed using deviance analysis (Crawley 1994). The different tests were worked out by model simplification using the software JMP$^{©}$ (Sall and Lehman 1996). In this kind of tests, models including (1) and not including (2) the variable of interest are compared by calculating the change in deviance $X^2 = 2(\mathrm{Ln}(L)_{\mathrm{model}\ 1} - \mathrm{Ln}(L)_{\mathrm{model}\ 2})$. This follows a χ^2 distribution with $N_1 - N_2$ degrees of freedom (N_i being the number of independent parameters estimated in model i; see McCullagh and Nelder 1983). Departure from a binomial distribution was tested, and when necessary, overdispersion was taken into account by replacing χ^2 test by Fisher's test (Sokal and Rohlf 1995). We first tested for a line effect and a nested population effect, both of which document genetic variation in juvenile desiccation tolerance in our design. Then we included a shell length effect, in order to evaluate how much of the genetic (between-line) and non-genetic (within-line) variation in desiccation tolerance is accounted for by differences in juvenile size. In

testing size effects, the population effects were ignored for the sake of simplicity, as the first analysis showed that they were very weak. All model simplifications were done sequentially, by first removing nested terms or interaction terms.

Adults

For adults, our data set consisted in the maximum duration of desiccation that each individual was able to survive. Because this variable did not follow a classical distribution, we analyzed it using non-parametric analysis of variance. We used Kruskal–Wallis test to assess a line effect, and for each line a population effect. We also tested for effects of shell length using Spearman rank correlation.

Classification of the morphs according to their invasive ability

A survey of 110 sites (chosen so as to cover most watersheds in Martinique) was carried out each year since 1994. This survey allowed us to follow the variation of the relative densities of all Thiarid lines in each site (Pointier et al. 1993). For each pair of lines, we determined the best-invading line as the one that increased in relative frequency most often when both lines were observed in the same site. Although not all possible pairs could be documented in our data set, all the available pairwise relationships happened to be transitive, that is, for any three lines A, B and C, when A > B and B > C, we also observed A > C. This allowed us to establish a single classification of all lines according to increasing invasive abilities: FAL < PAP < MAD < PDC < FDF < CPF < MA < TG. We used a Spearman rank correlation test to infer whether the variability in desiccation tolerance (for the juveniles and for the adults) could explain the variability in invasive abilities observed in the field.

The distribution of lines in Martinique among temporary and permanent sites

The 110 sites used to establish invasive history almost all pertain to the 'permanent, stable' type of habitat (permanent rivers) as this is by far the dominant habitat for Thiarids in Martinique. This data set cannot be used to document invasive history in the minority of 'temporary, unstable' habitats (some small rivers or streams, as well as isolated ponds), most of which are located in the southern part of the island. For this reason we tried in 2002 to increase our survey

by specifically adding 'temporary' sites (164 sites, of which 147 are of the permanent type, and 17 of the temporary type). Although we lack historical data on these sites, we expect that, under the null hypothesis that desiccation tolerance plays no role in relation to invasion, the relative representation of desiccation-tolerant and desiccation-sensitive lines be the same in both classes of sites. We tested whether the relative representation of three lines (PAP, MAD and TG) differed between the two kinds of sites using a g-test. We used these three lines because they are well represented in the 2002 data set, and representative of three contrasted situations: MAD is overall the most desiccation-tolerant line while TG is overall the most desiccation-sensitive line, and PAP is intermediate, taking into account both adults and juveniles.

Results

Juveniles

Histograms corresponding to survival rates for each population with their confidence intervals are represented in Figure 2. For both drying periods (3 and 15 h, respectively), there is an extremelypronounced line effect and a population effect on survival (Table 1).
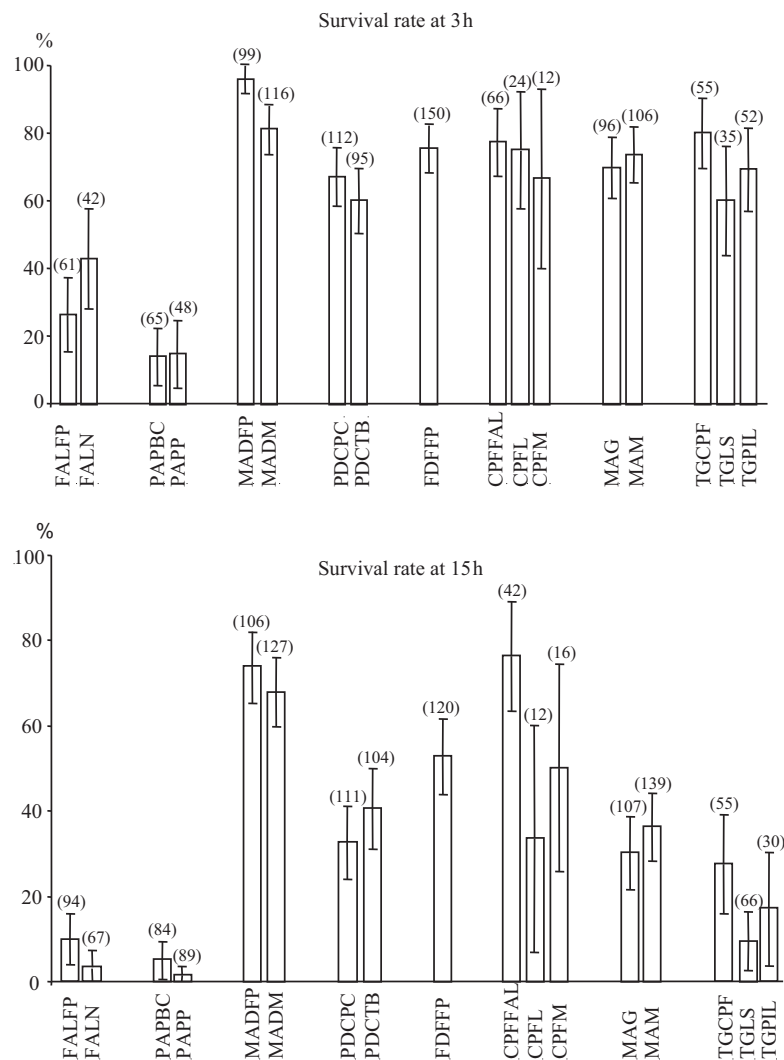

Figure 2. Survival rates of juveniles for each population with their confidence intervals (at 95%). The eight lines are ranked in an increasing order according to their invasive abilities. Numbers of individuals used in the experiment are given in parenthesis.

Although significant (because of the large sample size), the population effect explains a very small proportion of deviance compared to the line effect, and the line by line analysis of the population effect shows that this effect is only significant for MAD at 3 h ($P < 0.001$) and for CPF ($P = 0.01$) and TG ($P = 0.03$) at 15 h. The graphs in Figure 3 represent the fitted relationship between juvenile survival rate and length for each line. Juvenile survival increases with shell length. For both

Table 1. Results of the likelihood-ratio tests of lines, population and length effects on juvenile survival under drying conditions.

	Deviance	Δ dev	Δ ddl	P
3 h	$N = 1234$			
$1 + L + p(L)$	1612.93	28.98	11	0.006
$1 + L$	1641.91	266.04	7	<10E-6
1	1907.95			
$1 + L + lg + lg{*}L$	1350.94	7.57	7	0.372
$1 + L + lg$	1358.51	97.13	7	<10E-6
$1 + L + lg$	1358.51	283.40	1	<10E-6
$1 + lg$	1455.64			
15 h	$N = 1369$			
$1 + L + p(L)$	1647.29	29.39	11	0.004
$1 + L$	1676.68	411.65	7	<10E-6
1	2088.34			
$1 + L + lg + lg{*}L$	1317.01	17.18	7	0.016
$1 + L + lg$	1334.19	13.71	7	0.025
$1 + L + lg$	1334.19	342.48	1	<10E-6
$1 + lg$	1347.91			

Δ dev corresponds to changes of deviance due to the suppression of the bold-typed term. The tests are F or X^2 according to the presence or absence of overdispersion. L is the line effect, $p(L)$ the population effect nested within line, lg the shell length effect, and $lg{*}L$ is the shell length by line interaction. The term '1' symbolizes the constant term (overall mean).

drying periods (3 and 15 h), there is an extremely pronounced length effect on survival, even when the line factor is included in the model (Table 1). This means that both among- and between-line variation in survival is partly explained by variation in shell length. The deviance explained by the line effect is considerably reduced (97.13 vs 266.04 for the 3 h experiment, 13.71 vs 411.7 for the 15 h experiment) when shell length is included in the model, although the line effect remains significant. This indicates that most, but not all, of the variation among lines is explained by differences in juvenile size. The interaction between line and length effects is only significant at 15 h. Because the morphology of TG distinctly differs from that of all lines of *Melanoides*, we performed the same tests after removing TG from the sample. All results remain essentially similar, but for the disappearance of the shell length by line interaction (Δdev = 11, 7834, 6 *df*, NS). For the juveniles, the classification of the eight Thiarid lines according to increasing desiccation tolerance is essentially consistent between the 3- and 15-h experiments: PAP < FAL < TG < MA/PDC < CPF/FDF < MAD.

Adults
Figure 4 shows the adult mean survival time for the eight lines. According to the Kruskal–Wallis test ($P < 0.0001$), there is a highly significant line effect. The population effect is significant only within the MAD ($P = 0.0006$) and TG ($P = 0.022$) lines. The correlation between the mean shell length of a line and its mean survival time under desiccation is also significant (Spearman rank correlation: $P < 0.05$, Figure 4). The classification of the eight Thiarid lines according to increasing resistance to desiccation is the
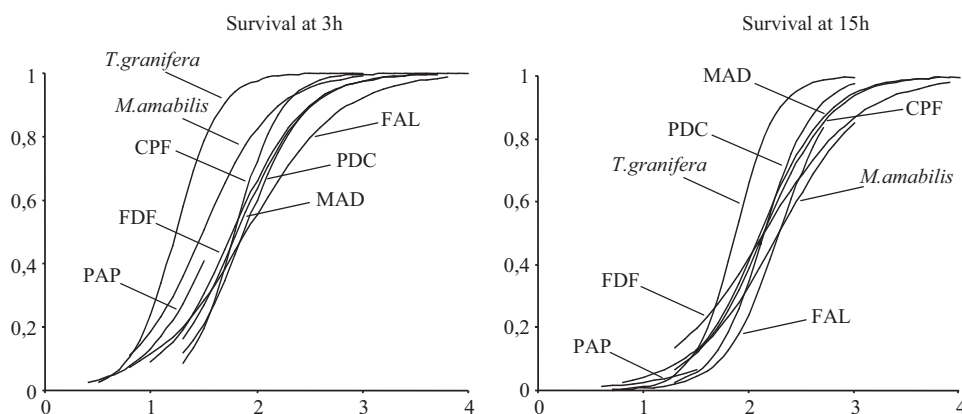

Figure 3. Logistic fit of juvenile survival rate as a function of length for the eight invasive Thiarid lines. Each fitted curve is represented only for the range of sizes actually observed in the experimental juveniles of the corresponding line.
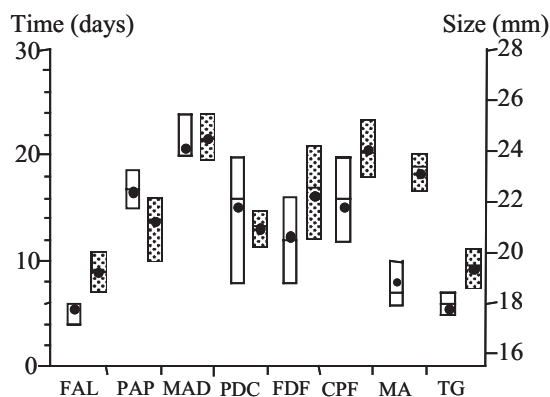
Figure 4. Adult survival time (on the left) and adult size (on the right, shaded) for each Thiarid line. The filled circles represent the means while the quantile boxes indicate the median as well as the 25th and 75th percentiles. The eight lines are ranked according to their increasing invasive abilities.

following: FAL < TG < MA < FDF < PAP < PDC < CPF <MAD for adults.

Relation between variability in desiccation tolerance and variability in invasive abilities

The results of the Spearman rank correlation test is nonsignificant for the juvenile desiccation tolerance as well as the adult desiccation tolerance. It can be seen in Figures 2 and 4 (where lines are ranked according to increasing invasive abilities), that no clear relationship emerges between survival under drying conditions and invasive abilities.

Distribution of lines between temporary and permanent sites

Twelve, two and six sites out of seventeen belonging to temporary habitats are respectively occupied by MAD, TG and PAP populations. In permanent habitats, the proportions are dramatically different, as 38 sites out of 147 harbour MAD populations while TG is found in 94 sites, and PAP in 89 sites. The null hypothesis H_0 of independence between line and type of habitat is strongly rejected ($G = -2.80$, 1 df, $P < 0.001$). Note that the temporary sites are mostly located in the southern part of the island where the climate is overall much dryer (Figure 5).

Discussion

All studied Thiarid lines seem to resist desiccation quite well at the adult stage, as they can survive at least a few days and up to a month under drying conditions. Prosobranchs could be expected to resist desiccation more successfully than Pulmonates, by virtue of their ability to close the aperture by the operculum (Brown 1994). However, this resistance to drought is much lower than observed for many Pulmonates which may survive several months or even more to the desiccation (Barbosa and Barbosa 1959; Cridland 1967; Véra et al. 1994). Survival time during drought may be further increased in the field, if snails can find relatively humid protected microhabitats in the soil (Sturrock 1970; Pointier and Combes 1976). Our estimates of adult survival times also coincide quite well with an estimation carried out on TG by Chaniotis et al. (1980), although our experimental drying conditions are somewhat different. Juveniles are logically less resistant to drought and survive hours rather than days. The most prominent feature of our data set is the extreme variation in desiccation tolerance observed among Thiarid lines, for both age classes. The difference in survival probability under desiccation between the most sensitive and the most resistant line is approximately 10-fold for juveniles (in both the 3- and 15-h experiments), and the maximum difference in survival time under desiccation reaches fourfold or more in adults (5 days vs 24 days). Although TG, the most morphologically and taxonomically distant line, is among the most sensitive, the bulk of the variation in sensitivity to desiccation is not due to the inclusion of distinct species. Indeed, the very closely related lines belonging to the species *M. tuberculata* together cover the entire range observed in the present experiment. This is in line with previous studies that have established the existence of pronounced differences among three of these lines for other life history traits (Pointier et al. 1992). Some population effects within lines for desiccation tolerance were also observed, but these effects were weak, in agreement with the idea that little genetic variation should be present within recently introduced parthenogenetic lineages.

The relative resistances of the eight lines are relatively similar according to the developmental stage (adults vs. juveniles), except for the PAP line. Indeed, the PAP line exhibits very poor resistance at the juvenile stage, whereas adults show a quite strong resistance. This can be explained because PAP adults are relatively large, whereas the juveniles are very small compared to the other lines. Indeed, as it has been demonstrated for other freshwater molluscs (Dudgeon 1981; Tucker et al. 1996), desiccation tolerance is mainly explained

Figure 5. Map of the Martinique island showing the distributions of PAP, MAD and TG in 2002. Circles and triangles represent permanent and temporary sites respectively. Filled and empty symbols represent occupied and non-occupied sites respectively.

by individual size. A common interpretation is that changes in surface to volume ratio, as these animals increase in size, may render larger individuals less susceptible to water loss (Dudgeon 1980).

The relationship between size and desiccation tolerance in juvenile TG differs from that of other Thiarid lines. This probably relies on its distinctive morphology, with a proportionally larger aperture, and hence evaporation surface, compared to *Melanoides* spp. with equivalent shell length (Pointier 2001).

The shell size effect, and the fact that adults are much more resistant to desiccation than juveniles within each line, suggest that as they grow older individuals progressively get more tolerant to desiccation. However, this does not contradict the interpretation that the differences observed among lines are essentially of genetic origin. Indeed, not only are there significant differences among lines when size is controlled for in the analysis, but also the large size differences observed among lines (especially at the juvenile stage) are themselves under genetic control, given that all experimental individuals were of similar ages and had similar environmental histories in the laboratory. In conclusion, Thiarid lines genetically differ in desiccation tolerance, both because their size at birth (in juveniles) or their maximum size (in adults) are genetically different and because of intrinsic, size-independent, genetic differences in susceptibility to water loss.

It is unfortunately difficult to predict *a priori* the ecological relevance of our measures of desiccation tolerance in the laboratory without a precise knowledge of the context in which temporary droughts take place in the field. However exposure to drying conditions in unstable or temporary habitats is probably a matter of days rather than hours, suggesting that adult rather than juvenile desiccation tolerance may

be an important factor for population persistence in such habitats. Whether desiccation tolerance is a limiting factor during passive migration is an even more difficult question. Little is known about migration, although aquatic birds have been shown to carry molluscs (Maguire 1963). Other factors linked to human activities may be also involved such as cars and cattle that often cross rivers. Unfortunately, we have little idea of the stage at which migration majoritarily occurs, and of the potential duration of the travel from one water body to another. Because we lack firm *a priori* expectations, we tested the correlation between desiccation tolerance and invasive ability for both developmental stages.

No positive correlation emerges between desiccation tolerance (at either adult or juvenile stage) and invasive ability according to our historical record of Thiarid invasions in Martinique. This suggests at first glance that desiccation stress was not a major determinant of the migration and establishment (or persistence) components of invasion. However, our historical records mainly bear on permanent rivers, which constitute the bulk of favorable habitats for Thiarids in Martinique. Given the overall good resistance to drought shown by Thiarids in this experiment, the degree of desiccation stress experienced in permanent and open habitats (periodic fluctuations in river margins and water flux) seems insufficient to limit invasion. For this reason, it appeared interesting to investigate the less common temporary, closed habitats such as ponds that are considerably affected by drought, and we accordingly increased our sampling effort in this direction. Three lines, TG, PAP and MAD, were sufficiently abundant and spatially widespread in Martinique in 2002 in order to compare their distributions among the two categories of sites. These three lines represent all the

range in desiccation tolerance, for adults as well as juveniles. Their distributions were highly unbalanced, as the desiccation-resistant MAD dominate temporary habitats while the reverse is true in permanent habitats. Symmetrically, the desiccation-sensitive TG dominates permanent habitat while it is nearly absent in temporary habitats. The repartition of PAP, the line with intermediate desiccation tolerance, is the most balanced among the two habitat types. Also, in permanent habitats, TG is the most invasive Thiarid according to our historical record, while MAD is nearly the less invasive line and PAP is intermediate. Several biases could potentially have affected our comparison of distributions between permanent and temporary habitats. The first one is spatial autocorrelation. Because invasion is a dynamic process, an invasive taxon taken at a given time after its introduction in the island, may not have had sufficient time to reach all parts of the island, which is problematic because most of our temporary habitats are located in a single region, that is, the relatively dry southern end of Martinique. Distributions could actually reflect the date and site of introduction of different lines rather than their intrinsic ability to invade different habitats. However, this possibility can be rejected because these three lines have been introduced more than 10 years ago and have had sufficient time to reach all parts of the island, as attested by their presence from the northernmost to the southernmost sites in 2002 (as well as in the previous years in our historical record). A second potential problem lies with metapopulation effects: sites exchange migrants and are therefore not independent. However, under the null hypothesis that habitat type plays no role in relation to invasion, this effect would tend to homogenize the occurrences of the three lines (MAD, PAP and TG) across habitats rather than to differentiate them. This is strengthened by the fact that the permanent rivers, which shelter huge populations, are doubtlessly the main sources of migrants. Note that, because of this asymmetry, the abundance of MAD in temporary habitats could be transient, and, being competitively excluded by TG and other lines in the predominant permanent habitats, it could go extinct in all habitats on the long run. Extinction is currently in process for the FAL line, which is restricted to three sites in 2002 while it was widespread throughout the island in the early eighties, before the introduction of the other lines (Pointier et al. 1993). Whether the advantage of MAD in temporary habitats will be sufficient for it to avoid extinction is not known.

To summarize, our data suggest that relative invasive capacity is dependent on the type of habitat and that, although desiccation tolerance is not a limiting factor for Thiarid invasion in general, it does limit the invasion of habitats most exposed to drought. This is in agreement with the correlation established for other molluscs (Machin 1975) between the ability to survive desiccation and the abundance in temporary habitats, although it had never been studied in an invasion context. Our study reinforces the growing evidence for differential invasion according to local characteristics in aquatic communities (Rosecchi et al. 2001; Hacker et al. 2001; Miller et al. 2002). For instance, Moyle and Light (1996) found that the most important factor determining the success of an invading fish in California streams and estuaries is the hydrologic regime. It has traditionally been difficult to tease apart the roles of the biotic component (e.g., the diversity of the resident species pool, Case 1990; Tilman 1997; Levine 2000) and of the match between the biology of invaders and the physical environment (Fausch et al. 2001; Ross et al. 2001; Holway et al. 2002) in determining ecosystem-level vulnerability to invasion. More studies on ecological invasion differentials between closely related invasive taxa could increase our predictive power on invasions, in addition to the more classical comparisons between invasive and non-invasive species.

Acknowledgements

References

Abbott RT (1952) A study of an intermediate snail host (*Thiara granifera*) of the oriental lung fluke (*Paragoninus*). Proceedings of the US National Museum 102: 71–116

Appleton CC (1978) Review of literature on abiotic factors influencing the distribution and life cycles of bilharziasis intermediate host snails. Malacological Review 11: 1–25

Barbosa FS and Barbosa I (1959) Observations on the ability of the snail *Australorbis nigricans* to survive out of the water in the laboratory. Journal of Parasitology 45: 627–630

Brown DS (1994) Freshwater Snails of Africa and their Medical Importance, 2nd edn. Taylor and Francis, London, 609 pp

Case TJ (1990) Invasion resistance arises in strongly interacting species-rich model competition communities. Proceedings of the National Academy of Sciences 87: 9610–9614

Chaniotis BN, Miles Butler J, Ferguson FF and Jobin WR (1980) Thermal limits, desiccation tolerance, and humidity reactions of *Thiara (Tarebia) granifera mauiensis* (Gastropoda: Thiaridae) host of the Asiatic lung fluke disease. Caribbean Journal of Sciences 16: 1–4

Crawley MJ (1993) GLIM for ecologists. Blackwell Scientific Publications, Oxford

Cridland CC (1967) Resistance of *Bulinus* (Physopsis) *globosus*, *Bulinus* (Ph.) *africanus*, *Biomphalaria pfeifferi* and *Lymnaea natalensis* to experimental desiccation. Bulletin of the World Health Organization 36: 507–513

Dudgeon D (1980) The Corbiculidae of Southern China. In: Morton BS (ed) Proceedings, First International Workshop on the Malacofauna of Hong Kong and southern China, pp 37–60. Hong Kong University Press

Dudgeon D (1981) Aspects of the desiccation tolerance of four species of benthic mollusca from plover cove reservoir, Hong Kong. The Veliger 24: 267–271

Everett RA (2000) Patterns and pathways of biological invasions. Trends in Ecology and Evolution 15: 177–178

Fausch KD, Taniguchi Y, Nakano S, Grossman GD and Townsend CR (2001) Flood disturbance regimes influence rainbow trout invasion success among five holarctic regions. Ecological Applications 11: 1438–1455

Hacker SD, Heimer D, Hellquist CE, Reeder TG, Reeves B, Riordan TJ and Dethier MN (2001) A marine plant (*Spartina anglica*) invades widely varying habitats: potential mechanisms of invasion and control. Biological Invasions 3: 211–217

Hill AM, Sinars DM and Lodge DM (1993) Invasion of an occupied niche by the crayfish *Orconectes rusticus*: potential importance of growth and mortality. Oecologia 94: 303–306

Holway DA, Suarez AV and Case TJ (2002) Role of abiotic factors in governing susceptibility to invasion: a test with argentine ants. Ecology 83: 1610–1619

Jabbour-Zahab R, Pointier JP, Jourdane J, Oviedo J, Bargues MD, Mas-Coma S, Angles R, Perera G, Khallayoune K and Renaud F (1997) Phylogeography and genetic divergence of some lymnaeid snails, intermediate hosts of human and animal fasciolasis with special reference to lymnaeids from the Bolivian Altiplano. Acta Tropica 64: 191–203

Jacob J (1958) Cytological studies of Melaniidae (Mollusca) with special reference to parthenogenesis and polyploidyII. A study of meiosis in the rare males of the polyploid race *M. tuberculata* and *M. lineatus*. Transactions of the Royal Society of Edinburgh 63: 433–444

Jarne P and Städler T (1995) Population genetic structure and mating system evolution in freshwater pulmonates. Experimentia 51: 482–497

Kolar CS and Lodge DM (2001) Progress in invasion biology: predicting invaders. Trends in Ecology and Evolution 16: 199–204

Levine JM (2000) Species diversity and biological invasions: relating local process to community patterns. Science 288: 852–854

Lockwood JL (1999) Using taxonomy to predict success among introduced avifauna: relative importance of transport and establishment. Conservation Biology 13: 560–567

Machin J (1975) Water relations. In: Fretter and Peake J (eds) Pulmonates, Vol I: Functional Anatomy and Physiology, pp 105–163. Academic Press, London

Maguire Jr B (1963) The passive dispersal of small aquatic organisms and their colonization of isolated bodies of water. Ecological Monographs 33: 161–185

McCullagh HP and Nelder JA (1983) Generalized Linear Models. Cambridge University Press, Cambridge, UK, 511 pp

Miller TE, Kneitel JM and Burns JH (2002) Effect of community structure on invasion success and rate. Ecology 83: 898–905

Moyle PB and Light T (1996) Fish invasions in California: do abiotic factors determine success? Ecology 77: 1666–1670

Pointier JP (1989) Conchological studies of *Thiara (Melanoides) tuberculata* (mollusca: gastropoda: thiaridae) in the French West Indies. Walkerana 3: 203–209

Pointier JP (1993) The introduction of *Melanoides tuberculata* (Mollusca: Thiaridae) to the island of Saint Lucia (West Indies) and its role in the decline of *Biomphalaria glabrata*, the snail intermediate host of *Schistosomia mansoni*. Acta Tropica 54: 13–19

Pointier JP (1999) Invading freshwater gastropods: some conflicting aspects for public health. Malacologia 41: 403–411

Pointier JP (2001) Invading freshwater snails and biological control in Martinique Island, French West Indies. Memorias do Instituto Oswaldo Cruz 96: 67–74

Pointier JP and Combes C (1976) La saison sèche en Guadeloupe et ses conséquences sur la démographie des mollusques dans les biotopes à *Biomphalaria glabrata* (Say, 1818), vecteur de la bilharziose intestinale. Terre et Vie 30: 121–147

Pointier JP and McCullough F (1989) Biological control of the snail hosts of *Schistosoma mansoni* in the Caribbean area using *Thiara* spp. Acta Tropica 46: 147–155

Pointier JP, Delay B, Toffart JL, Lefèvre M and Romero-Alvarez R (1992) Life history traits of three morphs of *Melanoides tuberculata* (Gastropoda: Thiaridae), an invading snail in the French West Indies. Journal of Molluscan Studies 58: 415–423

Pointier JP, Thaler L, Pernot AF and Delay B (1993) Invasion of the Martinique island by the parthenogenetic snail *Melanoides tuberculata* and the succession of morphs. Acta Oecologica 14: 33–42

Rahel FJ (2000) Homogenization of fish faunas across the United States. Science 288: 854–856

Ricciardi A and MacIsaac HJ (2000) Recent mass invasion of the North American great lakes by Ponto-Caspian species. Trends in Ecology and Evolution 15: 62–65

Reeve L (1860) Conchologica Iconica or illustrations of the shells of molluscous animals. Vol. 12, Pl. 33, Fig. 223

Rosecchi E, Thomas F and Crivelli AJ (2001) Can life-history traits predict the fate of introduced species? A case study on two cyprinid fish in southern France. Freshwater Biology 46: 845–853

Ross RM, Lellis WA, Bennett RM and Johnson CS (2001) Landscape determinants of nonindigenous fish invasions. Biological Invasions 3: 347–361

Sakai AK, Allendorf FW and Holt JS et al. (2001) The population biology of invasive species. Annual Review of Ecology and Systematics 32: 305–332

Sall J and Lehman A (1996) JMP, start statistics: a guide to statistics and data analysis using JMP and JMP IN® Software. Duxbury Press, 521 pp

Samadi S, Mavarez J, Pointier JP, Delay B and Jarne P (1999) Microsatellite and morphological analysis of population structure in the parthenogenetic freshwater snail *Melanoides tuberculata*:

insights into the creation of variability. Molecular Ecology 8: 1141–1153

Sokal RR and Rohlf FJ (1995) Biometry 3rd edn. WH Freeman & Company, New York, 887 pp

Stoddart JA (1985) Analysis of species lineages of some Australian thiarids (Thiaridae, Prosobranchia, Gastropoda) using the evolutionary species concept. Journal of Malacological Society of Australia 7: 7–16

Sturrock RF (1970) An investigation of some factors influencing the survival of St Lucian *Biomphalaria glabrata* deprived of water. Annals of Tropical Medicine and Parasitology 64: 365–371

Tilman D (1997) Community invasibility, recruitment limitation, and grassland biodiversity. Ecology 78: 81–92

Tucker JK, Janzen FJ and Paukstis GL (1996) Laboratory survivorship of aerially exposed pond snails (*Physella integra*) from Illinois. Transaction of the Illinois State Academy of Science 89: 225–231

Véra C, Brémond P, Labbo R, Meuchet F, Sellin E, Boulanger D, Pointier JP, Delay B and Sellin B (1994) Seasonal fluctuations in population densities of *Bulinus senegalensis* and *B. truncatus* (Planorbidae) in temporary pools in a focus of *Schistosoma haematobium* in Niger: implications for control. Journal of Molluscan Studies 61: 79–88

Welcomme RL (1992) A history of international introductions of inland aquatic species. ICES Marine Science Symposia 194: 3–14

Williamson MH and Fitter A (1996a) The characters of successful invaders. Biological Conservation 78: 163–170

Williamson MH and Fitter A (1996b) The varying success of invaders. Ecology 77: 1661–1666