Assessing environmental factors structuring populations and movement dynamics of the invasive snail *Tarebia granifera* in a subtropical Austral reservoir

By

Fhatuwani Makherana

Student Number: 11632066

A research thesis submitted in the fulfilment of the requirements of a

Master of Environmental Sciences (MENVSC)

Department of Geography and Environmental Sciences, Faculty of Science, Engineering and Agriculture, University of Venda

Supervisors: Dr Tatenda Dalu, Dr Ross N Cuthbert, Mr Farai Dondofema

December 2021

ABSTRACT

Invasive alien species continue to spread and proliferate in waterways worldwide, but environmental drivers of invasion dynamics lack assessment. Understanding alien species ability to self-disperse via locomotion following arrival to new environments is also critical for prediction of invasion success. The study assessed: (i) the distribution and abundance of *Tarebia granifera* and the potential drivers of population structure in Nandoni reservoir; and (ii) compared movement traits between two widespread invasive alien snails, *T. granifera* and *Physa acuta*, to assess their net distance and velocity and determine dispersal potential. *Tarebia granifera* was widespread at sites invaded, with abundances exceeding 500 individuals m^{-2} at impacted areas. *Tarebia granifera* was significantly associated with sediment (i.e., chlorophyll-*a*, Mn, sediment organic carbon (SOC) and organic matter (SOM)) and water (i.e., pH, conductivity, total dissolved solids (TDS)) variables. *Tarebia granifera* seemed to exhibit two recruitment peaks in November and March, identified via size-based stock assessment. *Tarebia granifera* displayed a significantly greater velocity and covered a significantly larger net distance than *Physa acuta*. The exploratory behaviour (i.e., mean, or absolute turning angles and straightness index) did not differ significantly between the two alien species; both species showed a slight tendency to turn counter clockwise. Overall, the study shows that there was higher snail abundance during the summer season, furthermore, sediment and water variables were found to be important in structuring *T. granifera* populations. The present study suggests a more rapid capacity to self-disperse in *T. granifera* than *P. acuta*, but a similar level of exploratory behaviour between the two species. The study provided autecological information and insights on the distribution and extent of spread of *T. granifera*, given the often-overlooked role of animal behaviour in promoting invasion, this information can help inform and predict the invasion pattern of invasive alien freshwater

snail. This information can also help in the development of invasive alien snail management action plans within the region and elsewhere.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS

I would like to express my special gratitude to Dr Tatenda Dalu for his support, understanding, encouragement, supervision, dedication, criticism, guidance, and endless efforts to make this thesis a success. I would like to thank my co-supervisors Dr Ross N Cuthbert and Mr Farai Dondofema, it was their guidance, encouragements, support, supervision, and criticism that made this thesis a success.

I would like to thank the Almighty God for the strength and wisdom. I am very much thankful to my family for the encouragement, love and support, my mom Mrs M Sinthumule, my dad Mr Michael T Makherana, my siblings: Miss T Makherana, Mr Junior T Makherana and Miss Z Sinthumule, and my late grandmothers, Mrs Tsanwani M Madima and Mrs M Makherana.

I would also like to give thanks to Mr Linton F Munyai, Mr Vincent T Netshituni and Miss Glencia M Chauke for the assistance and support they provided to make this thesis a success, more especially with field work.

I greatly acknowledge the financial support of the University of Venda Niche Grant (SES/18/ERM/10) and NRF Thuthuka Grant (117700) through my supervisor Dr Tatenda Dalu. Thanks to Kudzai Mpakairi for assisting with the distribution maps.

DECLARATION

I FHATUWANI MAKHERANA hereby declares that the dissertation for Master of Environmental science at the University of Venda, hereby submitted by me, has not been previously submitted for a degree at this university or any other university, that it is my own work and all reference material contained therein has been duly acknowledged.

Signature:______________________________ Date: 10 December 2021

PREFACE

This thesis comprises a general introduction (Chapter 1), results (Chapter 2–3) and a general synthesis (Chapter 4). The combined reference list at the end of the thesis ensures limited repetition. The result sections were organised as scientific papers, which are *currently in press* (see below):

Publication list

1. **Fhatuwani Makherana**, Ross N Cuthbert, Farai Dondofema, Ryan J Wasserman, Glencia M Chauke, Linton F Munyai and Tatenda Dalu. Distribution, drivers and population structure of the invasive alien snail *Tarebia granifera* in the Luvuvhu River, South Africa. *River Research and Applications* (***In press***)
2. **Fhatuwani Makherana**, Ross N Cuthbert, Cristián J Monaco, Farai Dondofema, Ryan J Wasserman, Glencia M Chauke, Linton F Munyai and Tatenda Dalu. Informing spread predictions of two alien snails using movement traits. *Science of the Total Environment* (***In press***)

CHAPTER 1: BACKGROUND

1.1. Background

An aquatic ecosystem refers to a complex web of relationships that exist between the abiotic and biotic components that exist within a water body (Olatunji, 2020). For an ecosystem to survive, a balance must be maintained among the consumers, decomposers and producers as well as the abiotic components. According to Irfan and Alatawi (2019), an aquatic ecosystem encompasses freshwater (i.e., reservoirs, lakes, ponds, rivers, streams, groundwater, wetlands) and marine (i.e., ocean, estuaries, salt marshes, coral reefs, mangroves) systems. It consists of fauna and flora which are either planktons, nektons or benthos, a variety of which use phenology-based cues such as day length and temperature to control important behaviours such as hatching, spawning and migration (Benbow et al., 2020).

An invaded system is an area that is invaded by invasive alien species that have been influenced by anthropogenic activities and includes both include both native and invasive alien species. For a species to be considered as an invasive alien species it starts as a native species that is then transported and introduced beyond its native environmental range (Blackburn et al., 2011), then establishes, reproduces, spreads and often poses effects on biodiversity or economies (Ricciardi, 2013). In most cases, this species poses risks to ecosystem services, native biodiversity, human health and socioeconomic status (Charles and Dukes, 2007; Cuthbert et al., 2021). Invasive alien species tend to be problematic as they are known to thrive better than native species (McNeely, 2001). The impacts of invasive alien species occur in both terrestrial and aquatic ecosystems (Mayfield et al., 2021).

Invertebrates play an important role in aquatic environments, as integral parts of the food chain their and are significant for ecosystem functionality, such as pollination, decomposition and nutrient cycling (Reck and Van der Ree, 2015). Invertebrates are a large group of organisms, amongst them are snails. Snails consist of approximately 30 000 marine, 30 000 terrestrial and 5 000 freshwater species (Alzurfi et al., 2019). Freshwater molluscs fall into two key groups namely bivalves and gastropods, that are found in a wide range of freshwater habitats (Seddon et al., 2011). In South Africa, molluscs are one of the largest invertebrate groups in marine, freshwater and terrestrial environments (van Wilgen et al., 2020). However, in South African freshwater ecosystems, there are over thirteen alien snails that are present, ten of which are known to have been introduced through shipping activities, ornamental plant and aquarium trade (Appleton and Nadasan, 2002; Karatayev et al., 2009; Appleton et al., 2009; Appleton and Miranda, 2015; van Wilgen et al., 2020).

Freshwater snails have an impact on aquatic primary production through their consumption of algae and plants (Alzurfi et al., 2019). Freshwater snails can be found living under sediments, at the bottom of large lakes and rivers, as well as small ponds and streams (van Oosterhout et al., 2013). In South Africa, thirteen invasive alien snails are known to have invaded freshwaters, major of which were introduced through aquarium or ornamental plant trade including *Tarebia granifera*, *Lymnea columella*, *Physa acuta* and *Aplexa marmorata* (Weyl et al., 2020).

Invasive *T. granifera* is of the family Thiaridae, common name ‘Quilted Melania’ (Appleton et al., 2009). *Tarebia granifera* occurs in freshwater bodies such as rivers, lakes, reservoirs, ponds and estuaries across the country (Yakovenko et al., 2018). It is native to South-East Asia and it has been reported to have invaded African countries such as Mozambique, Eswatini, South Africa and Zimbabwe, and other countries around the world (Miranda et al., 2010). *Tarebia granifera* was first described by Lamarck (1816) (Isnaningsih et al., 2017), however, the invasive alien snail was introduced to South Africa through aquarium trade during the early 1990s (Appleton and Nadasan, 2002). The rapid spread of *T. granifera* has been through both passive and active pathways (i.e., through weeds attached on trailers and boats or by attachment on bird feathers) (Jones et al., 2017). *Tarebia granifera* spreads rapidly due to its reproductive strategy, which is ovoviviparity and parthenogenesis; furthermore, its wide ranging tolerance to salinity and temperature also contribute to its successful dispersion (Miranda et al., 2011a).

Tarebia granifera can cause biodiversity loss if found in high densities, since it tends to dominate benthic aquatic habitats, resulting in resource competition and the loss or displacement of native species (Miranda et al., 2010; Weyl et al., 2020). Snail behavioural movement is in response to the local environment (i.e. search for food, mating, avoiding predation, and responding to chemical stimuli), the behaviour has an influence on the spread and dispersal rate of the snail (Cloyed and Dell, 2019). It is significant to understand the behaviour of these species. Behaviour affects how these species quickly spread and disperse (Clobert et al., 2009). Therefore, this study assessed environmental factors structuring populations and movement dynamics of the invasive snail Tarebia granifera in a subtropical Austral reservoir.

Animal movement is important for ecosystem functioning and the survival of the species (Holyoak et al., 2009; Tucker et al., 2018). Animals move in different ways either passively or actively (Nathan et al., 2008). Anthropogenic activities have resulted in the alteration of biodiversity, changes in habitat composition, and movement dynamics of many animals

(Tucker et al., 2018). Snails appear to be the most sensitive to habitat alteration (Nicolai and Ansart, 2017). Movement patterns of snails are often described by the competition for resources (i.e., food, space, predation avoidance) (Chapman, 2000). The rapid spread and dispersal of invasive alien species has been noted to cause declines in native species (Appleton et al., 2009). Furthermore, it is important to understand movement behaviour since it can provide insightful information about dispersal rates, the species spread (Frid and Dill, 2002), and invasion into new environments.

1.2. Problem statement

The main purpose for construction of Nandoni dam was to provide portable drinking water, and water for irrigation of farmlands (Manavhela and Spencer, 2012). Several studies have been conducted on the reservoir assessing the impacts of damming on the local communities, tourism development and water quality. *Tarebia granifera* invasions are particularly of concern, hence, this study will explore the relationship between water and sediment quality variables on the invasive snail *T. granifera* abundances and distribution in Nandoni reservoir. In South Africa, *T. granifera* was introduced around the year 1996 through aquarium trade as a stowaway with aquarium plants. Its distribution in South African reservoirs, particularly in Limpopo province, has not been studied. *Tarebia granifera* dominates aquatic communities and may pose risks to ecosystem services and indigenous biodiversity (Sakai et al., 2001).

1.3. Research aim and objectives

1.3.1. Aim

The main aim of the study was to assess environmental factors structuring population, and movement dynamics of the invasive snail *T. granifera* in a subtropical Austral reservoir

1.3.2. Specific objectives

The following are the objectives of the study:

- Assess *T. granifera* distribution and size patterns in relation to environmental characteristics in a reservoir situated on the Luvuvhu River system in South Africa.
- Compare the movement traits between two invasive alien snails with high invasion success: *T. granifera* and *P. acuta*.

1.4. Research hypotheses

- *Tarebia granifera* will be more abundant in summer (November), as this time can be associated with heavy rainfall and high temperature.
- *Physa acuta* will move faster than *T. granifera* due to differences in body sizes, with *P. acuta* being smaller in size while *T. granifera* is generally bigger.

1.5. Thesis outline

As highlighted in the preface, the thesis consists of general introduction (Chapter 1), two data chapters (Chapters 2 and 3) and a general conclusions chapter, (Chapter 4). Chapters 2 and 3 of the thesis focus on the distribution, drivers and population structure of the invasive alien snail *Tarebia granifera* in the Luvuvhu river, and inform spread predictions of two alien snails using movement traits. Finally, Chapter 4 provides an overall synthesis of the thesis and provides key conclusions and recommendations.

CHAPTER 2: DISTRIBUTION, DRIVERS AND POPULATION STRUCTURE OF THE INVASIVE ALIEN SNAIL *TAREBIA GRANIFERA* IN THE LUVUVHU RIVER, SOUTH AFRICA

2.1. Introduction

Thousands of alien species have spread to non-native ranges around the world in recent decades (Seebens et al., 2017), precipitating ecological impacts from reductions in fitness, to population declines, to extinctions (Bellard et al., 2016; Nunes et al., 2019). Aquatic systems are regarded as most vulnerable, experiencing high rates of invasion, and marked ecological and socio-economic impacts (Bailey et al., 2020; Cuthbert et al., 2021). In freshwaters, high connectivity coupled with lacklustre biosecurity permits rapid spread of invaders following their introduction (Coughlan et al., 2020), delaying management and potentially exacerbating control-related spending (Ahmed et al., 2021).

Molluscs are among the most notorious freshwater invaders (e.g., zebra mussel, *Dreissena polymorpha*; New Zealand mud snail, *Potamopyrgus antipodarum*) (Nentwig et al., 2018). Globally they have been introduced through accidental and intentional pathways (Yanai et al., 2017) and often exhibit particularly high invasiveness due to their small size and difficulty of detection at low population sizes or immature life stages (Zieritz et al., 2017). The subtropics have the greatest diversity of freshwater molluscs globally (De Kock and Wolmarans, 2002). Mollusc invasions could homogenise this biodiversity, but status and risks remain understudied, especially in the Global South. Bivalves and gastropods are found in a wide range of freshwater habitats (Seddon et al., 2011), being essential for aquatic primary production and consumption, feeding on algae, bacteria, zooplankton, detritus, dissolved organic material, diatoms, and plants (Alzurfi et al., 2019). Despite these services, invading molluscs have driven shifts in the structure and function of aquatic ecosystems, by engineering environments and shifting trophic dynamics as well as other ecological processes (Emery-Butcher et al., 2020). For example, invasive snails can increase phytoplankton biomass through release of nutrients via grazing activities and lead to exclusion of native species (Emery-Butcher et al., 2020; Miranda et al., 2010).

In South Africa, molluscs are one of the largest groups of invertebrates (Weyl et al., 2020), although incursions of alien species are a growing but overlooked concern. So far, there are over thirteen reported invasive snails in the country, most notably *Tarebia granifera* (Weyl et al., 2020). *Tarebia granifera* is native to south-east Asia and has reportedly invaded several African countries, such as Mozambique, Eswatini, South Africa and Zimbabwe, among others (Miranda et al., 2010). This alien snail was possibly introduced to South Africa through the aquarium trade during the early 1990s as a stowaway with aquarium plants (Appleton and Nadasan, 2002). *Tarebia granifera* occurs in low-lying and shallow areas of lotic and lentic freshwater and estuarine systems, but is also found in artificial water bodies, such as irrigation channels and reservoirs (Yakovenko et al., 2018; Weyl et al., 2020). Human-modified waterways can promote establishment and spread of *T. granifera* through disturbance, alongside canalisation for agricultural and industrial purposes (Miranda et al., 2010; Jones et al., 2017). The rapid spread of *T. granifera* has been through both passive (transferred through water or aquatic weeds that attach to the boat or trailers) and active (through attachment to waterfowl droppings or feathers) pathways (Jones et al., 2017).

Figure 2.1. Images of the quilted melania (*Tarebia granifera)*, with a shell length of 4 – 35 mm. Source: Gavin Snow

Invasion by *T. granifera* can lead to biodiversity loss if it occurs in high densities, as it tends to dominate benthic aquatic communities, leading to competition for resources and loss or displacement of native species (Miranda et al., 2010; Weyl et al., 2020). Globally, *T.*

granifera poses a major threat to resident communities, and it has been known to cause local extinction of native snails (Kesner and Kumschick, 2018; Zengeya et al., 2020). For example, the native thiarid *Melanoides tuberculata* appears to be declining due to pressure from rapidly spreading *T. granifera* (Appleton et al., 2009). However, studies have not established the drivers behind the successful spread of this species in aquatic ecosystems (but see Raw et al., 2013) and, centrally, which water or sediment chemistry drivers might promote invasion success. Thus, the spatiotemporal ecology of this widespread and high impact invasive alien snail and its management status is largely understudied.

This study assessed *T. granifera* distribution and size patterns in relation to environmental characteristics in a reservoir situated on the Luvuvhu River system in South Africa. The main aims of this study were to assess: (*i*) whether environmental variables and *T. granifera* population structure and composition differed among different reservoir sites subject to varying anthropogenic activity across seasons, (*ii*) how the distribution of *T. granifera* related to physicochemical parameters in Nandoni reservoir, and (*iii*) the key water or sediment variable drivers structuring the population within the system.

2.2. Materials and methods

2.2.1. Study area

Nandoni reservoir (with a centroid of 22°59'11" S, 30°36'16.19" E) is situated in Thulamela Municipality, Vhembe District in the Limpopo Province of South Africa (Figure 2.2) and is approximately 10 km from the town of Thohoyandou (Mbedzi et al., 2020). The reservoir lies along the Luvuvhu River with an earth-fill and concrete structure, with an approximate catchment area of 1380 km^2, total length of 2215 m, and a total capacity of 16.4 million m^3. The average air temperature around the reservoir is 23 °C and 17 °C during the summer and winter, respectively (DWAF, 2012). The average annual precipitation for the entire catchment varies between 610 and 800 mm, with a mean annual runoff of 519 million m^3 (Heath and Classen, 1990). The topography of the reservoir area is comprised of low−lying, undulating terrain which is underlain by a gneiss sequence of the Soutpansberg group. The soil in most parts has been eroded due to continuous agricultural activities.

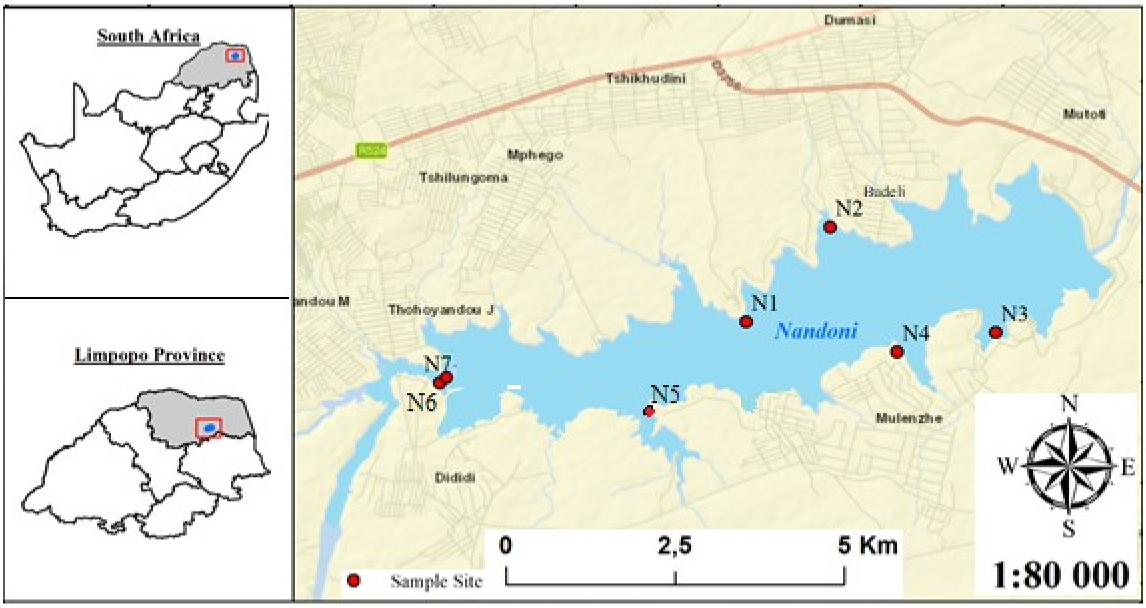

Figure 1.2. Study map highlighting the sites (N1–N7) surveyed in Nandoni Reservoir, South Africa.

The collection of samples occurred in spring (23 September 2020), summer (23 November 2020), autumn (18 March 2021) and winter (04 June 2021). Site selection was based on previous studies on the system (i.e., Dalu et al., 2019; Mbedzi et al., 2020) and according to human population density along the reservoir shorelines. In total, seven sites were selected around the reservoir: four sites (site 2 – Budeli village (estimated village population density (ePD) 2362), site 4 – Mulenzhe village (ePD 2566), site 6 – Dididi village (ePD 2312) and site 7 – Thohoyandou J (Muledane village: ePD 1428)), categorized as high ePD density sites; and three sites (site 1 – ePD 0, close to an agricultural college, site 5 – ePD 6, site 3 – ePD 4, at the outskirts of Mulenzhe village, in a bay adjacent to a fishing lodge) categorized as low ePD (Figure 2; see Mbedzi et al., 2020; https://census2011.adrianfrith.com/place/966). This range of populations reflects the gradient occurring at the reservoir, although it was not possible to sample 'pristine' conditions (or uninvaded ones), away from human influence, in the study site given that it is inherently human altered and widely invaded. 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. While not assessed formally, other snail species encountered were the invasive *Physa acuta*, as well as small Planorbidae and large Physidae taxa, with the latter two being found in very low abundances.

2.2.2. Physiochemical parameters

2.2.2.1. In-situ measurements

At each sampling site and season, conductivity (µS cm^{-1}), pH, total dissolved solids (mg L^{-1}), and water temperature (°C) were measured *in-situ* using a portable handheld Cyberscan Series multiparameter meter (Eutech Instruments) from three different locations spaced at least 2 m apart.

2.2.2.2. Sediment chemistry variables

Two integrated 1.5 kg sediment samples (*n* = 2) from three random areas within each site were collected across the different study sites and seasons. The sampling was done using acid-washed wooden splints and each integrated sample was placed in new polyethylene ziplock bags to avoid cross contaminates. The composite samples were immediately packed in a cooler box with ice and transported to the University of Venda Pollution laboratory for analysis within 24 h (Wang et al. 2015). In the laboratory, the samples were oven-dried at 60 °C for 72 h to a constant weight before being disaggregated in a porcelain mortar. The dried sediment samples were then homogenized using a riffle splitter, and thereafter a sediment subsample of 0.5 kg was separated and sent to BEMLAB, Cape Town for further analysis.

Triplicate benthic algal core samples were collected at each station using a perspex sediment corer of 20 mm internal diameter, inserted by hand into the sediment for benthic chlorophyll-*a* concentration determination (following Human et al. 2018). Cation elements (i.e., boron (B), calcium (Ca), magnesium (Mg), potassium (K), sodium (Na)), heavy metals (i.e., copper (Cu), iron (Fe), zinc (Zn)), sediment phosphorus (sed-P) and phosphate (sed-PO_4^{3-}) concentrations, sediment organic matter (SOM) and organic carbon (SOC), sediment pH, resistivity and stone count (<5 cm) were quantified for each site and season as described in detail in Dalu et al. (2021).

2.2.3. Sampling of *Tarebia granifera*

Tarebia granifera were collected from the seven different sites in each season, using two integrated samples collected from 3 quadrats (30 cm × 30 cm, sediment depth of 5 –10 cm) each, to quantify abundance and size characteristics. Snails were collected by randomly placing a quadrat in the shallow littoral zone of the reservoir at each site, with the entire contents of the quadrat collected using a handheld plastic spade and placed inside a plastic zip-lock bag. The samples were taken to the University of Venda Pollution Laboratory for further analyses. The collected samples were then sieved through a 2 mm mesh to separate *T. granifera* from sediments, before all snails were counted and measured (shell height and breadth), to the nearest 0.1 mm using a Vernier calliper. The samples were then placed in a labelled polyethylene bottles containing a 90 % ethanol solution. All field abundances were quantified as individuals per m^2.

2.2.4. Data analysis

To determine whether the ecosystem health based on water and sediment quality (log (x + 1) transformed) variables differed among sites (i.e., sites N1 – N7) and seasons (i.e., spring, summer, autumn, winter), a distance-based PERMutational ANalysis of VAriance (PERMANOVA; Anderson 2001) in PRIMER v6 add-on package PERMANOVA+ was used (Anderson et al. 2008). Each term in the analysis was tested using 9999 permutations (Anderson and ter Braak, 2003), with significant terms being investigated using *a posteriori* pair-wise comparison based on the PERMANOVA *t*-statistic (Anderson et al. 2008). We further tested whether there were significant differences in water and sediment chemistry variables and *T. granifera* abundances among the study sites and seasons using two-way ANOVA in SPSS v16.0 for Windows software (SPSS Inc. 2007). Before the ANOVA analyses, all data were assessed for normality and homogeneity of variance and were found to conform to parametric assumptions using the Shapiro–Wilk's W and Levene's tests, respectively.

Geographical positions of study locations were used to produce distribution maps based on the estimated abundances of invasive alien *T. granifera* using geographical information systems (ESRI, 2011). The programme FAO-ICLARM Stock Assessment Tool (FiSAT) was adopted to analyse *T. granifera* length frequency data (Sparre and Venema 1993). The computer models incorporated in FiSAT were used to estimate the von Bertalanffy growth function (VBGF) parameters i.e., *K* (growth coefficient, which is the relatively growth rate of the species) and *L*∞ (asymptotic length, which is the mean maximal length the snails would reach over an infinite period).

A Detrended Canonical Correspondence Analysis (DCCA) was used to determine whether unimodal or linear methods were most appropriate for ordination analysis. The gradient lengths from the DCCA analysis were examined, and since the longest gradient was shorter than 3.0, a linear constrained Redundancy Analysis (RDA) method was found to be the most appropriate for the data. The RDA, based on significant ($p < 0.05$) forward selected environmental variables, was used for analysis using 9999 Monte Carlo Permutations in Canoco version 5.1 (Ter Braak and Šmilauer 2012). To evaluate changes in *T. granifera* abundances among study sites and seasons, a hierarchial cluster analysis was carried out in PRIMER v6 (Anderson et al., 2008), in autopilot mode so as to allow the program to choose the best solution for each dimensionality (Kruskal and Wish 1978).

2.3. Results

2.3.1. Habitat characteristics

Nandoni reservoir ecosystem health based on the water and sediment chemistry variables differed significantly among study sites (Pseudo-$F_{6,55} = 4.115$, $p = 0.0001$) and seasons (Pseudo-$F_{3,55} = 9.450$, $p = 0.0001$). Significant pairwise differences ($p < 0.050$) were found across all season combinations, however, for sites no significant differences ($p > 0.050$) were observed for N2 *vs* N1, N3 and N4, N3 *vs* N4, N6 *vs* N4 and N7, N7 *vs* N4 and N5 *vs* N4 combinations, with system health deteriorating towards the winter season (Table 2.1). While variable, the summer often had high sediment and water concentrations and autumn had low concentrations (Table 2.2).

Table 2.1. Pairwise comparison results for the PERMANOVA highlighting the *t* (white) and *p* values (grey) for the seasons and sites. Bold values indicate significant differences at $p < 0.05$.

Seasons							
	Spring	Summer	Autumn	Winter			
Spring	**1.000**	**0.014**	**0.0002**	**0.0001**			
Summer	**1.925**	**1.000**	**0.0001**	**0.0001**			
Autumn	**3.026**	**3.512**	**1.000**	**0.0001**			
Winter	**3.203**	**3.728**	**2.914**	**1.000**			
Sites							
	N1	N2	N3	N4	N5	N6	N7
N1	1.000	0.290	**0.007**	**0.023**	**0.0001**	**0.001**	**0.004**
N2	1.107	1.000	0.336	0.263	**0.015**	**0.026**	**0.045**
N3	**2.397**	1.001	1.000	0.233	**0.001**	**0.011**	**0.026**
N4	**1.970**	1.161	1.208	1.000	0.057	0.055	0.253
N5	**4.669**	**2.449**	**3.241**	1.702	1.000	**0.022**	**0.024**
N6	**2.976**	**1.943**	**2.175**	1.667	**1.893**	1.000	0.367
N7	**2.874**	**1.876**	**1.909**	1.170	**1.853**	1.050	1.000

Sediment variables in summer, autumn and winter had pH values that were slightly acidic, and lowest in spring (Table 2.2). High sediment metal concentrations were recorded during summer (Table 2.2). Benthic chlorophyll-*a* concentration varied throughout the seasons, with a mean value of 139.5 g m^{-2} in winter and decreasing to a low concentration mean of 61.8 g m^{-2} in spring (Table 2.2). For water variables, temperature varied among all seasons (Table 2.2). In autumn, water pH was very low (mean 6.4) and peaked in spring (mean 8.6). Conductivity and TDS were generally very high in summer (Table 2.2).

Sediment and water variables displayed considerable heterogeneity among sites and seasons (Tables 2.2 and 2.3). All sediment variables except B, S, SOC and SOM differed significantly among sites, whereas pH, resistivity, stone count, Mn, S, SOM and chl-*a* differed among seasons (Table 2.3). Significant site-season interactions were evidenced for resistivity, Fe, and chl-*a* in addition. For water variables, temperature, pH and TDS differed consistently significantly among sites and seasons singularly (Table 2.3), while conductivity differed among seasons alone; temperature and pH also exhibit significant site-season interactions (Table 2.3).

Table 2.2. Physicochemical variables measured (± standard deviation) in Nandoni reservoir in September 2020 to June 2021. Abbreviations: B – boron, Ca – calcium, Cu – copper, Fe – iron, K – potassium, Mg – magnesium, Mn – manganese, Na – sodium, P – phosphorus, SOC – sediment organic carbon, SOM – sediment organic matter, S – sulphur, TDS – total dissolved solids, Zn – zinc.

Variables	Units	Spring	Summer	Autumn	Winter
Sediment					
pH		6.1±0.3	6.7±0.3	6.7±0.6	6.5±0.3
Resistivity	ohms	1912±314	1127±240	1981±515	1675±379
Stone	%	34.7±17.4	53.3±12.4	39.7±12.3	36.3±7.3
P	mg kg^{-1}	15.2±9.3	12.2±6.4	26.1±10.4	17.5±2.8
K	mg/kg	63.1±27.0	55.1±13.8	57.1±19.8	46.3±6.5
Ca	cmol(+) kg^{-1}	4.2±1.1	5.1±2.0	3.3±0.7	3.5±0.6
Mg	cmol(+) kg^{-1}	1.4±0.6	1.88±0.6	1.14±0.5	1.1±0.1
Na	cmol(+) kg^{-1}	0.15±0.04	0.21±0.1	0.18±0.1	0.16±0.03
Cu	mg kg^{-1}	5.1±0.8	5.5±2.7	4.6±1.5	4.5±0.8
Zn	mg kg^{-1}	5.6±1.5	2.8±0.8	4.3±1.7	3.6±1.0
Mn	mg kg^{-1}	91.1±34.0	139.5±72.9	109.4±32.6	63.1±15.3
B	mg kg^{-1}	0.3±0.1	0.20±0.04	0.20±0.06	0.19±0.04
Fe	mg kg^{-1}	161.1±29.8	246.0±85.8	200.1±55.4	151.6±15.0
SOC	%	1.2±0.5	1.4±0.4	0.75±0.19	0.97±0.12
S	mg kg^{-1}	18.8±8.8	38.6±16.9	15.7±5.7	21.1±5.0
SOM	%	4.6±2.6	13.7±3.2	13.6±5.5	15.4±11.8
Chlorophyll-*a*	g m^{-2}	61.8±12.4	100.3±40.7	118.0±49.5	139.5±32.5
Water					
Temperature	°C	29.8±0.6	29.8±0.9	31.2±0.2	21.2±0.2
pH		8.6±0.2	8.5±0.1	6.4±0.2	7.4±0.2
Conductivity	µS cm^{-1}	273.9±0.6	268.7±9.4	140.5±4.1	159.6±2.5
TDS	mg L^{-1}	165.9±2.8	167.2±1.0	70.3±2.0	79.6±1.4

Table 2.3. Two-way analyses of variance (ANOVA) based on sediment and water variables for sites and seasons. Bold values indicate significant differences at $p < 0.05$. See abbreviations in Table 2.2 for the parameters

Parameter	**Site**		**Season**		**Site × Season**	
	F	***p***	**F**	***p***	**F**	***p***
Sediment						
pH	**6.057**	**<0.001**	**4.430**	**0.011**	0.526	0.911
Resistivity	**4.176**	**0.004**	**7.506**	**0.001**	**3.769**	**0.001**
Stone	**2.900**	**0.024**	**3.277**	**0.035**	1.313	0.255
P	**3.836**	**0.006**	2.733	0.062	1.628	0.123
K	**3.124**	**0.017**	0.689	0.566	0.659	0.808
Ca	**5.310**	**0.001**	1.734	0.182	1.865	0.070
Mg	**6.769**	**<0.001**	1.452	0.248	0.572	0.879
Na	**4.830**	**0.002**	1.081	0.373	0.857	0.618
Cu	**7.869**	**0.000**	0.235	0.871	1.811	0.080
Zn	**2.436**	**0.050**	1.028	0.395	1.516	0.161
Mn	**3.461**	**0.011**	**2.958**	**0.049**	0.558	0.890
B	1.625	0.176	1.536	0.226	0.762	0.711
Fe	**3.764**	**0.007**	2.619	0.070	**3.752**	**0.001**
S	0.593	0.733	**8.110**	**<0.001**	1.627	0.124
SOC	2.094	0.085	2.468	0.082	1.179	0.339
SOM	0.568	0.752	**3.189**	**0.038**	1.377	0.220
Benthic chl-*a*	**2.638**	**0.036**	**9.405**	**<0.001**	**3.147**	**0.004**
Water						
Temperature	**4.822**	**0.001**	**6.564**	**<0.001**	**7.966**	**<0.001**
pH	**13.678**	**<0.001**	**20.297**	**<0.001**	**9.851**	**<0.001**
Conductivity	0.927	0.490	**7.657**	**<0.001**	1.139	0.366
TDS	**6.958**	**<0.001**	**42.233**	**<0.001**	1.665	0.111

2.3.2. Snail distribution and size patterns

Tarebia granifera abundances per m^2 were found to be significantly different across study seasons ($F_{3,55} = 41.824$, $p < 0.001$), but not among sites ($F_{6,55} = 1.614$, $p = 0.179$) or in interaction between these terms ($F_{18,55} = 0.967$, $p = 0.513$). Autumn snail abundances were low (range = 44–206 individuals m^{-2}, mean = 104 individuals m^{-2}) and peaked during the summer season (range = 161–517 individuals m^{-2}, mean = 368 individuals m^{-2}) (Figure 2.3). In general, sites associated with low population/household densities (i.e., N1, N3, N5) nearby had variable mean *T. granifera* abundances per m^{-2} (Figure 2.3).

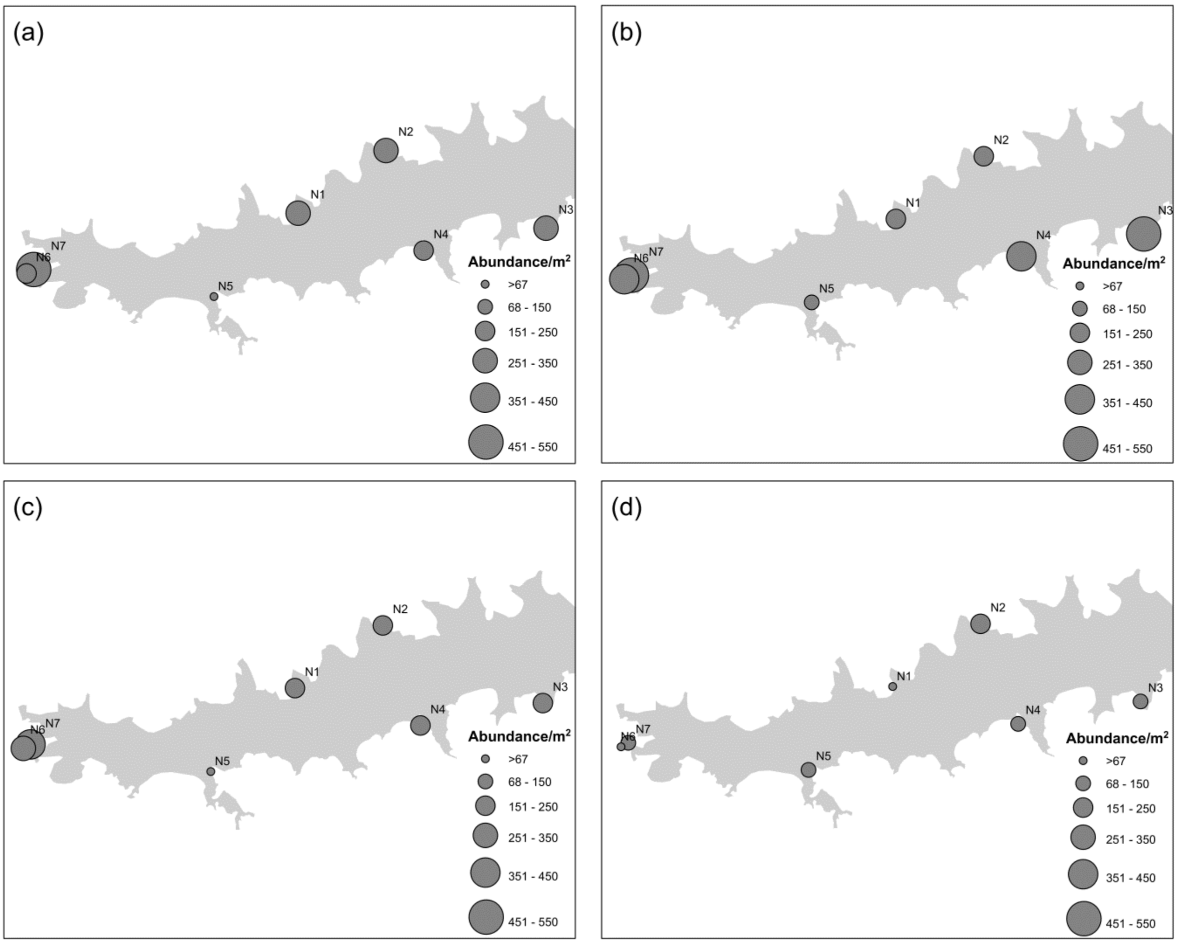

Figure 2.3. Distribution map of *Tarebia granifera* in the Nandoni reservoir of South Africa from (a) spring (September 2020), (b) summer (November 2020), (c) autumn (March 2021) and (d) winter (June 2021).

Considering length frequency distributions (Figure 2.4), size cohorts were clearly identifiable across seasons, with FiSAT identifying at least 6 size classes and two recruitment peaks in November and March. Thus, clear indications of growth were obtained from the length frequency distributions for all seasons. The growth coefficient (*K*) and asymptotic length (*L*∞) were 0.46 and 36.75 mm, respectively.

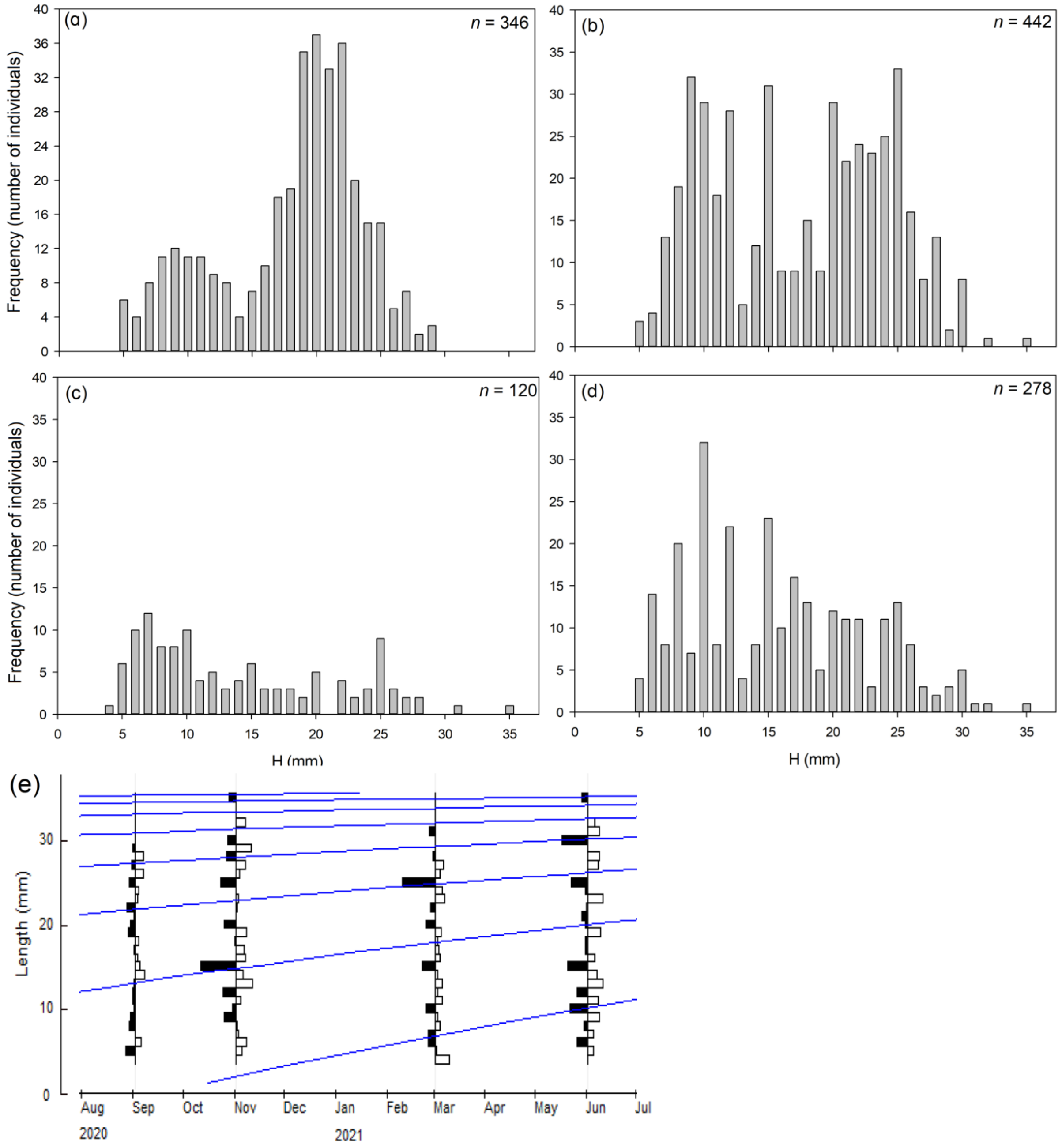

Figure 2.4. Frequency distributions of *Tarebia granifera* in Nandoni Reservoir from (a) spring (September 2020), (b) summer (November 2020), (c) autumn (March 2021) and (d) winter (June 2021), as well as (e) von Bertalanffy growth function plot and length frequencies, with the blue lines indicating the relative size (zonation of size classes) in time i.e., growth curve, and black and white bars the running average frequencies to emphasize positive and negative peaks (recruitment peaks shown by larger bars), respectively. Note that plot (e) is made with same data as plots (a) – (d), by dividing each of the frequency values by

the corresponding running mean frequency, and via the subtraction of 1 from each of the resulting quotients to remove potential sources of bias.

2.3.3. Influence of physicochemical variables on *Tarebia granifera* abundances

Redundancy analysis (RDA) first and second axes of the selected exploratory variables accounted for 36.4 % of the total *T. granifera* abundance variance. Of the 21 physicochemical variables, the abundance of *T. granifera* across the seven study sites and four seasons was found to be significantly associated with sediment (i.e., chlorophyll-*a*, Mn, SOC, SOM) and water (i.e., pH, conductivity, TDS) variables (Figure 2.5). Water pH, TDS and conductivity, sediment organic carbon and Mn were positively associated with the first axis while, SOM and benthic chlorophyll-*a* were negatively associated with the first axis (Figure 2.5). Summer sites were clearly separated along the first axis from the rest of the sites/seasons, whereas the spring sites showed a slight overlap with the autumn and winter sites. Summer site samples were associated with high *T. granifera* abundances which were associated to high pH, conductivity, TDS, Mn and SOC (Figure 2.5). Whereas most of the autumn and winter site samples were associated with low *T. granifera* abundances.

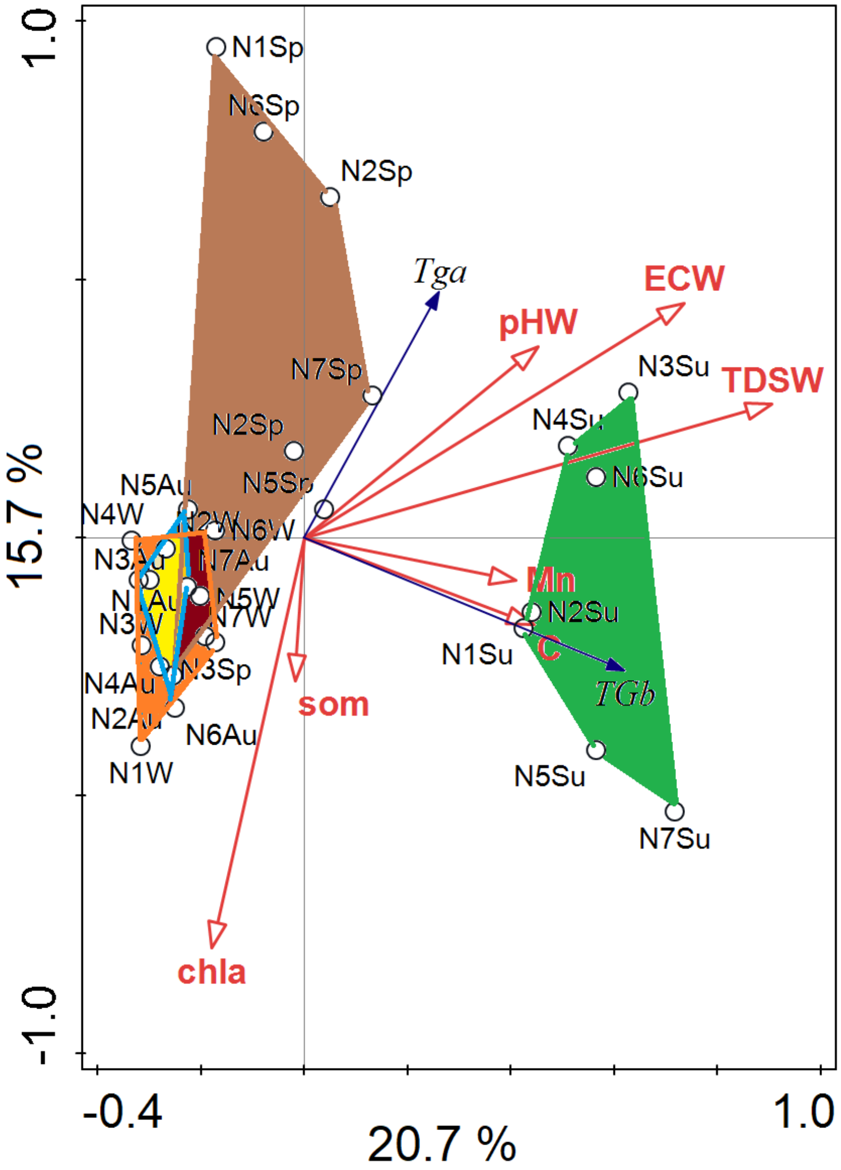

Figure 2.5. Redundancy analysis ordination biplot showing the relationship between measured significant environmental variables with *Tarebia granifera* abundances. Abbreviations: sites N1 – N7, letters after the site names: Au – autumn, Sp – spring, Su – summer, W – winter, TGa – *T. granifera* adults, TGb – *T. granifera* juveniles, chla – benthic chlorophyll-*a*, som – sediment organic matter, pHW – water pH, ECW – electrical conductivity in water, TDSW – water total dissolved solids, Mn – manganese, C – sediment organic carbon.

2.4. Discussion

This study assessed the invasion ecology of *T. granifera* in a tropical river-fed reservoir in southern Africa, across four seasons in relation to human densities, sediment and water chemistry variables. Overall, the study found that *T. granifera* was heterogeneously distributed among all four seasons, with peak littoral densities in summer which corresponded to changes in water and sediment variables. This summer peak corroborates other studies which recorded high densities seasonally as temperature peaked (Yong et al., 1987; Miranda et al., 2011b). In our study system, the summer peak could thus be associated with greater rainfall and water temperatures (Appleton and Nadasan, 2002). Further, peak abundances were associated with significant decreases in benthic chl-*a* concentrations, which could be related to grazing by the snails, with implications for food web transfer (Moslemi et al., 2012). As such, the *T. granifera* invasion of Nandoni reservoir has potentially altered a suite of ecosystem properties within the study system.

There were no significant differences in abundances among sites (while all were human-impacted and invaded), suggesting that the invasion is widespread and ubiquitous in this study system, and relatively unimpeded by human disturbances, such as car and laundry washing, bathing/swimming, and water abstraction on a daily basis that occur in densely-population areas. A lack of comparable uninvaded sites prohibited direct analysis of ecosystem-level effects of invasion here (Moslemi et al., 2012), with no uninvaded sites available on the reservoir. One can speculate that, since the species is abundant within the Limpopo River system where the study site is located, it likely migrated from the mainstem up to the current location, or has been dispersed by waterbirds and via passive dispersal through boats and fishing gear (see Appleton and Nadasan, 2002).

Tarebia granifera of different size classes (i.e., potential age groups) were recorded using stock assessments, which identified at least six different groups varying across the study seasons. In general, the shell height observed in Nandoni reservoir in this study was of a greater range compared to that observed in the KwaZulu Natal province of South Africa (range 0.8 to 22 mm) (Appleton and Nadasan, 2002), Havana (range 0 – 16 mm) (Yong et al., 1987) and the St. Lucia Estuary (range <1 – 29 mm) (Miranda et al., 2011b). Furthermore, larger size groups (>18 mm) or older cohorts dominated, whereas in the studies highlighted above, smaller snails and younger age groups were dominant. These differences could be attributed to favourable climate, flow conditions and resource availability (Miranda et al., 2011b), allowing older cohorts to dominate in Nandoni reservoir, or larger cohorts being competitively superior and smaller sizes moving to deeper waters that was not survey. The growth coefficient of 0.46 (estimated at 1.41 mm/month based on an $L\infty$ of 36.75 mm) was also double that observed in other studies (e.g., Chaniotis, 1980). Contrastingly, the densities (max of 544 individuals per m^2) observed in Nandoni reservoir were generally lower than those observed in other parts of South Africa of >1000 individuals per m^2 (Appleton and Nadasan, 2002; Miranda et al., 2011b). This might reflect a relatively early invasion stage, or the rich population dynamics that have been reported in invasive snails due to ‘boom-bust’ trends as populations grow and deplete resources (Perissinotto et al., 2014); such trends cannot be appreciated with irregular snapshot surveys in time. Alternatively, the system could have a relatively low carrying capacity. Nevertheless, this study provides a basis for understanding snail invasions, as little is known of the seasonal population fluctuations of *T. granifera* in relation to their environment.

In the present study, *T. granifera* abundances were significantly associated with sediment (i.e., benthic chlorophyll-*a*, Mn, SOC, SOM) and water (i.e., pH, conductivity, TDS) chemistry variables. The high benthic chl-*a*, SOC and SOM levels, observed especially during the summer months, might explain the high densities and sizes of *T. granifera* observed in the study area, since *T. granifera* sizes are mostly influenced by food availability and quality (Yong et al., 1987; Miranda et al., 2011b). The breaking down of SOM and SOC might have resulted in the release of nutrients that facilitated the growth of benthic algae which *T. granifera* feed on. Positive effects of rising pH could be attributed to the fact that *T. granifera* shells are eroded at low pH, as has been observed in other study systems where acidity precluded high population levels (Miranda et al., 2011b). The high conductivity and TDS levels observed, especially during spring and summer, may have contributed to high *T. granifera* densities, as in previous studies (e.g., Vazquez et al., 2016; Larson et al., 2020). Low conductivity tends to reduce growth and survival of snails (Larson et al., 2020), which might explain some of the low abundances observed during autumn and winter. Thus, at high conductivity and TDS levels, particularly during spring and summer, *T. granifera* will likely increase its growth and survival as it can adapt to acute high salinity stress and maintain a hypo-osmotic hemolymph (Larson et al., 2020); it has been found in very large densities in estuaries in South Africa of high conductivity levels.

While *T. granifera* was widespread in the focal sites in our study, and thus relatively unimpeded by disturbances associated with human activity, no *T. granifera* have been recorded on the more polluted Mvudi River which joins the Luvuvhu River before entering the reservoir. This could be attributed to contaminants and/or fast flowing waters due to wastewater runoff and discharge, which either impedes population growth through poor water quality or prevents population establishment and upstream spread due to high velocity; despite potential adaptations in invasive snails to different flow conditions (Kistner and Dybdahl, 2013). As with other invasive snails, adaptabilities to human disturbance and rates of parthenogenetic reproduction promote establishment in a range of conditions (Miranda et al., 2016). Despite a lack of impact studies in our study system, the rapid spread of *T. granifera* has reportedly displaced native gastropods. For example, Raw et al. (2013) also showed that native gastropods *Assiminea* cf. *capensis*, *M. tuberculata* and *Coriandria durbanensis* exhibited negative taxis response to chemical cues released by *T. granifera* at invaded sites in St. Lucia Estuary, South Africa. Similarly, Appleton et al. (2009) make anecdotal reports on *M. tuberculata* declines in many sites where *T. granifera* now occur in South Africa. Given the link between population dynamics and ecological impact (Parker et al., 1999), the factors that shape abundance and size structures in the present study may thus be the same which mediate impact. These results thus provide insights into population dynamics according to environmental variables in a heavily human-altered environment, but could be furthered by more resolute, widespread and longstanding investigations into the species.

2.5. Outlook

While the present study identified population characteristics and abiotic determinants of *T. granifera* abundances and sizes, it is still unclear what the ecological impacts are, and which species are being adversely affected in the region. There should thus be further studies on *T. granifera* in lakes and rivers to determine if and how native species assemblages are compromised, as well as assessments of populations at different depths of the system through time. Future work should also focus on improving monitoring of aquatic ecosystems that have not been invaded (e.g. through use of environmental DNA) and determining pathways, to ensure improved biosecurity such that further ecosystems are not invaded in future. Similarly, studies on physicochemical drivers and thresholds of *T. granifera* are necessary, to determine invasion debt in the region. Finally, environmentally-sound ways to manage invasive snail populations should be assessed.

CHAPTER 3: INFORMING SPREAD PREDICTIONS OF TWO ALIEN SNAILS USING MOVEMENT TRAITS

3.1. Introduction

Biological invasions are a growing global environmental concern and a prominent aspect of global change (Pyšek et al., 2020). Invasive alien species are those that have been introduced beyond their native range, establish and spread, often causing adverse effects on biodiversity (Ricciardi, 2013) and altering ecosystem functionality (Pyšek et al., 2020). Invasive alien species can be introduced through various pathways, either intentionally or accidentally (Hulme, 2015), challenging preventative management efforts. 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).

Molluscs are among the most impactful invasive alien species, with several notorious species listed in the “100 of the world’s worst” (Lowe et al., 2000), due to their degradation of biodiversity via competition for resources and displacement of native species (Weyl et al., 2020), as well as marked socio-economic effects (Cuthbert et al., 2021). Following arrival, alien molluscs rapidly disperse within and among freshwaters by human-mediated vectors, such as via attachment to fishing equipment and zoochory (Vinarski, 2017; Coughlan et al., 2017), but also via self and natural-dispersal through movement patterns and downstream drift, especially in gastropods (Croteau, 2010; Kappes and Haase, 2012). Furthermore, anthropogenic habitat changes can promote invasion through disturbance, alongside canalisation for agricultural and industrial purposes via increased habitat connectivity (Miranda et al., 2010; Jones et al., 2017).

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 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). For example, the rapid spread of *T. granifera* appeared to cause a decline of the native thiarid *Melanoides tuberculata* in South Africa (Appleton et al., 2009).

Understanding invasive alien species behavioural traits is significant since such traits influence spread and dispersal (Clobert et al., 2009). This study compared the movement traits between two invasive alien snails with high invasion success: *T. granifera* and *P. acuta.* The study compared the behavioural responses of the two species by assessing: (*i*) net distance and velocity to determine dispersal potential; (*ii*) turning angles (both absolute and relative) and straightness index as proxies of exploratory behaviour. It was hypothesised that

P. acuta will move faster than *T. granifera.* This can be associated with body sizes with *P. acuta* being smaller in size while *T. granifera* is generally bigger in size.

3.2. Materials and methods

3.2.1. Sampling

Adult individuals of *P. acuta* and *T. granifera* were collected by hand from Nandoni reservoir (22°59'11" S, 30°36'16.19" E) littoral zones (water depth mean 0.5 m), situated in the Thulamela Municipality, Vhembe District in the Limpopo Province of 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. *T. 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. Prior to the experiments, immediately after collection all the snails were acclimatized for 48 hours in filtered (63-µm mesh) source water at 26 ± 1.5 °C under 12h:12h day night regime.

3.2.2. Snail density estimation

To determine snail densities, random quadrat (30 × 30 cm) sampling was done at 7 sites around Nandoni reservoir littoral zones using a hand shovel at a water depth of approximately 5 – 10 cm (see Chapter 2). All snails were identified to species level, counted and measured.

3.2.3. Movement assays and data preparation

To describe the trajectories followed by individuals (n = 40 per species), an open-field arena was used over a 4-day period i.e., 20 individuals per day (between 0700 and 1700) for each size-matched individual within species at 26.5 ± 1.5 °C under a 40 W incandescent bulb lighting. The mean heights of *T. granifera* and *P. acuta* were 15.8 ± 1.1 (SD) mm and 8.1 ± 0.5 (SD) mm, respectively. The species were not sexed, as that involved dissection, and *T. granifera* trials were ran first, followed by *P. acuta* trials. 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. 3.1). At the beginning of each trial, a snail 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 seconds. The laminated grid was thoroughly washed between trials to prevent snails tracing the mucus trail left by previous individuals.

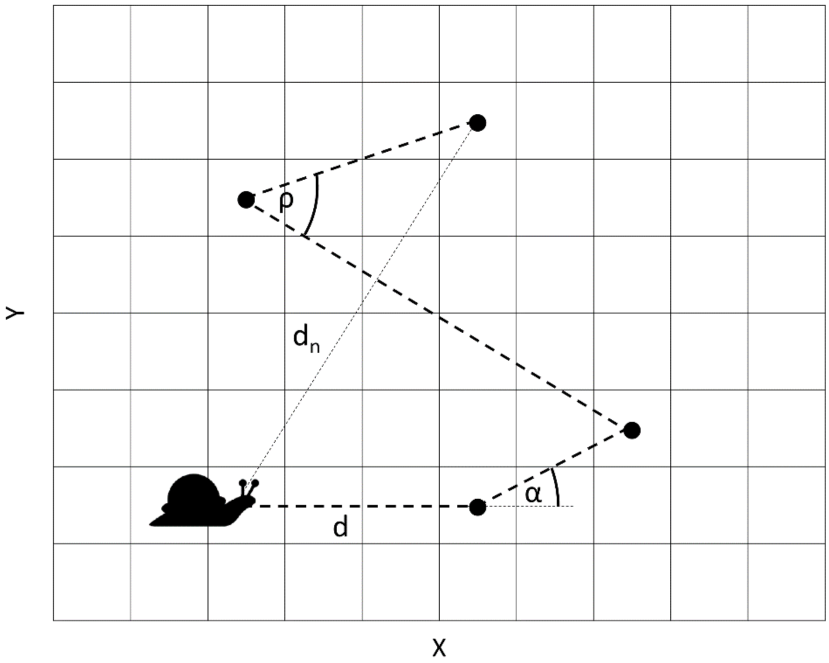

Figure 3.1. Schematic representation of movement essays used to describe the trajectories followed by *Physa acuta* and *Tarebia granifera* individuals, within an XY grid. Grid squares were 2 × 2 cm^2. The snail marks the starting position of the trial, and each black dot represents successive positions, occupied at 30 second 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

We used the XY-coordinate position of individuals recorded every 30 seconds to describe their trajectories, and estimate displacement ability (i.e., velocity and net distance) and exploratory behaviour (i.e., absolute, and relative turning angles, and straightness index; Fig. 3.1). 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). 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. 3.1). 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.

3.2.4. Statistical analyses

To investigate the effect of species on the movement traits (i.e., velocity, net distance, turning angles, and straightness index), we used non-parametric Kruskal-Wallis tests computed in R (R Core Team, 2019).

3.4. Results

The density of *T. granifera* and *P. acuta* in the field ranged between 104–368 and 15–619 individual’s m^{-2}, respectively (see Chapter 2).

The species comparison of movement traits showed that *P. acuta* moved significantly slower (Kruskal-Wallis test, $\chi^2 = 5.31$, df = 1, $p = 0.021$) and covered a significantly lower net distance (Kruskal-Wallis test, $\chi^2 = 4.87$, df = 1, $p = 0.027$) than *Tarebia granifera* (Figs. 3.2A and 3.2B). This suggests that *T. granifera* can disperse and spread further than *P. acuta*.

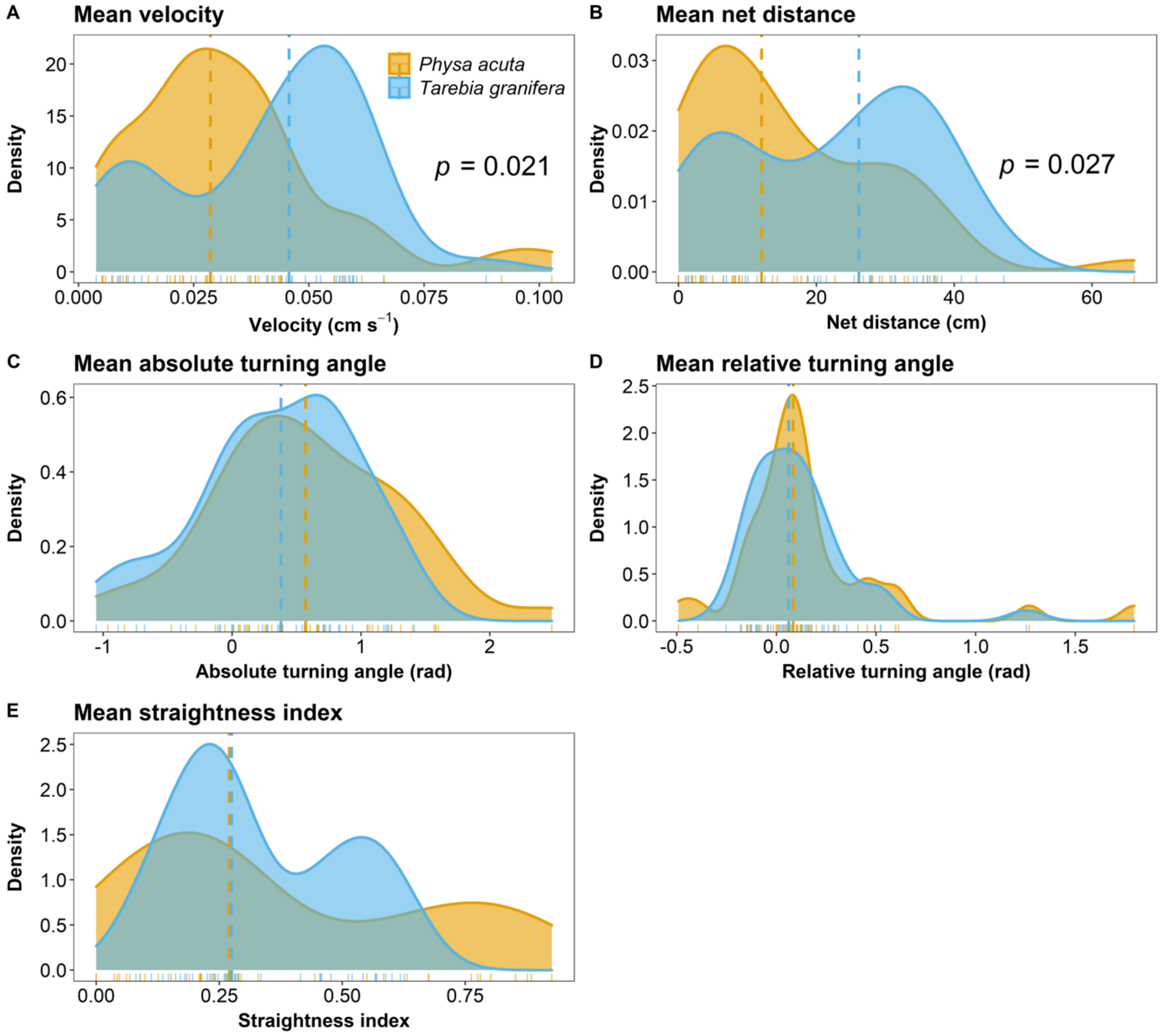

Figure 3.2. Density plots illustrating the distribution of movement traits of *Physa acuta* (orange) and *Tarebia granifera* (light blue). (A) velocity and (B) net distance provide information about the species ability to displace, while (C) absolute turning angle (i.e., α), (D) relative turning angle (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.

In contrast, the movement traits associated with individuals' exploratory behaviour did not differ significantly between the two species (Figs. 3.2C, 3.2D, and 3.2E). Individuals from both species showed a slight tendency to turn counter clockwise (positive turning angle values; Figs. 3.2C and 3.2D). 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. 3.2E).

3.5. Discussion

Both assessed snails are successful invaders, and therefore provide a model to assess spread and dispersal traits in gastropods. 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, however, exhibited similar levels of exploratory behaviour, characterized by relatively low straightness indices that could promote spread and dispersal to new areas by individuals.

The hypothesis was rejected with *T. granifera* moving faster than *P. acuta.* It was hypothesised that *P. acuta* will move faster than *T. granifera*. This can be associated with body sizes with *P. acuta* being smaller in size while *T. granifera* is generally bigger in size.

Importantly, in this 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), while *P. acuta* height ranges from 0.1 to 12 mm (Saha et al., 2016; Nunes, 2010). Our size classes therefore reflect species-level differences and the averages found in the sampled area. While speed might be intuitively expected to relate positively with size, Snider and Gilliam (2002) highlighted that smaller individuals *T. granifera* tended to move faster compared to larger individuals, this was due to resource availability, in contrast to our results. Such differences might also emanate from experimental context, as it is important to consider the microscale and behavioural mechanisms producing the observed responses. For example, responses could have been linked to searching for food. Indeed, snails' movement patterns are often explained by the competition for resources (Chapman, 2000), and both snail species assessed here tend to outcompete native species for food resources and space and not limited to the two factors (Miranda and Perissinotto, 2012). Availability of food has an influence in the movement of the snails, in this study there was no food provided in the area-restricted arenas, one might speculate that larger individuals i.e., *T. granifera* will slow down in natural environments when food resources are abundant, but small individuals i.e., *P. acuta* will speed up through areas where food resources have been reduced (Snider and Gilliam, 2008). Several studies have highlighted that current velocity, predation threat and abiotic and biotic variables might also affect snail movement behaviour in natural environments (Fraser et al., 2006; Snider and Gilliam, 2008).

The study results showed that *T. granifera* and *P. acuta* moved at a mean velocity of ~0.45 cm s^{-1} and ~0.30 cm s^{-1}, respectively, suggesting that the former has a higher capacity to spread. These findings suggest that *P. acuta* here moved faster compared to a previous study by Bernot et al. (2005) and Brown et al. (2012) who observed mean 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 hours before the experiment and placed in toxic ionic liquid solution for experiment (Bernot et al., 2005). In the study by Brown et al. (2012), snails were chronically exposed to Triclosan concentrations. Under field conditions, *P. acuta* was also shown to move faster than *Bulinus tropicus* of similar size, under same current velocity conditions, which gives it a competitive advantage over native snails (Appleton, 2003). However, Appleton (2003) showed that *T. granifera* can move at a velocity of 120 cm s^{-1} in rivers of KwaZulu Natal Province of South Africa, approximately three times faster than *T. granifera* movements observed in the current study.

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 counter clockwise turning angles, with such behavioural responses being considered as exploratory (Raw et al., 2015). O'Brien et al. (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. The stop-and-go movements that snails performed during the experiments did not occur at obvious places and might have corresponded to a random search for favourable stopping places i.e., areas that might have food and also movement oriented in a direction that is likely to change with each stop. Importantly, such random search behaviour could facilitate colonization of new areas in aquatic environments, enabling rapid dispersal of individual snails (i.e., propagules) to found widespread populations after invasion. Equally, these traits could enhance the probability of being entrained in anthropogenic or natural vectors via encounters which promote gastropod dispersal (e.g., fishing gear, boats or via zoochory) (Kappes and Haase, 2012; Coughlan et al., 2017).

In conclusion, 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 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.

CHAPTER 4: GENERAL SYNTHESIS

4.1. General discussion

Invasive species are a growing global concern (Pyšek et al., 2020) with thousands of these species having successfully spread to non-native ranges (Seebens et al., 2017). Aquatic ecosystems are vulnerable and tend to experience high invasion rates, ecological and socio-economic impacts (Bailey et al., 2020; Curthbert et al., 2021). Freshwater molluscs are amongst the most successful and impactful invaders (Nentwig et al., 2018). The invasion of *T. granifera* and *P. acuta* is of concern since these species tend to outcompete and displace native species, leading to an imbalanced ecosystem (Appleton, 2003). It is important to understand the behaviour of these species since the behaviour plays a role in dispersal and spread (Clobert et al., 2009).

There is little knowledge about the environmental factors that influence the distribution, abundance, and movement dynamics of *T. granifera* in Limpopo reservoirs, particularly in Nandoni reservoir. To the author's knowledge, this is the first study on the invasion of *T. granifera* to be carried in Nandoni reservoir or the Luvuvhu river system. Although several studies have been conducted in Nandoni reservoir, such as Gumbo et al. (2016), Dalu et al. (2019) and Sinthumule (2021), these studies focused on water quality, pollution, and economic opportunities, respectively. The purpose of this study was to investigate environmental factors (water and sediment) structuring populations and movement dynamics of the invasive snail *T. granifera* in a subtropical Austral reservoir. One of the key findings of the study was that *T. granifera* was widely distributed across the reservoir, and its distribution and abundance are associated with sediments and water variables (see Chapter 2). Several other studies have indicated that *T. granifera* has successfully invaded and spread across

South African provinces such as Limpopo, Mpumalanga, and KwaZulu Natal, and prefers sandy habitats and shallow water environments (Appleton, 2003; Appleton et al., 2009; Miranda et al., 2010; Appleton and Miranda, 2015a). The findings of this study indicate that physicochemical variables have a significant influence on the abundance and distribution of *T. granifera.*

The results of this study indicate that *T. granifera* was unevenly distributed across all four seasons (i.e., winter, autumn, spring, summer) and in all the seven selected sites N1–N7 (Chapter 2). This study is in agreement with studies conducted in KwaZulu Natal reservoirs, lakes, and estuaries, showing that physicochemical variables, such as chlorophyll-a, manganese, sediment organic matter, and organic carbon, temperature, pH, conductivity and total dissolved solids are significant variables that influenced the distribution and abundance of *T. granifera* populations (Chapter 2) (Appleton and Nadasan, 2012; Miranda et al., 2011b; Miranda et al., 2010).

The shell height of *T. granifera* in this study was slightly greater (range 0–35 mm) than that of Appleton and Nadasan (2002) in KZN (range 0.8–22 mm), Yong et al. (1987) Havana (range 0–16 mm) and Miranda et al. (2011b), the St. Lucia Estuary (range <1–29 mm), while *P. acuta* was a smaller snail (0.1–12 mm) (Saha et al., 2016; Nunes, 2010), again consistent with this study (Chapters 2 and 3). Throughout the investigation, large *T. granifera* were found to be the most prevalent. Larger snails have a lower possibility of passive transfer (i.e., other animals) (Anderson et al., 2007). *Physa acuta* is generally a smaller snail, and in densely populated areas, smaller snails are driven by either a shortage of resources or chemical cues passed among individuals (Anderson et al., 2007).

One of the objectives of this study was to compare the movement traits between two invasive alien snails *T. granifera* and *P. acuta*. This study provided baseline information on alien snails' movement and further improves understanding of how these two species spread, disperse, and invade new environments. *Tarebia granifera* and *P. acuta* have invaded many river systems across South Africa (Appleton, 2003) including the Luvuvhu River System. A key finding of the investigation was that *T. granifera* moves faster than *P. acuta* (Chapter 3). The result is consistent with the published literature. For example Bernot et al. (2005) and Brown et al. (2012) both observed that *P. acuta* is generally a slower moving snail. In terms of exploratory behaviour, both snails respond in a similar way. Furthermore, the results show that *P. acuta* covered a significantly lower net distance, which suggests that *T. granifera* had a higher capacity to spread than *P. acuta*. Snails' behaviour during movement in their natural habitat can be influenced by current speed, predator danger, and abiotic and biotic factors (Fraser et al., 2006; Snider and Gilliam, 2008). The study is important since it provides important information and insights towards the distribution, abundance, and the extent of spread of *T. granifera* and also provided valuable information on the movement traits of *T. granifera* and *P. acuta.*

4.2. Conclusions and recommendations

In conclusion, snail abundance is influenced by physicochemical factors, and its movement behaviour is highly related to population dynamics and spread. *Tarebia granifera* and *P. acuta* are considered to be amongst the most successful invaders; therefore, it is significant to understand the invasion success of these two snails in Nandoni reservoir and Limpopo water bodies as a whole. The present study has clearly demonstrated the physicochemical variables that influence the distribution and abundance of *T. granifera*; however, the ecological impacts of *T. granifera* remain unclear. Therefore, there is a need for future studies that will investigate the impacts, growth, reproduction, and feeding dynamics of *T. granifera*, and further assess the abundances of native mollusc species in relation to *T. granifera* invasions. Future studies should focus on monitoring aquatic ecosystems that have not yet been invaded by *T. granifera* and aim to improve on biosecurity and ensure that no further invasion occurs. Passive dispersal of the snail may occur through weed on boats and boat trailers; therefore, it is recommended that boats must be checked and cleaned before taking off, and at the point of arrival, any weed that might be attached must be removed and disposed of safely. Future studies should also attempt to explore how other general habitat factors (i.e., aquatic macrophytes, wave exposure) affect species distribution.

REFERENCES

Ahmed, D. A., Hudgins, E. J., Cuthbert, R. N., Kourantidou, M., Diagne, C., Haubrock, P. J., Leung, B., Liu, C., Leroy, B., Petrovskii, S., and Courchamp, F. (2021). Managing biological invasions: the cost of inaction. *Research Square*, DOI: 10.21203/rs.3.rs-300416/v1

Alzurfi, S. K., Algburi, J. B., Taher, M. M., Alhachami, L. H., and Zwain, K. A. (2019). Mollusca Diversity in Aquatic Ecosystem. *ARPN Journal of Engineering and Applied Sciences*, 14, 7277–7283.

Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26, 32–46.

Anderson, M. J., and ter Braak, C. J. F. (2003). Permutation tests for multi-factorial analysis of variance. *Journal of Statistical Computation and Simulation,* 73, 85–113.

Anderson, M. J., Gorley, R. N., and Clarke, K. R. (2008). *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods.* PRIMER-E, Plymouth, UK.

Anderson, T. K and Weaver, K. F., and Guralnick R. P. (2007). Variation in adult shell morphology and life-history traits in the land snail *Oreohelix cooperi* in relation to biotic and abiotic factors. *Journal of Molluscan Studies*, 73, 129-137

Appleton, C. C. (2003). Alien and invasive fresh water gastropoda in South Africa. *African Journal of Aquatic Sciences*, 28, 69–81.

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

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

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

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

Bailey, S. A., Brown, L., Campbell, M. L., Canning-Clode, J., Carlton, J. T., Castro, N., Chainho, P., Chan, F., Creed, J., Curd, A., Darling, J., Fofonoff, P., Galil, B., Hewitt, C., Inglis, G., Keith, I., Mandrak, N., Marchini, A., Mckenzie, C., and Zhan, A. (2020). Trends in the detection of aquatic non-indigenous species across global marine, estuarine and freshwater ecosystems: A 50-year perspective. *Diversity and Distributions*, 26, 1780-1797.

Bellard, C., Cassey, P., and Blackburn, T. M. (2016). Alien species as a driver of recent extinctions. *Biology Letters*, 12, 1-5.

Benbow, M. E., Receveur, J. P. and Lamberti, G. A. (2020). Death and decomposition in aquatic ecosystems. *Frontiers in Ecology and Evolution*, 8, 1–12.

Benhamou, S. (2004). How to reliably estimate the tortuosity of an animal's path: straightness, sinuosity, or fractal dimension? *Journal of Theoretical Biology*, 229, 209–220.

Bernot, R. J., Kennedy, E. E. and Lamberti, G. A. (2005). Effects of ionic liquids on the survival, movement, and feeding behaviour of the freshwater snail, *Physa acuta. Environmental Toxicology and Chemistry*, 24, 1759–1765.

Blackburn, T. M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarošík, V., Wilson, J. R. U. and Richardson, D. M. (2011). A proposed unified framework for biological invasions. *Trends in Ecology and Evolution*, 26, 333–339.

Brancatelli, G. I. E. and Zalba, S. M. (2018). Vector analysis: a tool for preventing the introduction of invasive alien species into protected areas. *Nature Conservation*, 24, 43-63.

Brown, J., Bernot, M. J. and Bernot, R. J. (2012). The influence of TCS on the growth and behaviour of the freshwater snail, *Physa acuta*. *Journal of Environmental Science and Health Part 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. *Ecological Modelling*, 197, 516–519.

Chaniotis, B. N., Butler J. M., Ferguson F. F. and Jobin, W. R. (1980). Bionomics of *Tarebia granifera* (Gastropoda: Thiaridae) in Puerto Rico, an Asian vector of *Paragonimiasis westermani. Caribbean Journal of Science*, 16, 81–89.

Chapman, M. G. (2000). A comparative study of differences among species and patches of habitat on movements of three species of intertidal gastropods. *Journal of Experimental Marine Biology and Ecology*, 244, 181–201.

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

Cloyed, C. S., and Dell, A. I. (2019). Resource distribution and internal factors interact to govern movement of a freshwater snail. *Proc. R. Soc. B,* 286, 1-8.

Coppolino, M. L. (2009). Land snail abundance and diversity with associated ecological variables in six southern Illinois counties. MSc Dissertation, Southern Illinois University, Carbondale, Illinois.

Coughlan, N. E., Cuthbert, R. N., and Dick, J. T. A. (2020). Aquatic biosecurity remains a damp squib. *Biodiversity and Conservation*, 29, 3091–3093.

Coughlan, N. E., Stevens, A. L., Kelly, T. C., Dick, J. T. A. and Jansen, M. A. K. (2017). Zoochorous dispersal of freshwater bivalves: An overlooked vector in biological invasions? *Knowledge and Management of Aquatic Ecosystems*, 418, 1–8.

Croteau, E. K. (2010). Causes and consequences of dispersal in plants and animals. *Nature Education Knowledge*, 3, 1-12

Cuthbert, R. N., Pattison, Z., Taylor, N. G., Verbrugge, L., Diagne, C., Ahmed, D. A., Leroy, B., and Angulo, E., Briski, E., Capinha, C., Catford, J., Dalu, T., Essl, F., Gozlan, R., Haubrock, P., Kourantidou, M., Kramer, A., Renault, D., Wasserman, R., and. Courchamp, F. (2021). Global economic costs of aquatic invasive alien species. *Science of the Total Environment*, 775, 145238.

Cuthbert, R. N., Diagne, C., Haubrock, P. J., Turbelin, A. J. and Courchamp, F. (2021). Are the “100 of the world’s worst” invasive species also the costliest? *Biological Invasions*. DOI: 10.1007/s10530-021-02568-7.

Dalu, T., and Chauke, R. (2020). Assessing macroinvertebrate communities in relation to environmental variables: the case of Sambandou wetlands, Vhembe Biosphere Reserve. *Applied Water Science*, 10, 1–11.

Dalu, T., Malesa, B., and Cuthbert, R. N. (2019). Assessing factors driving the distribution and characteristics of shoreline macroplastics in a subtropical reservoir. *Science of the Total Environment*, 696, 133992.

Darwall, W. R. T., Smith, K. G., Allen, D. J., Holland, R. A, Harrison, I. J. and 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. and Wolmarans, C. T. (2007). Distribution and habitats of the alien invader freshwater snail *Physa acuta* in South Africa. *Water SA*, 33, 717–722.

DWAF. (2012) Development of a reconciliation strategy for the Luvuvhu and Letaba water supply system: literature review report. Department of Water Affairs, Pretoria.

Emery-Butcher, H. E., Beatty, S. J., and Robson, B. J. (2020). The impacts of invasive ecosystem engineers in freshwaters: A review. *Freshwater Biology*, 65, 999–1015.

ESRI (Environmental Systems Research Institute). (2011). ArcGIS Desktop: Release 10. Environmental Systems Research Institute, Redlands, CA.

Fraser, D. F., Gilliam, J. F., Daley, M. J., Le, A. N. and Skalski, G. T. (2001). Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. *American Naturalist*, 158, 124–135.

Frid, A., and Dill, L. (2002). Human-caused Disturbance Stimuli as a Form of Predation Risk. *Conservation Ecology*, 6, 1–11.

Gumbo, J., Dzaga, R., and Nethengwe, N. (2016). Impact on Water Quality of Nandoni Water Reservoir Downstream of Municipal Sewage Plants in Vhembe District, South Africa. *Sustainability*, 8, 1–16.

Charles, H. L., and Dukes, J. S. (2007). Impacts of Invasive Species on Ecosystem Services. *Ecological Studies,* 198, 217–237.

Holyoak, M., Casagrandi, R., Nathan, R., Revilla, E., Spiegel, O. (2009). Trends and Missing Parts in the Study of Movement Ecology. *Proceedings of the National Academy of Sciences America*, 105, 19060–19065.

Hulme, P. E. (2015). Invasion pathways at a crossroad: Policy and research challenges for managing alien species introductions. *Journal of Applied Ecology*, 52, 1418–1424.

Irfan, S., and Alatawi, A. M. M. (2019). Aquatic ecosystem and biodiversity: a review. *Open journal of Ecology*, 9, 1–13.

Isnaningsih, N. R., Basukiriadi, A. and Marwoto, R. M. (2017). The Morphology and Ontogenetic *Tarebia granifera* (Lamarck, 1822) from Indonesia (Gastropoda: Cerithioidea: Thiaridae). *Treubia*, 44, 1–14.

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

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

Kappes, H., and Haase, P. (2012). Slow, but steady: dispersal of freshwater molluscs. *Aquatic Sciences*, 74, 1–14.

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

Kesner, D., and Kumschick, S. (2018). Gastropods alien to South Africa cause severe environmental harm in their global alien ranges across habitats. *Ecology and Evolution*, 8, 8273–8285.

Kistner, E. J., and Dybdahl, M. F. (2013). Adaptive responses and invasion: the role of plasticity and evolution in snail shell morphology. *Ecology and Evolution*, 3, 424–436.

Kruskal, J. B., and Wish, M. (1978). Multidimensional Scaling. Sage University Paper series on Quantitative Applications in the Social Sciences. Sage Publishers, Beverly Hills and London.

Larson, M. D., Dewey, J. C., and Krist, A. C. (2020). Invasive *Potamopyrgus antipodarum* (New Zealand mud snails) and native snails differ in sensitivity to specific electrical conductivity and cations. *Aquatic Ecology*, 54, 103–117.

Lowe, S., Browne, M., Boudjelas, S., and De Poorter, M. (2000). 100 of the World's worst invasive alien species a selection from the global invasive species database. The Invasive Species Specialist Group (ISSG), Auckland.

Mayfield A. E., Seybold, S. J., Haag, W. R., Johnson, M. T., Kerns, B. K., Kilgo, J. C., Larkin, D. L., Lucardi, R. D., Moltzan, B. D., Pearson, D. E., Rothlisberger, J. D., Schardt, J. D., Schwartz, M. K., and Young, M. K. (2021) Impacts of Invasive Species in Terrestrial and Aquatic Systems in the United States. In: Poland T. M., Patel-Weynand T., Finch D. M., Miniat C. F., Hayes D. C., Lopez V. M. (eds) Invasive Species in Forests and Rangelands of the United States. Springer, Cham.

Manavhela, P. and Spencer, J. P. (2012). Assessment of the potential for sustainable community tourism development: A study at the Nandoni Dam in Limpopo Province, South Africa. *African Journal for Physical, Health Education, Recreation and Dance*, 18, 535–551.

Mbedzi, R., Cuthbert, R. N., Wasserman, R. J., Murungweni, F. M. and Dalu, T. (2020). Spatiotemporal variation in microplastic contamination along a subtropical reservoir shoreline. *Environmental Science and Pollution Research*, 27, 23880–23887.

Measey, J. (2019). A global meta-analysis of the ecological impacts of alien species on native amphibians. Proceedings of the Royal Society B: *Biological Sciences*, 286, 1–10.

McNeely, J. (2001). Invasive species: a costly catastrophe for native biodiversity. *Land Use and Water Resources Research*, 1, 1–10.

Miranda, N. A. F., and Perissinotto, R. (2014). Benthic assemblages of wetlands invaded by *Tarebia granifera* (Lamarck, 1822) (Caenogastropoda: Thiaridae) in the iSimangaliso Wetland Park, South Africa. *Molluscan Research*, 34, 40–48.

Miranda, N. A. F., John Measey, G., Peer, N., Raw, J. L., Perissinotto, R., and Appleton, C. C. (2016). Shell crushing resistance of alien and native thiarid gastropods to predatory crabs in South Africa. *Aquatic Invasions*, 11, 303–311.

Miranda, N. A. F., Perissinotto, R., and Appleton, C. C. (2010). Salinity and temperature tolerance of the invasive freshwater gastropod *Tarebia granifera. South African Journal of Science*, 106, 1–8.

Miranda, N. A. F., Perissinotto, R., and Appleton, C. C. (2011a). Feeding dynamics of the invasive gastropod *Tarebia granifera* in coastal and estuarine lakes of northern KwaZulu-Natal, South Africa. *Estuarine, Coastal and Shelf Science*, 91, 442–449.

Miranda, N. A. F., Perissinotto, R., and Appleton, C. C. (2011b). Population structure of an invasive parthenogenetic gastropod in coastal lakes and estuaries of northern KwaZulu-Natal, South Africa. *PLoS ONE*, 6, 1–9.

Miranda, N. A. F., and 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., and Appleton, C. C. (2010). Salinity and temperature tolerance of the invasive freshwater gastropod *Tarebia granifera. South African Journal of Science*, 106, 1–8.

Moslemi, J. M., Snider, S. B., MacNeill, K., Gilliam, J. F., and Flecker, A. S. (2012). Impacts of an invasive snail (*Tarebia granifera*) on nutrient cycling in tropical streams: the role of riparian deforestation in Trinidad, West Indies. *PLoS One*, 7, 1–10.

Nathan, R., Getz, W., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., and Smouse, P. E. (2008). A Movement Ecology Paradigm for Unifying Organismal Movement Research. *Proceedings of the National Academy of Sciences*, 105, 19052–19059.

Nentwig, W., Bacher, S., Kumschick, S., Pyšek, P., and Vilà, M. (2018). More than "100 worst" alien species in Europe. *Biological Invasions*, 20, 1611–1621.

Nicolai, A., and Ansart, A. (2017). Conservation at a slow pace: Terrestrial gastropods facing fast-changing climate. *Conservation Physiology*, 5, 1–14.

Nunes, A. L., Fill, J. M., Davies, S. J., Louw, M., Rebelo, A. D., Thorp, C. J., Vimercati. G., and 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 - Serie Zoologia*, 100, 275–279.

Olatunji, O. (2020). *Aquatic biopolymers: understanding their industrial significance and environmental implications*. Switzerland: Springer Open.

Parker, I. M., Simberloff, D., Lonsdale, W. M., Goodell, K., Wonham, M., Kareiva, P. M., Williamson, M. H., Von Holle, B. M. P. B., Moyle, P. B., Byers, J. E., and Goldwasser, L. (1999). Impact: Toward a framework for understanding the ecological effects of invaders. *Biological invasions*, 1, 3–19.

Perera, G., and Yong, M. (1984). The influence of some abiotic factors on the distribution of freshwater mollusks on the Isle of Youth (Isle of Pines), Cuba. *WALKERANA - Freshwater Mollusk Conservation* Society, 2, 131–139.

Perissinotto, R., Miranda, N. A. F., Raw, J. L., and Peer, N. (2014). Biodiversity census of lake St Lucia, iSimangaliso Wetland Park (South Africa): Gastropod molluscs. *ZooKeys*, 43, 1–43.

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. and Richardson, D. M. (2020). Scientists' warning on invasive alien species. *Biological Reviews*, 95, 1511–1534.

R Core Team, (2019). R: A language and environment for statistical computing. Vienna, Austria.

Raw, J. L., Miranda, N. A. F. and Perissinotto R. (2013). Chemical Cues Released by an Alien Invasive Aquatic Gastropod Drive Its Invasion Success. *PLoS ONE*, 8, e64071.

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

Reck, H., and van der Ree, R. (2015). Insects, snails and spiders: The role of invertebrates in road ecology. In: Van der Ree, R. Smith, D. J. and Grilo, C. (eds) Handbook of Road Ecology. John Wiley & Sons, UK.Ricciardi, A. (2013). Invasive species. In: Meyers, R. A. J. (ed.) Encyclopedia of Sustainability Science and Technology. Springer, Canada.

Saha, C., Chakraborty, J., Pramanik, S., Parveen, S., and Aditya, G. (2016). Observations on abundance and fecundity of the invasive snail *Physa acuta* in West Bengal, India: Implications for management. *Journal of Entomology and Zoology Studies*, 4, 490–497.

Seddon, M., Appleton, C., Van Damme, D., and Graf D. L. (2011). Freshwater molluscs of Africa: diversity, distribution, and conservation. In: Darwall, W., Smith, K., Allen, D., Holland, R., Harrison, I. and Brooks, E. (eds.), The Diversity of Life in African Freshwaters: Under Water, Under Threat: An Analysis of the Status and Distribution of Freshwater Species Throughout Mainland Africa. IUCN, Gland.

Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., Pagad, S., Pyšek, P., Winter, M., Arianoutsou, M., Bacher, S., Blasius, B., Brundu, G., Capinha, C., Celesti-Grapow, L., Dawson, W., Dullinger, S., Fuentes, N., Jäger, H., and Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, 8, 1–9.

Sinthumule, N.I., 2021. Window of Economic Opportunity or Door of Exclusion? Nandoni Dam and Its Local Communities. *Sustainability,* 13, 1–15.

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

Sparre, P., and Venema, S. C. (1993). Introduction to tropical fish stock assessment. Part I: Manual. FAO Fisheries Technical Paper 306.1, Review 1. Food and Agriculture Organization of the United Nations. Rome.

Tucker, M., Böhning-Gaese, K., Fagan, W., Fryxell, J., Moorter, B., Alberts, S., Ali, A., Allen, A., Attias, N., Avgar, Tal Bartlam B. H., Bayarbaatar, B., and Belant, J., Bertassoni, A., Beyer, D., Bidner, L., van Beest, F., Blake, S., Blaum, N., and Mueller, T., (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*, 359, 466–469.

van Oosterhout, C., Mohammed, R. S., Xavier, R., Stephenson, J. F., Archard, G. A., Hockley, F. A., Perkins, S. E. and Cable, J. (2013). Invasive freshwater snails provide resource for native marine hermit crabs. *Aquatic Invasions*, 8, 185–191.

van Wilgen, B. W., Measey, J., Richardson, D. M., Wilson, J. R. and Zengeya, T. A. (2020). Biological Invasions of South Africa. Springer Nature, Cham.

Vazquez, R., Ward, D. M., and Sepulveda, A. (2016). Does water chemistry limit the distribution of New Zealand mud snails in Redwood National Park? *Biological Invasions*, 18, 1523–1531.

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. *Biological Invasions*, 19, 1299–1314.

Wang, Q., Hamilton, P. B., and Kang, F. (2014). Observations on attachment strategies of periphytic diatoms in changing lotic systems (Ottawa, Canada). *Nova Hedwigia*, 99, 239–253.

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

Yakovenko, V., Fedonenko, O., Klimenko, O., and Petrovsky, O. (2018). Biological control of the invasive snail species *Melanoides tuberculata* and *Tarebia granifera* in Zaporizka Nuclear Power Plant cooling pond. *Ukrainian Journal of Ecology*, 8, 975–982.

Yanai, Z., Dayan, T., Mienis, H. K., and Gasith, A. (2017). The pet and horticultural trades as introduction and dispersal agents of non-indigenous freshwater molluscs. *Management of Biological Invasions*, 8, 523–532.

Yescott, R. E., and Hansen, E. L. (1976). Effect of manganese on *Biomphalaria glabrata* infected with *Schistosoma mansoni*. *Journal of Invertebrate Pathology*, 28, 315–320.

Yong, M., Sanchez, R., Perera, G., Ferrer, R., and Amador, O. (1987). Seasonal studies of two populations of *Tarebia granifera*. *WALKERANA - Freshwater Mollusk Conservation Society*, 2, 159–163.

Zengeya T. A., Kumschick S., Weyl O. L. F., and van Wilgen B. W. (2020). An evaluation of the impacts of alien species on biodiversity in South Africa using different assessment methods. In: van Wilgen, B., Measey, J., Richardson, D. M., Wilson, J. R. and Zengeya, T.A. (eds), Biological Invasions in South Africa. Springer Nature, Cham.

Zieritz, A., Gallardo, B., Baker, S.J., Britton, R., van Valkenburg, J., Verreycken, H., and Aldridge, D. (2017). Changes in pathways and vectors of biological invasions in Northwest Europe. *Biological Invasions*, 19, 269–282.