Science of the Total Environment 811 (2022) 152364

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Informing spread predictions of two alien snails using movement traits

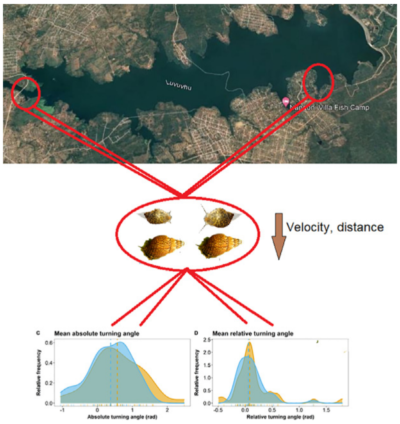
Fhatuwani Makherana [a], Ross N. Cuthbert [b,c], Cristián J. Monaco [d], Farai Dondofema [a], Ryan J. Wasserman [e,c], Glencia M. Chauke [a], Linton F. Munyai [a], Tatenda Dalu [c,f,g,*]

[a] Aquatic Systems Research Group, Department of Geography and Environmental Sciences, University of Venda, Thohoyandou 0950, South Africa
[b] GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, 24105 Kiel, Germany
[c] South African Institute for Aquatic Biodiversity, Makhanda 6140, South Africa
[d] IFREMER, IRD, Institute Louis-Malardé, University of the Polynésie française, EIO, 98725 Taravao, Tahiti, French Polynesia
[e] Department of Zoology and Entomology, Rhodes University, Makhanda 6140, South Africa
[f] Aquatic Systems Research Group, School of Biology and Environmental Sciences, University of Mpumalanga, Nelspruit 1200, South Africa
[g] Wissenshaftskolleg zu Berlin Institute for Advanced Study, Berlin 14193, Germany

HIGHLIGHTS

- *Tarebia granifera* and *Physa acuta* densities ranged between 161 and 517 and 15–619 individuals m^{-2}, respectively.
- *P. acuta* moved significantly slower and covered a significantly shorter net distance.
- Movement traits associated with exploratory behaviour were similar among species.
- Variation in straightness index trait was 1.6-fold greater for *P. acuta* (CV = 79.9).
- Study provides baseline information on alien snails in the Austral subtropical regions.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 5 November 2021
Received in revised form 5 December 2021
Accepted 9 December 2021
Available online 14 December 2021

Editor: Damia Barcelo

Keywords:
Dispersal potential
Freshwater ecosystem

ABSTRACT

Invasive alien species are a growing global problem, and aquatic ecosystems have been regarded as particularly vulnerable. Biological invasions can alter ecosystem functioning, threaten native biodiversity and burden the global economy. Understanding alien species ability to disperse via locomotion following arrival to new environments is critical for prediction of spread rates. Here, we quantified in-field densities and compared movement traits between two widespread invasive alien snails, *Tarebia granifera* and *Physa acuta*. We measured the: (*i*) net distance and velocity to determine dispersal potential; and (*ii*) turning angles (both absolute and relative) and straightness index as proxies for exploratory behaviour. *Tarebia granifera* exhibited a significantly greater velocity and covered a significantly larger net distance (i.e., greater spread rate) than *Physa acuta*. In-field densities were marked for both species (*T. granifera*: mean 351 individuals m^{-2}; *P. acuta*: mean 235 individuals m^{-2}), but differed spatially. The exploratory behavior (i.e., mean or absolute turning angles and straightness index) did not differ significantly between the two alien species;

---

* Corresponding author at: Aquatic Systems Research Group, School of Biology and Environmental Sciences, University of Mpumalanga, Nelspruit 1200, South Africa.
E-mail address: dalutatennda@yahoo.co.uk (T. Dalu).

http://dx.doi.org/10.1016/j.scitotenv.2021.152364

Invasive non-native species
Physa acuta
Tarebia granifera

both species showed a slight tendency to turn counterclockwise. The present study suggests a more rapid capacity to self-disperse in *T. granifera* than *P. acuta*, which could facilitate rapid spread within and between aquatic systems. Thus, this current study highlights the often-overlooked role of animal behaviour in promoting invasion; this autecological information can help inform predictive models for the spread of alien snails within freshwater ecosystems.

1. Introduction

Biological invasions are a growing global environmental concern and a prominent aspect of global change (Pyšek et al., 2020). The ability to spread following introduction is a critical aspect of the invasion process (Blackburn et al., 2011). Rapid self-dispersal or association with anthropogenic vectors is likely conducive to high invasion success (Clobert et al., 2009; Brancatelli and Zalba, 2018). Active spread may be particularly important in aquatic environments that are highly interconnected and have pronounced biosecurity challenges (Coughlan et al., 2020). Furthermore, anthropogenic habitat changes can promote invasion through environmental disturbance and artificially increased habitat connectivity (e.g., irrigation systems and canals; Miranda et al., 2010; Jones et al., 2017). Thus, following introduction, groups such as alien molluscs rapidly disperse within and between freshwaters through human-mediated vectors, including via attachment to fishing equipment and zoochory (Vinarski, 2017; Coughlan et al., 2017), but also via self and natural-dispersal by movement patterns and downstream drift (Croteau, 2010; Kappes and Haase, 2012).

Molluscs cause degradation of biodiversity via competition for resources and displacement of native species (Weyl et al., 2020), as well as marked socio-economic impacts (Cuthbert et al., 2021). In Africa, fourteen alien gastropod species have been reported, including the notorious freshwater snails *Tarebia granifera* and *Physa acuta* (Darwall et al., 2011). *Tarebia granifera* is native to south-east Asia and has invaded several African countries, such as Mozambique, Eswatini, South Africa and Zimbabwe, as well as South and North America (Appleton, 2003; Appleton et al., 2009; Miranda et al., 2010; Appleton and Miranda, 2015a). *Physa acuta* is native to North America and has invaded countries such as Namibia, Mozambique, South Africa and Zimbabwe (De Kock and Wolmarans, 2007). Both *P. acuta* and *T. granifera* were introduced to South Africa through the aquarium trade in the 1950s and 1990s, respectively (Appleton, 2003). These two snail species have negative impacts on the ecosystem and are successful invaders, due to their high reproductive capacity, ability to outcompete native species, and potential to rapidly colonise waterbodies and migrate upstream (De Kock and Wolmarans, 2007; Appleton, 2003). In South Africa, for example *T. granifera* and *P. acuta* at high densities negatively affect benthic invertebrate diversity and displace native snails, with *T. granifera* also causing economic damage, having been highlighted to damage water supply machinery pumping from reservoirs (Appleton et al., 2009). Understanding IAS behavioral traits is significant since such traits influence spread and dispersal (Appleton and Nadasan, 2002; Clobert et al., 2009; Karatayev et al., 2009), and thus this study compared the movement traits between *T. granifera* and *P. acuta*. We compared the behavioral responses of the two species by assessing: (*i*) net distance and velocity to determine dispersal potential; and (*ii*) turning angles (both absolute and relative) and straightness index as proxies of exploratory behaviour. We hypothesized that since *T. granifera* is a more recent invasion that is very rapidly spreading, it will move faster and travel in straighter lines than *P. acuta*.

2. Materials and methods

2.1. Snail density estimation

To determine snail density, haphazard quadrat (30 × 30 cm) sampling was done at 7 sites (see Fig. 1) in the Nandoni reservoir littoral zones using a hand shovel at a water depth of approximately 5–10 cm. All snails were identified to species level and counted. Nandoni reservoir is situated in the Limpopo Province of South Africa (Fig. 1). The reservoir has a catchment area of 1380 km^2 and a total volume of 16.4 million m^3. The average air temperature is a range between 17 and 23 °C, annual rainfall of 610–800 mm and annual runoff of 519 million m^3 (Mbedzi et al., 2020). The sites were highly variable in terms of substrate embeddedness, with site 1 being dominated by silt and sand, site 2 by clay, silt and boulders, site 3 by clay, silt, sand and stones/rocks, site 4 by silt and clay, site 5 by clay, site 6 by silt and clay, and site 7 by sand and stones/rocks (see Table S1 for coordinates).

2.2. Experimental sampling

Adult individuals of *P. acuta* and *T. granifera* were collected from littoral zones (water depth mean 0.3 ± 0.15 m) by hand from Nandoni reservoir (22°59′11″ S, 30°36′16.19″ E; Limpopo Province, South Africa). The snails were transported to a laboratory at the University of Venda in source water with stones for habitat in 6 × 20 L buckets containing approximately 15–20 individuals each. *Tarebia granifera* and *P. acuta* were collected 2 days apart in October 2020. Individuals from each species were maintained in separate, open buckets with 15–20 individuals per bucket in source water with constant aeration. All snails were acclimatized for 48 h in filtered (63-μm mesh) source water at 26 ± 1.5 °C under a 12 h:12 h day:night regime.

2.3. Movement assays and data preparation

The mean heights of *T. granifera* and *P. acuta* used in the experiments were 15.8 ± 1.1 (SD) mm and 8.1 ± 0.5 (SD) mm, respectively. To describe the trajectories followed by individuals ($n = 40$ per species), we used an open-field arena over a 4-day period i.e., 20 individuals per day (between 0700 and 1700 h) for each size-matched individual within species at 26.5 ± 1.5 °C under 40 W incandescent bulb lighting. The arena consisted of a 66.5 cm × 50 cm × 50 cm tank containing approximately 10 L source water with dark walls and a laminated grid (2 × 2 cm^2 squares) overlaid on the bottom (Fig. 2). At the beginning of each trial, a snail facing north was placed on the marked centre of the grid and allowed to move freely for a 30 min observation period. A GoPro camera (HERO8 Black), suspended 50 cm above the arena, captured an image every 30 s. At the end of each trial, the laminated grid was thoroughly washed to prevent snails tracing the mucus trail left by previous individuals and water replaced to remove any traces of chemical cues.

We used the *XY*-coordinate position of individuals recorded every 30 s to describe their trajectories, and estimate displacement ability (i.e., velocity and net distance) and exploratory behavior (i.e., absolute and relative turning angles, and straightness index; Fig. 1). Straight lines were interpolated between consecutive positions. The velocity, distance, and turning angles were determined using the R package *adehabitat* (Calenge, 2006). Step velocity (cm s^{-1}) was calculated based on the distance (d, cm) covered on each 30-second time interval, and averaged for each individual. The overall net distance (d_n, cm) was computed between the initial and final positions of each snail. As the individual moved, we computed the absolute (α) and relative (ρ) turning angles (rad), whereby α is the angle resulting between the x-axis and the step path, while ρ is the mean angle resulting between successive step paths (Fig. 1). We calculated the *straightness index* as the ratio between d_n and the sum of d covered on the trajectory (i.e., path length). Thus, the level of exploration increases asymptotically for values of *straightness index* ranging between 0 and 1.

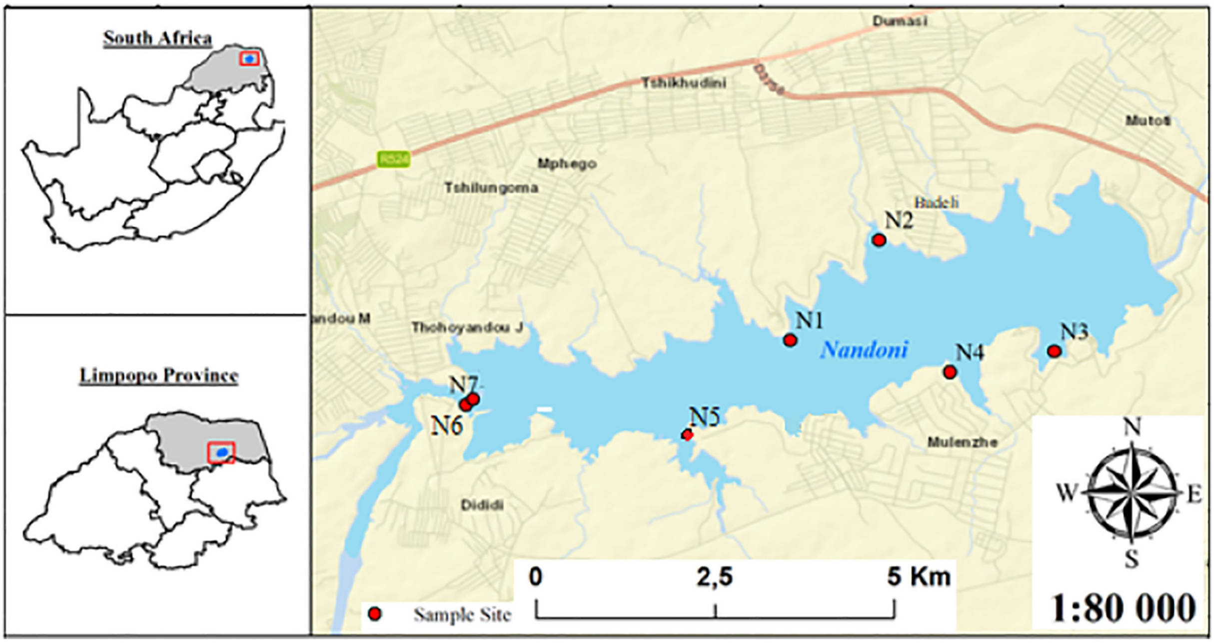


Fig. 1. Study map highlighting the seven study sites (i.e., N1–N7) sampled in Nandoni Reservoir, South Africa for snails.

2.4. Statistical analyses

Differences in densities among sites and species were examined using a non-parametric Kruskal-Wallis (KW) test. Equally, to investigate the effect of species on the movement traits (i.e., velocity, net distance, turning angles, and straightness index), we used non-parametric KW tests computed in R (R Core Team, 2019). Relative frequency distributions were determined to visualize differences in movement traits between species considering the replicated trials per species.

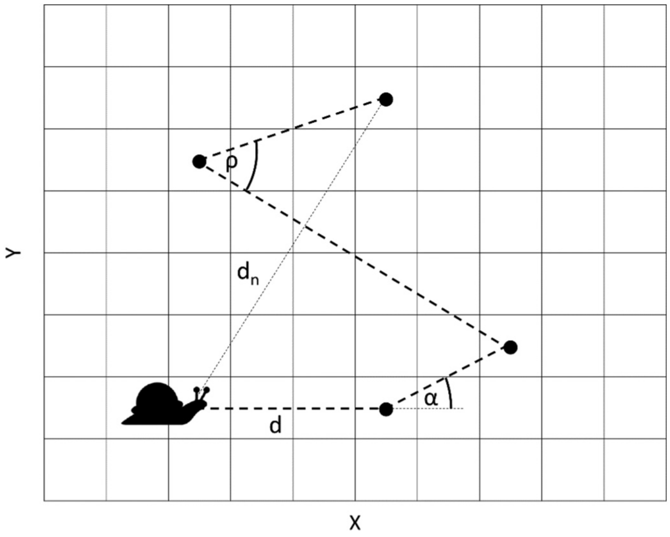


Fig. 2. Schematic representation of movement assays used to describe the trajectories followed by *Physa acuta* and *Tarebia granifera* individuals, within an XY grid. Grid squares were 2 × 2 cm^2. The snail marks the starting position of the trial, and each black dot represents successive positions, occupied at 30 s intervals. The d and d_n are the step distance and the overall net distance covered, respectively. Displacement velocity at each step was calculated based on d and time (i.e., 30 s). The α and ρ are the absolute and relative turning angles, respectively.

3. Results

The densities of *T. granifera* and *P. acuta* in the field ranged between 161 and 517 (mean 351 ± 136) and 15–619 (mean 235 ± 143) individuals m^{-2}, respectively. We observed significant differences among study sites for *P. acuta* (KW, H = 2.432, df = 6, p = 0.018) and between species (KW, H = 3.117, df = 2, p = 0.001) but no significant differences for *T. granifera* among sites (KW, H = 1.614, df = 6, p = 0.179). The species-level comparison of movement traits showed that *P. acuta* moved significantly slower (KW, H = 5.31, df = 1, p = 0.021) and covered a significantly shorter net distance (KW, H = 4.87, df = 1, p = 0.027) than *Tarebia granifera* (Fig. 3A, B). This suggests that *T. granifera* can disperse and spread further than *P. acuta* per unit time.

In contrast, the movement traits associated with individuals' exploratory behaviour did not differ significantly between the two species (Fig. 3C–E). Individuals from both species showed a slight tendency to turn counterclockwise (positive turning angle values; Fig. 2C, D). This departure from a straight path was also indicated by the non-zero mean straightness index. Despite the similar mean straightness index values between species, the variation in this trait was 1.6-fold greater for *P. acuta* (CV = 79.9) than *T. granifera* (CV = 50.5) (Fig. 2E).

4. Discussion

Both of the assessed snails are successful invaders, and therefore provide a model to assess spread and dispersal traits in gastropods. Here, these species exhibited marked field densities, but there were significant differences in the net distance that each species covered, whereby *P. acuta* covered significantly lesser distance and moved slower than *T. granifera*. Both species also exhibited similar levels of exploratory behaviour, characterized by relatively low straightness indices that may promote spread and dispersal to new areas by individuals. Similar to differences found here between species in terms of their size, Snider and Gilliam (2005) highlighted that at low resource densities, large *T. granifera* individuals moved faster than small individuals. That study also found that population and environmental heterogeneities both influenced individual movement behaviors, and their interaction may drive movement variation terms of both advection and diffusion rates. Clampitt (1973) additionally highlighted that *P. acuta* moved rapidly, suggesting an adaptation to their

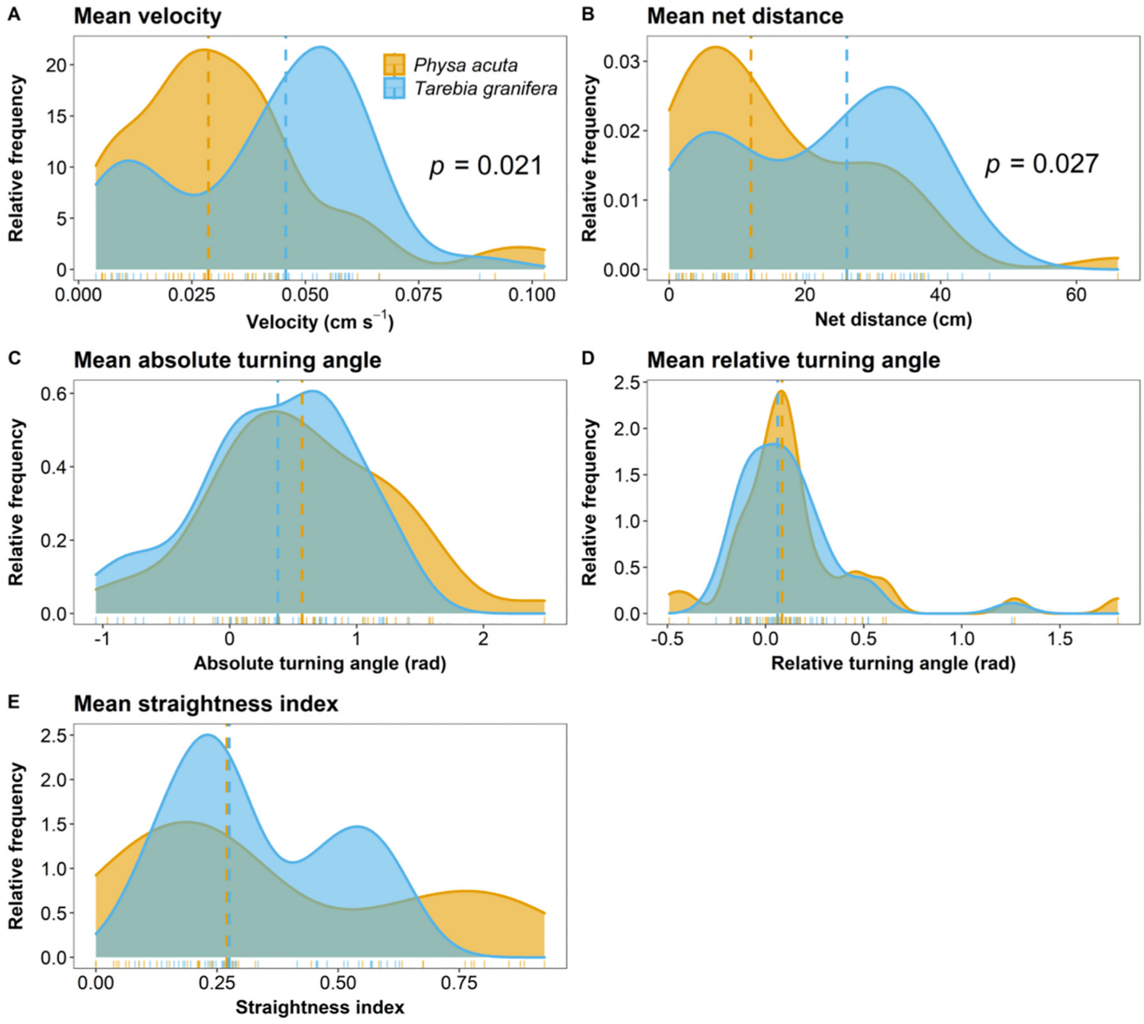


Fig. 3. Relative frequency distributions of movement traits of *Physa acuta* (orange) and *Tarebia granifera* (light blue). (A) velocity and (B) net distance provide information about the species ability to displace, while (C) absolute turning angle (i.e., α), (D) relative turning angle (i.e., ρ), and (E) straightness index inform about individuals' exploratory behaviour. Mean trait values were calculated using the trajectories followed by 40 snails per species. The vertical dashed lines represent median values for the species. The individual data points are represented by the *rug* on the *x*-axis.

foraging on more exposed and uniform substrata, such as lake and river sediments. These results highlight additional context-dependencies that may alter movement traits in the focal species, such as size, resource availability and substratum.

The results here showed that *T. granifera* and *P. acuta* moved at a median velocity of $\sim$0.45 cm s^{-1} and $\sim$0.30 cm s^{-1}, respectively, suggesting that the former has a higher capacity to spread. These findings suggest that *P. acuta* assessed here moved faster compared to previous studies by Bernot et al. (2005) and Brown et al. (2012), who observed average velocities of 0.13 cm s^{-1} and 0.05–0.09 cm s^{-1}, respectively; at least two times slower than the current study. The contrasting results, however, are likely due to the different methods used. Bernot et al. (2005) starved the snails for 24 h before the experiment and placed them in a toxic ionic liquid solution for experimentation (Bernot et al., 2005). In the study by Brown et al. (2012), snails were chronically exposed to Triclosan concentrations, and thus the aims of these studies pertaining to toxicity likely dampened observed movement traits. Under field conditions, *P. acuta* has been also shown to move faster than *Bulinus tropicus* of a similar size, under matched current velocity conditions, which gives it a competitive advantage over native snails (Appleton, 2003). This variability thus indicates multiple contexts that influence behavioral traits which require further elucidation.

Importantly, in our study, *T. granifera* and *P. acuta* where not of the same size, as the mean heights for the snails were 15.8 and 8.1 mm, respectively. In general, *T. granifera* is a larger snail with a height ranging from 0.8 to 29 mm (Appleton et al., 2009; Appleton and Miranda, 2015b), whereas *P. acuta* height ranges from 0.1 to 12 mm (Saha et al., 2016; Núñez, 2010). Our size classes therefore reflect species-level differences and the averages found in the sampled area. Interspecific differences might also emanate from experimental context, as it is important to consider the microscale and behavioral mechanisms producing the observed responses. For example, responses could have been linked to searching for food. Indeed, snails' movement patterns are often explained by competition for resources (Chapman, 2000), and both snail species assessed here tend to outcompete native species for food resources and space (Miranda and Perissinotto, 2012); although food was not provided in arenas within the current study. Several studies have also highlighted that current velocity, predation threat and other abiotic and biotic variables might also affect snail movement behavior in natural environments (Snider and Gilliam, 2008).

The tortuosity of an organism's path can be reliably measured by the straightness index, which is based on whether the organism performed a random search or oriented movement (Benhamou, 2004). Here, the straightness indices were similar between species, with *T. granifera* and *P. acuta* exhibiting predominantly counterclockwise turning angles, with such behavioral responses being considered as exploratory (Raw et al., 2015). However, although not fully investigated in the current study, O'Brien (1990) highlighted that many animals perform “saltatory searching”, which consists of natural movement: they move forward, take a brief pause, and then move forward again. From the current study, the straightness index was the most relevant index for exploratory behaviour as the response was extremely variable for both species, with the snails showing both high (close to 1) and low values (close to 0). The median was low (close to 0.25), however, revealing that they did not follow a straight line (i.e., a tendency to explore the arena). We believe that the approach reveals a baseline response of the snails, as there was no stimulus or stressor present. The approach therefore allows surfacing the intrinsic responses of both species, without the ‘noise’ added by other environmental forcings, and could aid future comparisons under relevant contexts. Importantly, such random search behaviors could facilitate colonization of new areas in aquatic environments, enabling rapid dispersal of individual snails (i.e., propagules) to generate widespread populations after invasion. Equally, these traits could enhance the probability of being entrained in anthropogenic or natural vectors via chance encounters which promote gastropod dispersal (e.g. fishing gear, boats or via zoochory) (Kappes and Haase, 2012; Coughlan et al., 2017).

5. Conclusions

The present study provides baseline information on alien snail movements considering two highly successful invaders within the Austral subtropical region, improving our understanding of how these species disperse and invade new environments. Because the present study only assessed the snails under stagnant water conditions, it is unclear how the snails would behave under flowing water conditions and/or in the presence of food. Future studies should therefore investigate how snail movement traits influence their dispersal rates under flowing water conditions, different resource conditions, between populations, and when the snail species are size matched.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.152364.

CRediT authorship contribution statement

FM: Investigation, Data curation, Formal analysis, Writing – original draft, review & editing; TD: Conceptualization, Investigation, Methodology, Data curation, Formal analysis, Funding acquisition, Supervision, Writing – original draft, review & editing; RNC: Conceptualization, Methodology, Formal analysis, Supervision, Writing – original draft, review & editing; CJM: Methodology, Formal analysis, Writing – original draft, review & editing; FD: Visualisation, Investigation, Supervision, Writing – review & editing; LFM: Investigation, Visualisation, Writing – review & editing; RJW: Visualisation, Writing – review & editing; GCM: Visualisation, Investigation, Writing – review & editing.

Declaration of competing interest

All authors declare no conflict or financial interests exist for the manuscript.

Acknowledgements

We greatly acknowledge the research financial support of the University of Venda Niche Grant (SES/18/ERM/10) and NRF Thuthuka Grant (117700). TD and RC acknowledge fellowship funding from the Wissenshaftskolleg zu Berlin Institute for Advanced Study/Stellenbosch Institute for Advanced Study and Alexander von Humboldt Foundation, respectively.

References

Appleton, C.C., 2003. Alien and invasive fresh water Gastropoda in South Africa. Afr. J. Aquat. Sci. 28, 69–81.

Appleton, C.C., Miranda, N.A.F., 2015a. Two Asian freshwater snails newly introduced into South Africa and an analysis of alien species reported to date. Afr. Invertebr. 56, 1–17.

Appleton, C., Miranda, N.A.F., 2015b. Molluscs. In: Griffiths, C., Picker, M., Day, J. (Eds.), Freshwater Life: A Field Guide to the Plants And Animals of Southern Africa. Penguin Random House Struik, Cape Town.

Appleton, C.C., Nadasan, D.S., 2002. First report of Tarebia granifera (Lamarck, 1816) (Gastropoda: Thiaridae) from Africa. J. Molluscan Stud. 68, 399–402.

Appleton, C.C., Forbes, A.T., Demetriades, N.T., 2009. The occurrence, bionomics and potential impacts of the invasive freshwater snail Tarebia granifera (Lamarck, 1822) (Gastropoda: Thiaridae) in South Africa. Zool. Meded. 83, 525–536.

Benhamou, S., 2004. How to reliably estimate the tortuosity of an animal's path: straightness, sinuosity, or fractal dimension? J. Theor. Biol. 229, 209–220.

Bernot, R.J., Kennedy, E.E., Lamberti, G.A., 2005. Effects of ionic liquids on the survival, movement, and feeding behavior of the freshwater snail, Physa acuta. Environ. Toxicol. Chem. 24, 1759–1765.

Blackburn, T.M., Pyšek, P., Bacher, S., Carlton, J.T., Duncan, R.P., Jarošík, V., Wilson, J.R.U., Richardson, D.M., 2011. A proposed unified framework for biological invasions. Trends Ecol. Evol. 26, 333–339.

Brancatelli, G.I.E., Zalba, S.M., 2018. Vector analysis: a tool for preventing the introduction of invasive alien species into protected areas. Nat. Conserv. 24, 43–63.

Brown, J., Bernot, M.J., Bernot, R.J., 2012. The influence of TCS on the growth and behavior of the freshwater snail, Physa acuta. J. Environ. Sci. Health A 47, 1626–1630.

Calenge, C., 2006. The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. Ecol. Model. 197, 516–519.

Chapman, M.G., 2000. A comparative study of differences among species and patches of habitat on movements of three species of intertidal gastropods. J. Exp. Mar. Biol. Ecol. 244, 181–201.

Clampitt, P.T., 1973. Substratum as a factor in the distribution of pulmonate snails in Douglas Lake, Michigan. Malacologia 12, 379–399.

Clobert, J., Le Galliard, J.F., Cote, J., Meylan, S., Massot, M., 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecol. Lett. 12, 197–209.

Coughlan, N.E., Stevens, A.L., Kelly, T.C., Dick, J.T.A., Jansen, M.A.K., 2017. Zoochorous dispersal of freshwater bivalves: an overlooked vector in biological invasions? Knowl. Manag. Aquat. Ecosyst. 418, 1–8.

Coughlan, N.E., Cuthbert, R.N., Dick, J.T.A., 2020. Aquatic biosecurity remains a damp squib. Biodivers. Conserv. 29, 3091–3093.

Croteau, E.K., 2010. Causes and consequences of dispersal in plants and animals. Nat. Educ. Knowl. 3, 1–12.

Cuthbert, R.N., Diagne, C., Haubrock, P.J., Turbelin, A.J., Courchamp, F., 2021. Are the “100 of the world’s worst” invasive species also the costliest? Biol. Invasions https://doi.org/10.1007/s10530-021-02568-7.

Darwall, W.R.T., Smith, K.G., Allen, D.J., Holland, R.A., Harrison, I.J., Brooks, E.G.E., 2011. The diversity of life in African freshwaters: Underwater, under threat. An Analysis of the Status And Distribution of Freshwater Species Throughout Mainland Africa. IUCN, Gland, Switzerland.

De Kock, K.N., Wolmarans, C.T., 2007. Distribution and habitats of the alien invader freshwater snail Physa acuta in South Africa. Water SA 33, 717–722.

Jones, R.W., Hill, J.M., Coetzee, J.A., Avery, T.S., Weyl, O.L.F., Hill, M.P., 2017. The abundance of an invasive freshwater snail Tarebia granifera (Lamarck, 1822) in the Nseleni River, South Africa. Afr. J. Aquat. Sci. 42, 75–81.

Kappes, H., Haase, P., 2012. Slow, but steady: dispersal of freshwater molluscs. Aquat. Sci. 74, 1–14.

Karatayev, A.Y., Burlakova, L.E., Karatayev, V.A., Padilla, D.K., 2009. Introduction, distribution, spread, and impacts of exotic freshwater gastropods in Texas. Hydrobiologia 619, 181–194.

Mbedzi, R., Cuthbert, R.N., Wasserman, R.J., Murungweni, F.M., Dalu, T., 2020. Spatiotemporal variation in microplastic contamination along a subtropical reservoir shoreline. Environ. Sci. Pollut. Res. 27, 23880–23887.

Miranda, N.A.F., Perissinotto, R., 2012. Stable isotope evidence for dietary overlap between alien and native gastropods in coastal lakes of northern KwaZulu-Natal, South Africa. PLoS ONE 7, 1–13.

Miranda, N.A.F., Perissinotto, R., Appleton, C.C., 2010. Salinity and temperature tolerance of the invasive freshwater gastropod Tarebia granifera. S. Afr. J. Sci. 106, 1–8.

Núñez, V., 2010. Differences on allocation of available resources, in growth, reproduction, and survival, in an exotic gastropod of Physidae compared to an endemic one. Iheringia Ser. Zool. 100, 275–279.

O'Brien, T.G., 1990. A comparison of 3 survey methods for estimating relative abundance. Crocodiles: Proceedings of the 10th Working Meeting of the Crocodile Specialist Group, Gainesville, Florida, USA, 23 to 27 April 1990. 2. IUCN, p. 91.

Pyšek, P., Hulme, P.E., Simberloff, D., Bacher, S., Blackburn, T.M., Carlton, J.T., Wayne Dawson, W., Essl, F., Foxcroft, L.C., Genovesi, P., Jeschke, J.M., Kühn, I., Liebhold, A.M., Mandrak, N.E., Meyerson, L.A., Pauchard, A., Pergl, J., Roy, H.E., Seebens, H., van Kleunen, M., Vila, M., Wingfield, M.J., Richardson, D.M., 2020. Scientists' warning on invasive alien species. Biol. Rev. 95, 1511–1534.

R Core Team, 2019. R: A Language And Environment for Statistical Computing (Vienna, Austria).

Raw, J.L., Miranda, N.A.F., Perissinotto, R., 2015. Chemical cues released by heterospecific competitors: behavioural responses of native and alien invasive aquatic gastropods. Aquat. Sci. 77, 655–666.

Saha, C., Chakraborty, J., Pramanik, S., Parveen, S., Aditya, G., 2016. Observations on abundance and fecundity of the invasive snail Physa acuta in West Bengal, India: implications for management. J. Entomol. Zool. Stud. 4, 490–497.

Snider, S., Gilliam, J., 2005. Movement patterns of an invasive freshwater snail: an efficient modelling approach. Paper presented at the 2005 Annual Meeting of the Ecological Society of America, Montreal, Canada.

Snider, S.B., Gilliam, J.F., 2008. Movement ecology: size-specific behavioral response of an invasive snail to food availability. Ecology 89, 1961–1971.

Vinarski, M.V., 2017. The history of an invasion: phases of the explosive spread of the physid snail Physella acuta through Europe, Transcaucasia and Central Asia. Biol. Invasions 19, 1299–1314.

Weyl, O.L.F., Ellender, B.R., Wassermann, R.J., Truter, M., Dalu, T., Zengeya, T.A., Smit, N.J., 2020. Alien freshwater fauna in South Africa. In: van Wilgen, B., Measey, J., Richardson, D.M., Wilson, J.R., Zengeya, T.A. (Eds.), Biological Invasions in South Africa. Springer Nature, Switzerland.