Distribution and habitats of the alien invader freshwater snail *Physa acuta* in South Africa

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Abstract

This article focuses on the geographical distribution and habitats of the invader freshwater snail species *Physa acuta* as reflected by samples taken from 758 collection sites on record in the database of the National Freshwater Snail Collection (NFSC) at the Potchefstroom Campus of the North-West University. This species is currently the second most widespread alien invader freshwater snail species in South Africa. The 121 different loci ($^{1}/_{16}$- degree squares) from which the samples were collected, reflect a wide but discontinuous distribution mainly clustered around the major ports and urban centres of South Africa. Details of each habitat as described by collectors during surveys were statistically analysed, as well as altitude and mean annual air temperatures and rainfall for each locality. This species was reported from all types of water-bodies represented in the database, but the largest number of samples was recovered from dams and rivers. Chi-square and effect size values were calculated and an integrated decision tree constructed from the data which indicated that temperature, altitude and types of water-bodies were the important factors that significantly influenced the distribution of *P. acuta* in South Africa. Its slow progress in invading the relatively undisturbed water-bodies in the Kruger National Park as compared to the recently introduced invader freshwater snail species, *Tarebia granifera*, is briefly discussed.

Keywords: *Physa acuta*, invasive species, freshwater snail, geographical distribution, habitat preferences

Introduction

Physa acuta was not mentioned in the monograph by Connollyi (1939) after an in-depth revision of extensive mollusc material collected by himself and many other researchers in South Africa. Although the oldest record of *Physa acuta* in the National Freshwater Snail Collection (NFSC) dates back to 1954 from the Umsindusi River (KwaZulu-Natal), the first report in print for South Africa was established in 1964 by Van Bruggen (1964) from a single locality in Pretoria. Since then it has invaded many water-bodies in several river systems in South Africa (Hamilton-Attwell et al., 1970; De Kock et al., 1989; Appleton, 2003) and is currently considered the second most widespread alien invasive freshwater snail species in this country. In their review of introduced freshwater snails worldwide, Madsen and Frandsen (1989) concluded that the aquarium trade was probably to blame for the distribution of several of the common species, including *P. acuta*, a view supported by Appleton (2003) in his account of the alien and invasive freshwater gastropods in South Africa. *Physa acuta* which is widespread in water-bodies of the old world may have originated in North America and has become invasive on 4 continents (Appleton, 2003). According to Dillon et al. (2002) the identification of a new-world cognate has been complicated by the confused systematics and taxonomy of the Physidae in America and more than 40 species of physids are currently recognised in the United States. However, in the course of their research these authors were unable to detect evidence of reproductive isolation among six populations of snails from two continents and came to the conclusion that all should be referred to the oldest available nomen, *P. acuta*. On the strength of results of a taxonomic study by Hamilton-Attwell et al. (1970), the 200 samples of Physidae on record in the database of the NFSC at that stage, were identified as *P. acuta*. The remainder of the total number of 758 samples on record in the database for this species were also subsequently identified as *P. acuta*.

The first report in print of the presence of *Aplexa marmorata*, another species of the physid family in South Africa, was by Appleton et al. (1989) from specimens collected near Durban, KwaZulu-Natal in 1986. According to Appleton (2003) it has since then become widespread in the Durban area. The presence of *A. marmorata* was also established in 11 water-bodies in surveys conducted in the Kruger National Park since 1995 (De Kock and Wolmarans, 1998; De Kock et al., 2002; Wolmarans and De Kock, 2006). According to Appleton and Dana (2005) this invader species could have been introduced to Mozambique a century earlier than its first discovery in South Africa. The shell of *A. marmorata* can quite easily be confused with that of *P. acuta*; however, the posterior end of the foot of *A. marmorata* is darkly pigmented and pencil-like and its copulatory organ differs from that of *P. acuta* in that it does not have a conspicuous, externally visible preputial gland (Appleton et al., 1989).

Extensive research has been done in South Africa on several aspects of the biology of *P. acuta* (Appleton and Brackenbury, 1989; Appleton and Branch, 1989; Brackenbury and Appleton, 1991); Brackenbury and Appleton, 1993). The geographical distribution of this species in South Africa was reported by Hamilton-Attwell et al. (1970) and updated by De Kock et al. (1989).

By comparison with the freshwater snail genera *Bulinus* and *Biomphalaria* which are well-known intermediate hosts of human and animal diseases, *P. acuta* is rather innocuous having no role in transmission of any significant snail-borne disease.

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Received 24 April 2007; accepted in revised form 5 July 2007.

However, due to its superior reproductive capacity (Appleton and Brackenbury, 1998), ability to migrate upstream (Appleton and Branch, 1989) and to quickly recolonise a water-body (Brackenbury and Appleton, 1993), amongst others, this species could have a negative impact on indigenous freshwater molluscs in particular and on the biodiversity of freshwater habitats in general. This paper focuses on the geographical distribution and habitats of *P. acuta* currently on record for South Africa in the NFSC database.

Methods

Details of the habitats of all samples of *P. acuta* that could be located on a 1:250 000 topo-cadastral map series of South Africa, dating from 1956 until 2007, were extracted from the NFSC database. The number of loci ($^1/_{16}$ square degrees) in which the collection sites were located, was distributed in intervals of mean annual air temperature and rainfall, as well as intervals of mean altitude, to illustrate the frequency of occurrence of this species within specific intervals. Rainfall, temperature and altitude data were obtained in 2001 from the Computing Centre for Water Research, University of KwaZulu-Natal (disbanded since). A temperature index was calculated for all mollusc species in the database from their frequencies of occurrence within the selected temperature intervals and the results used to rank them in order of association with low to high climatic temperatures. The method of calculation is discussed in detail in our earlier publications (De Kock and Wolmarans, 2005a; b). Chi-square values were calculated to determine the significance in difference between the frequency of occurrence in, on, or at the different options for each variable, such as type of water-body, type of substratum or temperature interval. In addition an effect size (Cohen, 1977) was calculated for all the different variables discussed in this paper. The effect size is an index which measures the degree of discrepancy between the frequency distribution of a given species in the set of alternatives for a given variable such as water-bodies, as compared to the frequency distribution of all other mollusc species in the database in the set of alternatives for the same variable (Cohen, 1977). According to this author values for this index in the order of 0.1 and 0.3 indicate small and moderate effects respectively, while values in the order of 0.5 and higher indicate practically significant large effects. More details of the significance and interpretation of specific values calculated for this statistic in a given situation, is discussed in our earlier publications (De Kock and Wolmarans, 2005a; b).

An integrated decision tree (Breiman et al., 1984) was also constructed from the data. This statistical model enables the selection and ranking of those variables that can maximally discriminate between the frequency of occurrence of a given species under specific conditions when compared to all other species in the database. This was accomplished by making use of the SAS Enterprise Miner for Windows NT Release 4.0, April 19, 2000 programme and Decision Tree Modelling Course Notes (Potts, 1999).

Results

The 758 samples of *P. acuta* that could be pinpointed on our maps were collected from 121 different loci of which 57 were reported earlier by Hamilton-Attwell et al. (1970) and an additional 43 by De Kock et al. (1989) (Fig. 1). Although this species was reported from all types of water-bodies represented in our database, the largest number of samples was collected in dams (253) and rivers (162) (Table 1). However, the samples recovered from irrigation furrows (5.3%), water-holes (4.9%), channels (4.7%) and ditches (3.8%) each represented a higher percentage of the total number of collections of any mollusc species in a specific water-body (Table 1). The frequency of occurrence of *P. acuta* in dams differed significantly from all the other types of water-bodies except from pans, ponds, rivers and swamps (chi-square values ranging from χ=34.18, *df* =1; p<0.05 to χ=7.52, *df* =1; p<0.05).

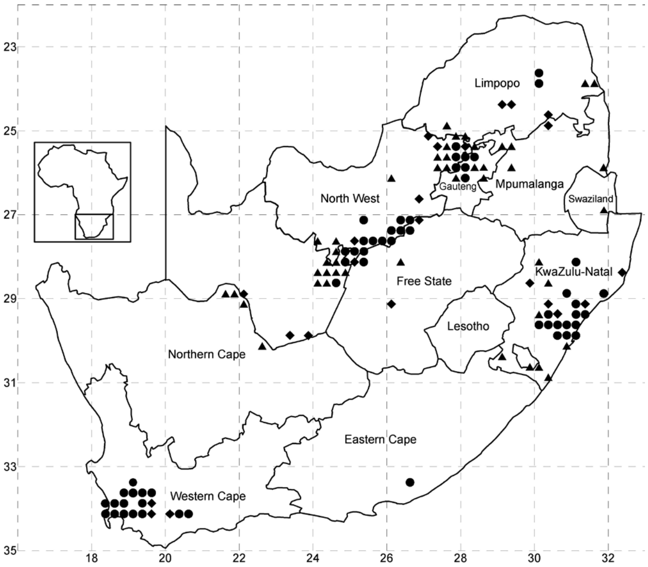

Figure 1
The geographical distribution of Physa acuta in $^1/_{16}$ square degree loci in South Africa.
● *loci reported by Hamilton-Attwell et al. (1970)*
▲ *loci reported by De Kock et al. (1989)*
♦ *loci recorded in the database of the NFSC since 1989*

TABLE 1
Types of water-bodies in which *Physa acuta* was found in 758 collection sites recorded during surveys

Water-bodies	A	B	C	D
Channel	8	1.1%	169	4.7%
Concrete dam	4	0.5%	221	1.8%
Dam	253	33.3%	8 400	3.1%
Ditch	24	3.2%	636	3.8%
Irrigation furrow	6	0.8%	113	5.3%
Pan	1	0.1%	306	0.3%
Pond	7	0.9%	1 566	0.4%
Quarry	2	0.3%	122	1.6%
River	162	21.4%	7 507	2.2%
Spring	8	1.1%	301	2.7%
Stream	88	11.6%	7 211	1.2%
Swamp/Marsh	25	3.3%	2 076	1.2%
Vlei	2	0.3%	103	1.9%
Waterhole	11	1.5%	225	4.9%
Effect size w = 0.45 (moderate to large)				

A Number of times collected in a specific water-body
B % of the total number of collections (758) on record for this species
C Number of times any mollusc was collected in a specific water-body
D % occurrence of this species in the total number of collections in a specific water-body

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ISSN 0378-4738 = Water SA Vol. 33 No. 5 October 2007
ISSN 1816-7950 = Water SA (on-line)

TABLE 2 Water conditions in the habitats of *Physa acuta* as described during surveys									
	Type		Current speed			Turbidity		Salinity	
	Perennial	Seasonal	Fast	Slow	Standing	Clear	Muddy	Fresh	Brackish
A	518	49	56	210	310	443	92	335	15
B	68.3%	6.5%	7.38%	27.7%	40.9%	58.4%	12.1%	44.2%	2.0%
C	22 432	5 350	2 229	9 501	16 147	20 408	6 438	24 089	657
D	2.3%	0.9%	1.6%	2.2%	1.9%	2.2%	1.4%	1.4%	2.3%
E	*w* = 0.27 (small to moderate effect)		*w* = 0.09 (small effect)			*w* = 0.16 (small effect)		*w* = 0.09 (small effect)	

A Number of times collected in a specific water condition
B % of the total number of collections (758) on record for this species
C Number of times any mollusc was collected in a specific water condition
E Effect size values calculated for each factor

The largest number of samples by far was reported from habitats in which the water conditions were described as perennial, standing, clear and fresh (Table 2) and the presence of aquatic vegetation was recorded for 80.7% of the sampling sites. Its frequency of occurrence in habitats with perennial water differed significantly from that in seasonal water ($p<0.05$) and a significant difference was likewise found between frequencies of occurrence in clear water as compared to the number of times it was reported from habitats with muddy water.

Although the frequency of occurrence reported for habitats with a stony substratum (232) was less than for habitats with a muddy substratum (247) it represented a higher percentage (2.9%) of the total number of collections of any mollusc species in habitats with a specific substratum (Table 3). A significant difference could therefore be indicated between the frequencies of occurrence of this species in habitats with these two types of substrata (χ=21.75, df =1; $p<0.05$).

The largest number of samples was recovered from habitats with loci falling within the 16 to 20˚C temperature interval (720) and this also represented a higher percentage (3.0%) of the total number of collections within a specific interval (Table 4). The frequency of occurrence within this temperature interval therefore differed significantly from the interval ranging from 21 to 25˚C (χ=57.73, *df* =1; $p<0.05$). Regarding rainfall, 58.4% of the samples were recovered from loci falling within the interval ranging from 601 to 900 mm. However, the 296 samples falling within the interval ranging from 301 to 600 mm represented a marginally higher percentage (2.5%) of the frequency of occurrence of any mollusc species within a specific interval. No significant difference could be shown between the frequencies of occurrence of habitats falling within these two rainfall intervals (χ=1.75, *df* =1; $p>0.05$). The majority of samples (582) were recovered from sites falling within the altitude interval ranging from 1 001 to 1 500 m and its frequency of occurrence within this interval differed significantly from all the other altitude

TABLE 3 Substratum types in the habitats of *Physa acuta* as described during surveys				
	Substratum types			
	Muddy	Stony	Sandy	Decomposing material
A	247	232	113	20
B	32.6%	30.6%	14.9%	2.6%
C	12 835	7 934	6 523	632
D	1.9%	2.9%	1.7%	3.2%
E	*w* = 0.23 (small to moderate effect)			

A Number of times collected in a water-body with a specific substratum
B % of the total number of collections (758) on record for this species
C Number of times any mollusc was collected in a water-body with a specific substratum
D % occurrence of this species in the total number of collections in a water-body with a specific substratum
E Effect size values calculated for substrata

TABLE 4 Frequency distribution of the 758 collection sites of *Physa acuta* in selected intervals of mean annual air temperature and rainfall and mean altitude in South Africa										
	Temperature intervals (°C)		Rainfall intervals (mm)				Altitude intervals (m)			
	16 - 20	21 - 25	0 - 300	301 - 600	601 - 900	901- 1 200	0 - 500	501 - 1 000	1 001 - 1 500	1 501 - 2 000
A	720	38	12	296	443	7	114	36	582	26
B	95.0%	5.0%	1.6%	39.1%	58.4%	0.9%	15.0%	4.7%	76.8%	3.4%
C	24 298	4 276	975	11 994	19 799	1 203	6 747	4 491	14 918	6 998
D	3.0%	0.9%	1.2%	2.5%	2.2%	5.8%	1.7%	0.8%	3.9%	0.37%
E	*w* = 0.33 (moderate effect)		*w* = 0.17 (small effect)				*w* = 0.67 (large effect)			

A Number of times collected in a locality falling within a specific interval
B % of the total number of collections (758) on record for this species
C Number of times any mollusc was collected in a locality falling within a specific interval
D % occurrence of this species in the total number of collections within a specific interval
E Effect size values calculated for each factor

TABLE 5
Frequency distribution in temperature intervals and temperature index of *Physa acuta* as compared to all mollusc species in the database of the National Freshwater Snail Collection

Mollusc species	Number of samples	5 –10°C	11 - 15°C	16 - 20°C	21 - 25°C	26 - 30°C	[1]Index	[2]SD	[3]CV	Effect size
Pisidium viridarium	636	201	270	163	2		1.947	0.764	39.22	-5.171
Lymnaea truncatula	723	95	281	343	4		2.354	0.709	30.14	-3.258
Pisidium casertanum	5		2	3			2.600	0.548	21.07	-2.103
Pisidium langleyanum	627	18	173	430	6		2.676	0.544	20.33	-1.745
Pisidium costulosum	425	1	138	282	4		2.680	0.492	18.34	-1.728
Bulinus tropicus	8 448	32	2326	5860	230		2.744	0.502	18.31	-1.426
Gyraulus connollyi	969		185	777	7		2.816	0.406	14.40	-1.088
Ceratophallus natalensis	1 797		299	1430	68		2.871	0.433	15.09	-0.829
Burnupia (all species)	2 778	7	287	2384	100		2.928	0.380	12.97	-0.565
Ferrissia (all species)	540		72	420	47	1	2.957	0.476	16.09	-0.425
Bulinus reticulatus	296		6	287	3		2.990	0.174	5.83	-0.273
Assiminea umlaasiana	2			2			3.000	0.000	0.00	-0.225
Tomichia cawstoni	4			4			3.000	0.000	0.00	-0.225
Tomichia diferens	10			10			3.000	0.000	0.00	-0.225
Tomichia lirata	2			2			3.000	0.000	0.00	-0.225
Tomichia ventricosa	89			89			3.000	0.000	0.00	-0.225
Tomichia tristis	81			79	2		3.025	0.156	5.16	-0.109
Unio caffer	76		6	63	6	1	3.026	0.461	15.24	-0.102
Physa acuta	758			720	38		3.048	0.213	7.00	0.000
Bulinus depressus	552			519	33		3.060	0.237	7.76	0.055
Arcuatula capensis	15			14	1		3.067	0.258	8.42	0.088
Lymnaea columella	2 302		81	1977	243	1	3.071	0.371	12.07	0.109
Lymnaea natalensis	4 721		205	3802	713	1	3.108	0.429	13.79	0.282
Assiminea bifasciata	17			15	2		3.118	0.332	10.65	0.327
Gyraulus costulatus	736		20	580	135	1	3.159	0.437	13.84	0.521
Bulinus forskalii	1 209		17	985	204	3	3.160	0.409	12.95	0.524
Pisidium ovampicum	6			5	1		3.167	0.408	12.89	0.557
Sphaerium capense	25		1	17	7		3.240	0.523	16.14	0.901
Bulinus africanus group	2 930		9	2155	760	6	3.260	0.450	13.82	0.997
Corbicula fluminalis africana	390		1	291	94	4	3.267	0.437	13.38	1.030
Tomichia natalensis	23			16	7		3.304	0.470	14.24	1.204
Thiara amarula	10			6	4		3.400	0.516	15.19	1.653
Assiminea ovata	5			3	2		3.400	0.548	16.11	1.653
Melanoides victoriae	49			29	19	1	3.429	0.540	15.75	1.787
Biomphalaria pfeifferi	1 639		5	880	751	3	3.459	0.508	14.69	1.929
Septaria tesselaria	2			1	1		3.500	0.707	20.20	2.122
Coelatura framesi	6			3	3		3.500	0.548	15.65	2.122
Neritina natalensis	16			8	8		3.500	0.516	14.75	2.122
Bulinus natalensis	245		2	97	146		3.588	0.510	14.20	2.534
Segmentorbis planodiscus	27			9	18		3.667	0.480	13.10	2.905
Segmentorbis angustus	32			7	25		3.781	0.420	11.11	3.442
Melanoides tuberculata	305			64	237	4	3.803	0.430	11.30	3.546
Pisidium pirothi	23			4	19		3.826	0.388	10.13	3.653
Chambardia wahlbergi	44			5	37	2	3.932	0.398	10.11	4.149
Aplexa marmorata	9				9		4.000	0.000	0.00	4.469
Bellamya capillata	31				31		4.000	0.000	0.00	4.469
Eupera ferruginea	169			6	157	6	4.000	0.267	6.68	4.469
Lentorbis carringtoni	8				8		4.000	0.000	0.00	4.469
Lentorbis junodi	12				12		4.000	0.000	0.00	4.469
Segmentorbis kanisaensis	9				9		4.000	0.000	0.00	4.469
Chambardia petersi	28			1	26	1	4.000	0.272	6.80	4.469
Cleopatra ferruginea	73				71	2	4.027	0.164	4.08	4.598
Lanistes ovum	41				38	3	4.073	0.264	6.47	4.813

[1]Index: Temperature index; [2]SD: Standard deviation; [3]CV: Coefficient of variance

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ISSN 0378-4738 = Water SA Vol. 33 No. 5 October 2007
ISSN 1816-7950 = Water SA (on-line)

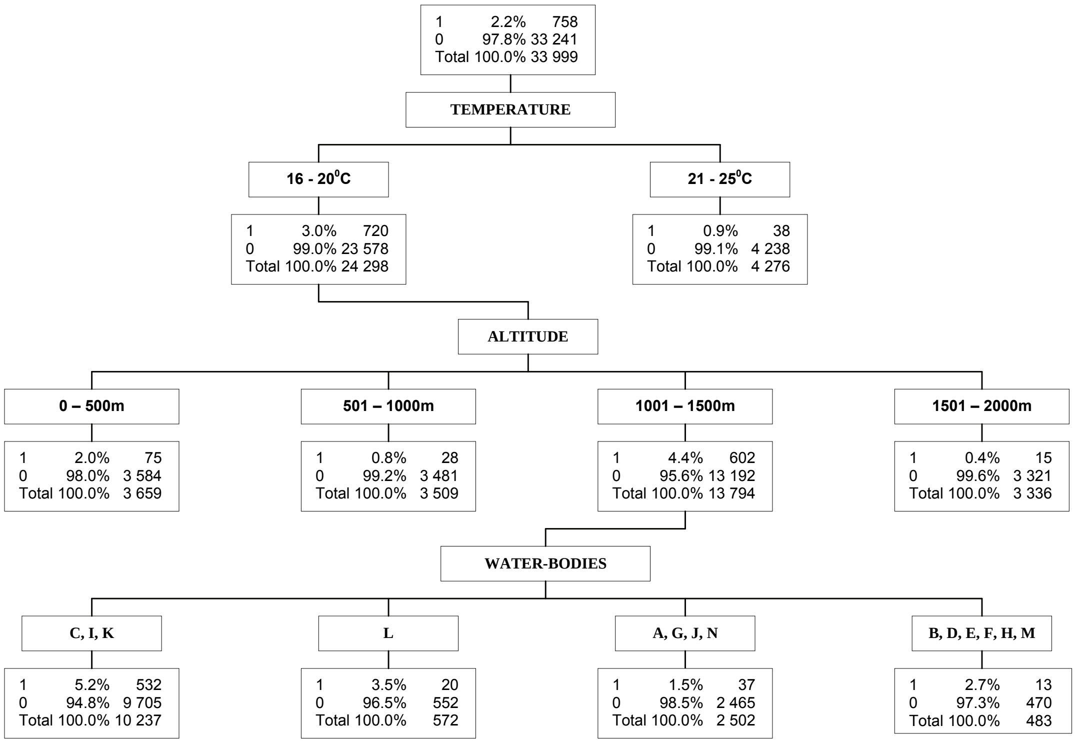

Figure 2
Decision tree of the frequency of occurrence of Physa acuta *for each variable as compared to the frequency of occurrence of all the other species in the database of the NFSC.*
0: percentages and frequencies of all other species,
1: percentages and frequencies of P. acuta*. Water-bodies: A: channel, B: concrete dam, C: dam, D: ditch, E: irrigation furrow, F: pan, G: pond, H: quarry, I: river, J: spring, K: stream, L: swamp, M: vlei, N: waterhole*

intervals (chi-square values ranging from χ=9.43, *df*=1; p<0.05 to χ =219.49, *df* =1; p<0.05). The temperature index (3.048) calculated for *P. acuta* ranked it 19th out of 53 species in respect of its association with low temperatures and the effect sizes indicated that this species differed significantly (*w*=/>0.5) in this regard from 38 of the other species (Table 5). The effect size values calculated for all the other parameters to determine the possible effect they could have had on the geographical distribution of *P. acuta* as depicted in Fig. 1, are presented in Tables 1 to 4. From these values it can be deduced that altitude, temperature and type of water-body played an important role in this respect (*w*= />0.5). These findings are supported by the results of the decision tree analysis (Fig. 2) which selected the same 3 factors as being important in establishing the geographical distribution of this species as reflected by the samples in the NFSC database.

Discussion

The decision-tree analysis grouped dams, rivers and streams together and indicated that the frequency of occurrence of *P. acuta* in these three types of water-bodies in the temperature interval ranging from 16 to 20˚C and the altitude interval ranging from 1 001 to 1 500 m differed significantly from all the other types of water-body (Fig. 2). This supports the statement by Brown (1994) that *P. acuta* is particularly common in both stagnant and flowing waters. An important attribute to exploit both lotic and lentic water-bodies is its relatively high tolerance of current velocities reported by Appleton (2003). It is therefore not surprising that a considerable number of samples of *P. acuta* in our database were recovered from water-bodies with current velocities ranging from slow to fast flowing (Table 2). The apparent lack of any association with submerged aquatic vegetation (Appleton, 2003) is supported by the fact that 36 of the samples in the NFSC database were collected in habitats reported to be without any higher vegetation. However, *P. acuta* commonly occurs on the roots of floating water hyacinths (*Eichhornia crassipes*) in backwaters of the Vaal River as observed during regular excursions with our students.

Although coordinated, extensive freshwater snail surveys by government and local health authorities were discontinued during the early 1980s, samples of *P. acuta* from 21 new loci were recorded in the NFSC database since the report by De Kock et al. (1989) (Fig. 1). One reason for its success as invader is suggested to be its high fecundity rate reported by Appleton and Brackenbury (1989) which proved to be superior to that of several common indigenous pulmonates, including *Bulinus tropicus* which is considered to be the most widespread freshwater snail in South Africa (De Kock et al., 2002). *Physa acuta* has become one of the most abundant snail species in the Vaal River over the past decade and has also been recovered in several small water-bodies within the Potchefstroom Municipal boundaries (North-West Province); however, it has not yet been found in the Mooi River (a tributary of the Vaal River) which meanders through Potchefstroom. This is rather surprising in view of its capability to migrate rapidly upstream as established by Appleton and Branch (1989) in the Liesbeeck River (Western Cape Province). Its slow progress in invading the Kruger National Park, as compared to other invasive snail species, was also observed by the authors during the surveys mentioned earlier. This could possibly be explained by the fact that *P. acuta*, commonly known as the 'sewage snail', seems to have difficulty in establishing itself far away from human activities and in Africa is associated with polluted water (Brown, 1994). From their studies in the Umsindusi River (KwaZulu-Natal) Brackenbury and Appleton (1993) concluded that *P. acuta* is better equipped than the indigenous snail species for establishing itself in newly disturbed habitats and may have become, like other invasives, a species associated with man. This could account for its absence in the relatively less disturbed habitats in the Mooi River and also for its slow progress in invading the water-bodies in the Kruger National Park where the impact of human activities is relatively small.

Scrutiny of the results in Table 5 shows that the most successful alien invader freshwater snail species in South Africa, *L. columella* (De Kock et al., 1989) was recovered from habitats located in loci falling within four of the temperature intervals, while the samples of *P. acuta* were recorded from only two of these intervals. Whether this reflects a narrower tolerance range in respect of temperature than that of *L. columella* and therefore could possibly have contributed to its more limited geographical distribution in South Africa than that of the latter species, needs further investigation.

In spite of a number of attributes contributing towards its success as an invader, amongst others a superior and adaptable reproductive ability, tolerance of higher current velocities than its indigenous counterparts (Brackenbury and Appleton, 1993) and rapid directional movement (Appleton 2003), the results of a recent study to establish the progress of alien invasive snail species in the Kruger National Park suggest that *P. acuta* might be a less aggressive invader than either *Aplexa marmorata* or *Tarebia granifera* (De Kock and Wolmarans, 2007). In view of the alarming progress that *T. granifera* has been making in invading water-bodies in the Kruger National Park, as observed by the authors during the surveys mentioned earlier and in KwaZulu-Natal (Appleton, 2005) since its presence in South Africa was first reported by Appleton and Nadasan (2002), its ecological impact could be far greater than that of *P. acuta* that has been present in South Africa for more than 6 decades.

The asynchronous nature of the collected material in the database could have an impact upon ecological variables and could confound some of the observations and conclusions drawn from the data. It is therefore unfortunate that the large-scale and routine coordinated snail surveys conducted in South Africa by state and local health authorities were discontinued in the early 1980s. At this point in time nobody really knows whether the intermediate host snails of medically and veterinary important parasitic diseases such as schistosomiasis and fascioliasis have extended the range of their geographical distribution in South Africa. Serious efforts should also be made to keep track of the progress made in their invasion of new water-bodies by the number of introduced alien mollusc species already present in South Africa. From the results of routine surveys, the database of the NFSC could be updated and monitoring of economically important snail-borne diseases at public health levels could also be facilitated.

Acknowledgements

The authors wish to thank the following persons and institution: Professors HS Steyn, head of the Statistical Consulting Service and DA de Waal of the Centre for Business Mathematics and Informatics of the of the North-West University, Potchefstroom Campus for their assistance in processing the data and the North-West University for infrastructure and financial support.

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