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Population irruption of the clam *Meretrix morphina* in Lake St Lucia, South Africa

The thick-shelled clam *Meretrix morphina*, previously referred to as *Meretrix meretrix*, now occurs in the west Indian Ocean region, along the eastern seaboard of Africa, from the Red Sea to the Mlalazi Estuary, close to the Tugela River. Its presence in South Africa is only of recent recording. *Meretrix morphina* was detected for the first time in Lake St Lucia in 2000. The population declined and was not detected from 2005 until 2011, most likely as a result of a severe drought that resulted in widespread desiccation and hypersalinity in the lake. The system then experienced increased freshwater input resulting in lower salinities from 2011 until 2014, during which time *M. morphina* reappeared and their population gradually increased. In 2015, *M. morphina* became abundant in St Lucia, attaining unprecedented densities of 447 ind./m². Biomass, expressed as a fresh weight, varied in the different basins of St Lucia, ranging from 195 g/m² at Lister's Point to 1909.8 g/m² at Catalina Bay. However, in 2016, when drought conditions returned, *M. morphina* disappeared. This species appears to thrive under brackish salinities and high temperatures. It is able to establish large populations with high biomass and can become dominant. However, *M. morphina* is sensitive to desiccation and hypersaline conditions. This clam has substantial commercial value and is exploited along the African east coast, particularly in Mozambique. In future, it may feature more prominently in South African estuaries. However, the ecology of *M. morphina* is still largely unknown.

Significance:

- First record of population irruption of *M. morphina* in South Africa.
- Report on the largely unknown ecology of a commercially valuable bivalve.
- Update on the taxonomy and poleward spread of *M. morphina*.

Introduction

The thick-shelled clam *Meretrix morphina* (Lamarck, 1818) has previously been reported erroneously as *Meretrix meretrix* (Linnaeus, 1758) in the western Indian Ocean^{1,2} because of an invalid synonymy which has only recently been rectified³. The species is restricted to the shores of the west Indian Ocean, but has occasionally been reported from South African coastal waters, mainly as dead shells.¹ Branch et al.² and Kilburn and Rippey⁴ have stated that *M. morphina* does not occur naturally south of Maputo Bay, Mozambique; however, this species has recently been recorded in the St Lucia and Mlalazi estuaries. This occurrence represents another case of poleward range expansion, probably in response to global warming, as many such cases have already been documented along the South African coastline.⁵ The mode of introduction into Lake St Lucia remains unresolved, but possible means involve either transport of veligers from Maputo Bay via the southward flowing Agulhas Current or human-mediated introduction of adults as bait for recreational fishing.⁶

The St Lucia system is Africa's largest estuarine lake, a Ramsar Wetland of International Importance and a crucial part of the iSimangaliso UNESCO World Heritage Site.⁷ It represents one of the most important nursery areas for estuarine dependent marine species along the southeast African coast and is regarded as a hotspot of biodiversity and centre of endemism.⁸ Historically, this system has undergone cyclical periods of alternating dry and wet conditions, culminating in floods and prolonged droughts.⁹ The flow of fresh water into St Lucia is also affected by anthropogenic activities in its catchments and in the mouth region of the estuary.^{10,11} The system is presently exposed to desiccation, prolonged mouth closure and the development of hypersalinity during dry phases.¹² For a detailed review of hydrodynamics in St Lucia see Stretch et al.⁹ and Lawrie and Stretch¹¹.

In Lake St Lucia, a viable *M. morphina* population was recorded for the first time in July 2000.⁵ The population then declined and was not detected in the lake, most likely because of a severe drought that caused widespread desiccation and hypersalinity in the region from 2005 until 2011.⁵ The system then experienced increased freshwater input, resulting in lower salinities from 2011 until 2014, during which time live *M. morphina* reappeared and their population gradually increased. In 2015, *M. morphina* became overwhelmingly abundant in St Lucia. As *M. morphina* is likely to have a major ecological impact when it occurs in such large numbers, information is needed on its biology and ecology in order to fully understand its role in the system. The aim of this study was to document the unprecedented population irruption of *M. morphina* in Lake St Lucia, as well as to identify some possible implications of its presence on the ecology of the system.

Materials and methods

Lake St Lucia consists of three lake basins, known as South Lake, North Lake and False Bay. Sampling sites were selected to represent the South Lake (Catalina Bay and Charter's Creek) and False Bay/North Lake (Lister's Point) (Figure 1). Routine measurements of physico-chemical parameters (temperature, salinity, O₂ concentration, turbidity, pH) were taken using a YSI 6600V2 multiprobe. In addition, total suspended solids (TSS, mg/L) were determined by gravimetric analysis and chlorophyll-*a* concentrations (mg/L) were determined fluorometrically during quarterly surveys, conducted in January/February, April/May, July/August and November/December of

each year at the representative stations from 2008 to 2015 (for more details refer to Pillay and Perissinotto¹³). Salinity and water level data were obtained from Ezemvelo KZN Wildlife.

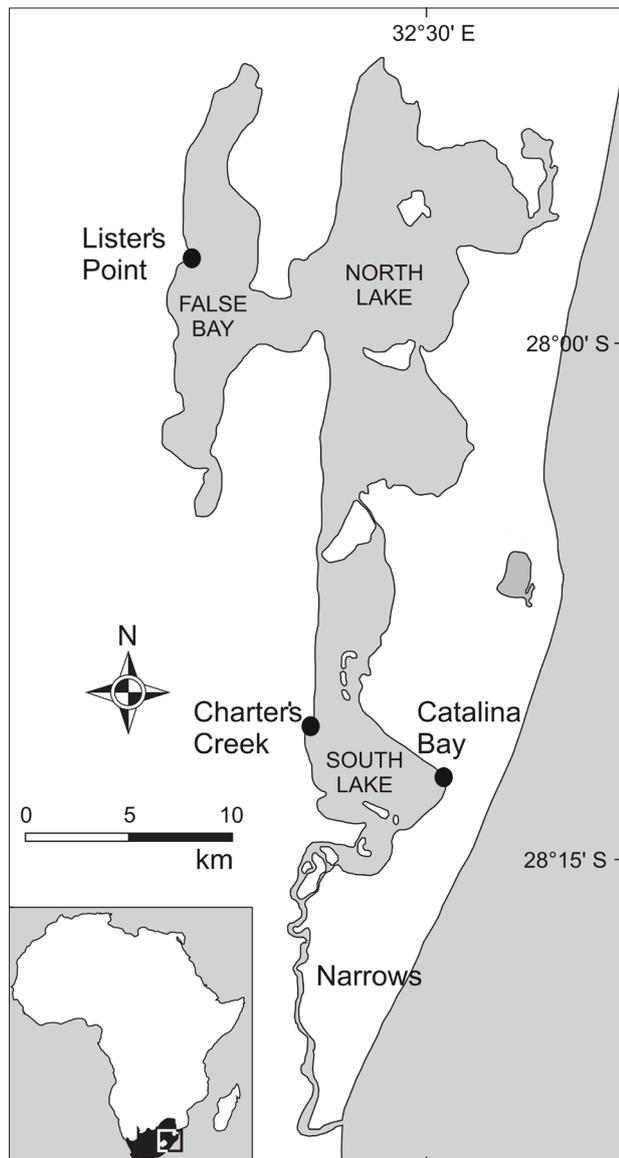


Figure 1: Map of Lake St Lucia. Black dots indicate dedicated sampling sites.

Benthic macrofaunal collections were undertaken on each occasion using a Zabalocki-type Ekman grab (sampling area = 0.0236 m², depth = 150 mm). At each visit, three replicate samples per site were collected, with each sample comprising the content of three grabs pooled together. After a thorough extraction process, involving repeat stirring and filtration, each macrofaunal sample was preserved using 4% formalin.¹³ A survey was also undertaken in November 2015 to assess the prevailing ecological conditions and the densities of the *Meretrix morphina* population during its irruption. Two 1x1-m quadrants were randomly positioned at Catalina Bay, Charter's Creek and Lister's Point. The sediment within each quadrant was extracted to a depth of 150 mm and passed through a 1000- μ m sieve. All bivalves collected on the sieve were preserved in 10% formalin and taken to the laboratory for identification, enumeration and measurement. The dominant species collected were *Brachidontes virgiliae*, *Dosinia hepatica*, *Salmacoma litoralis*, *Solen cylindraceus* and *Tellinides kilburni*.⁶ For each species, individuals of various shell lengths were weighed to determine total fresh weight (shell and wet tissue, g). This measure was used to determine biomass per square metre. Only fresh weight biomass and shell length is reported here to allow for direct preliminary comparisons with previous studies.^{14,15}

Distance-based linear modelling (DISTLM^{16,17,18}) was run in the PERMANOVA package of PRIMER v. 6. This program was used to perform permutational regression (9999 random permutations) to test for linear relationships between *M. morphina* abundance (response) and key environmental variables (temperature, salinity, dissolved O₂ concentration, turbidity, pH, chlorophyll-a, TSS concentrations, lake water level and year – predictors). Data collected when *M. morphina* were present during the years 2010–2015, in the three sampling sites, were included (21 sample points). The response variable (*M. morphina* density) was first converted to a Euclidean distance matrix. A stepwise selection procedure was used, incorporating the corrected Akaike Information Criterion (AICc)¹⁹ as the selection criterion to measure the relative goodness of fit for each model.

Results and discussion

The presence of *M. morphina* in Lake St Lucia and Mlalazi Estuary adds to the growing record of species displaying a poleward migration in South Africa.^{5,20} The southernmost distribution of *M. morphina* was previously recorded as Maputo Bay and Inhaca Island (25°57'S). The new records from St Lucia (28°13'S) and Mlalazi (28°57'S) have now substantially extended this distribution southwards.

Bivalve dominance shifts were previously recorded from St Lucia.⁶ These shifts appear to be related to flood and drought states of the system, more specifically, its associated salinity regime.²¹ St Lucia was previously dominated by *B. virgiliae* during wet phases and by *S. cylindraceus* during the preceding drought phase²² (Figure 2). However, during 2015, instead of the expected irruption of *S. cylindraceus*, *M. morphina* dominated (Figure 2, Table 1). The salinity tolerance range of *S. cylindraceus* is 15–65²³, whereas *M. morphina* was recorded in salinities of 7.5–58.2 during the current study (see also^{24–27}). Both species are euryhaline, but *M. morphina* may have established itself ahead of *S. cylindraceus* during low salinity conditions prevailing during the few years leading up to 2015. Whereas *B. virgiliae* has a sedentary habit and *S. cylindraceus* tends to burrow vertically in the substrate, *M. morphina* burrows vertically and horizontally. The more dynamic burrowing behaviour of *M. morphina* may allow it to better avoid predation, optimise foraging and escape unfavourable environmental conditions.²⁸ The stepwise AICc analysis selected water temperature, salinity, turbidity and total suspended solids as the most parsimonious model explaining a high percentage (80.3%) of the variation in *M. morphina* density (Table 2). Although *M. morphina* can tolerate high salinity, the model indicates that it performs better at lower salinity. An increase in water temperature is expected to raise the metabolism of bivalves, thus influencing activities such as feeding and burrowing. A combination of salinity and temperature affects the growth of *M. morphina*. Thanh and Thung²⁹ reported an optimal combination with salinity of 20 and temperature of 27 °C for the growth of *M. meretrix* juveniles. The highest average biomass of *M. morphina* was recorded at Catalina Bay in 2015, at an average salinity of 24 and temperature of 26 °C (Table 1).

St Lucia *M. morphina* appear to attain greater density and biomass compared with other populations along the African coast.^{13,14} The size and biomass of Maputo Bay populations may be depressed by human harvesting and high pollution levels¹⁴, whereas the St Lucia populations are not harvested and reside within a protected area. Predation pressure may also have been lower in St Lucia as a result of the adverse effect of the drought on fish populations.³⁰ Molluscivorous fish, crustaceans and birds are present in both areas, but their comparative impact on bivalve populations is unknown. Notably, *M. morphina* has a strong shell that is thicker than that of most other bivalves in St Lucia, which may also give it an advantage against certain predators. However, *M. morphina* can reach larger sizes and greater biomass than other dominant bivalves in Lake St Lucia (Figures 3 and 4). The maximum densities attained by *B. virgiliae* were >10 000 ind./m², two orders of magnitude higher than those of *S. cylindraceus* or *M. morphina*. The maximum shell length of *B. virgiliae*²¹ was 25 mm while *S. cylindraceus*³¹ and *M. morphina*⁶ reached lengths of 95 mm and 70 mm, respectively. Based on estimated values, *M. morphina* fresh weight biomass during 2015 was 1909.8 g/m² at Catalina Bay (Table 1).

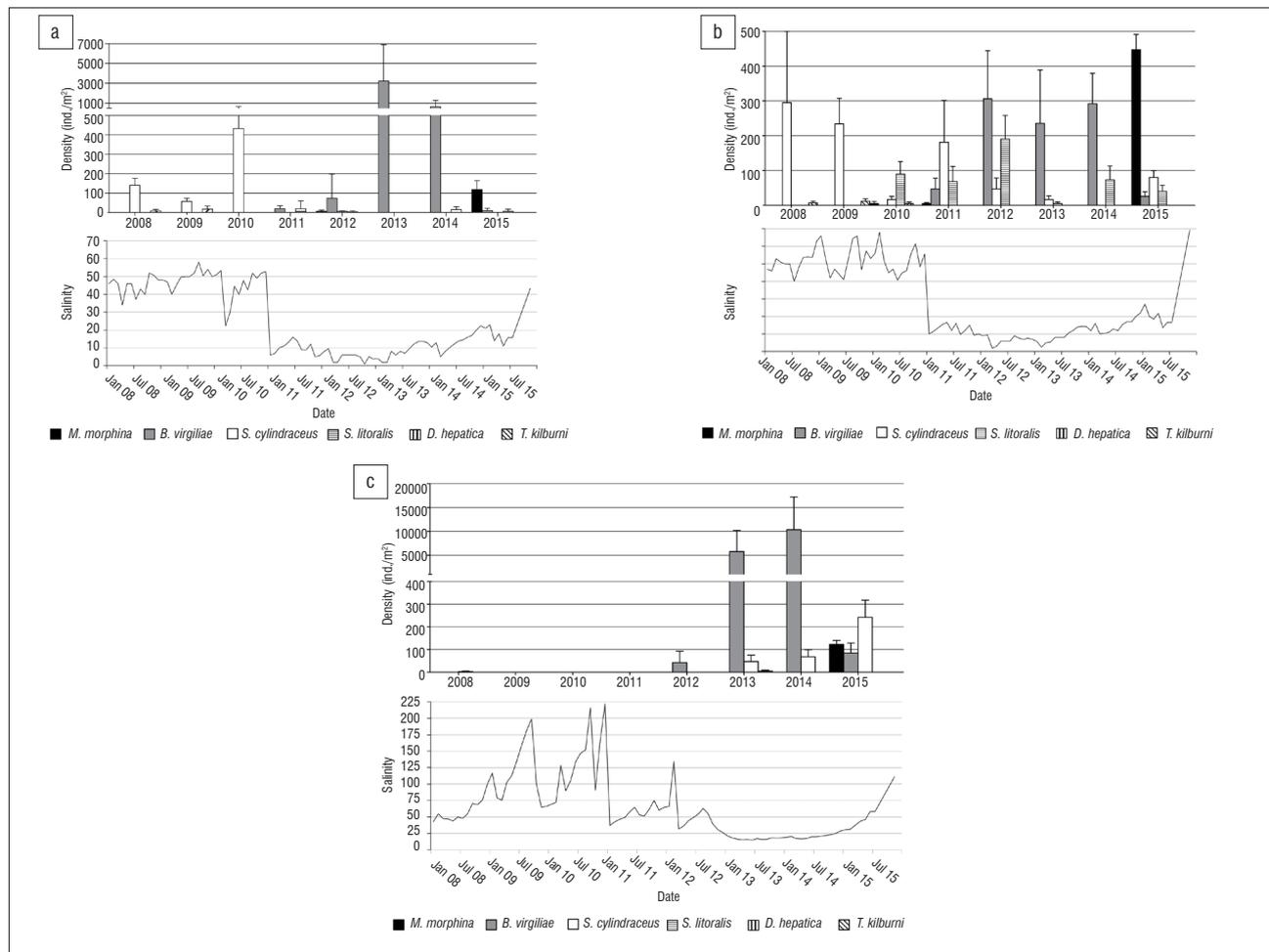


Figure 2: Population density (ind./m²) of bivalves (*Meretrix morphina*, *Brachidontes virgiliae*, *Dosinia hepatica*, *Salmacoma litoralis*, *Solen cylindraceus* and *Tellinides kilburni*) and average salinity at (a) Catalina Bay, (b) Charter's Creek and (c) Lister's Point from 2008 to 2015. Error bars show s.e. Samples were collected by Ekman grab.

Table 1: The estimated density, shell length and fresh weight biomass (mean±s.d.) of *Meretrix morphina* at three sites within Lake St Lucia in 2015

	Temperature (°C)	Salinity	Turbidity (NTU)	Total suspended solids (mg/L)	Density (ind./m ²)	Shell length (mm)	Biomass (g/m ²)
Catalina Bay	26.39	23.59	3.73	93.6 ± 3.8	117.8 ± 46.1	38 ± 11	1909.8 ± 1037.5
Charter's Creek	24.97	30.94	16.42	102.5 ± 26.9	447.3 ± 106.9	29 ± 15	215.5 ± 263.0
Lister's Point	23.82	61.47	206.325	229.3 ± 119.4	122.4 ± 43.2	20 ± 10	195.5 ± 27.0

Table 2: Distance-based linear model of *Meretrix morphina* abundance (response) against environmental variables (predictors) measured in Lake St Lucia from 2010 to 2015. Sequential tests for stepwise model ($r^2 = 0.80$), and percentage of multivariate flux variation explained by the model are presented. The most parsimonious model includes water temperature (°C), salinity, turbidity (NTU) and total suspended solids (TSS, mg/L).

Model	AICc	SS (trace)	Pseudo - F	P	Prop.	Cumul.	res. df
Temperature	210.8	1.25650	6.20	0.021	0.246	0.2460	19
Temperature + TSS	207.56	95381	5.93	0.028	0.187	0.433	18
Temperature + TSS + Salinity	206.43	52677	3.78	0.068	0.103	0.536	17
Temperature + TSS + Salinity + Turbidity	191.95	1.36200	21.68	0.001	0.267	0.803	16

Relationship between dbRDA coordinate axes and orthonormal X variables (multiple partial correlations)

Axis	Explained variation out of fitted model (%)	Explained variation out of total variation (%)	Temperature	TSS	Salinity	Turbidity
1	100	80.3	0.649	0.631	-0.338	0.257

Recruits, juveniles and large *M. morphina* adults were present in 2015 (Figure 3), indicating that the population was healthy and growing. However, at the end of 2015, as lake levels dropped and hypersaline conditions developed, the population was stranded and exposed to sudden desiccation. Thus, there was mass mortality of *M. morphina* (Figure 5). During this time, large flocks of birds, including seagulls and cormorants, were seen feeding on stranded *M. morphina* (personal observation). In 2016, this species was not detected in St Lucia. However, *M. morphina* may irrupt again in future.

High densities of *M. morphina* can play an important ecological role in becoming major consumers of suspended organic matter¹⁵ and their presence may be correlated with patterns of suspended particle loads and turbidity (Tables 1 and 2). However, the feeding behaviour of these clams is influenced by time of day, habitat type, food concentration,

salinity and body size, among other factors.^{15,32} Further studies, including comparative feeding analyses among different bivalve species, are needed to accurately address the effects of *M. morphina* on resident taxa and the environment.

While *M. meretrix* has been studied because of its commercial value^{32,33}, there is a substantial lack of knowledge regarding the ecology of *M. morphina*. In Lake St Lucia, *M. morphina* appears to thrive under brackish salinities and high temperatures. It is able to establish large populations with high biomass and can become one of the most dominant bivalve species in the system. However, like many other sympatric bivalves, *M. morphina* is sensitive to exposure to desiccation and hypersaline conditions. As the distribution range of *M. morphina* expands, further studies are needed to assess its ecological interactions in new habitats.

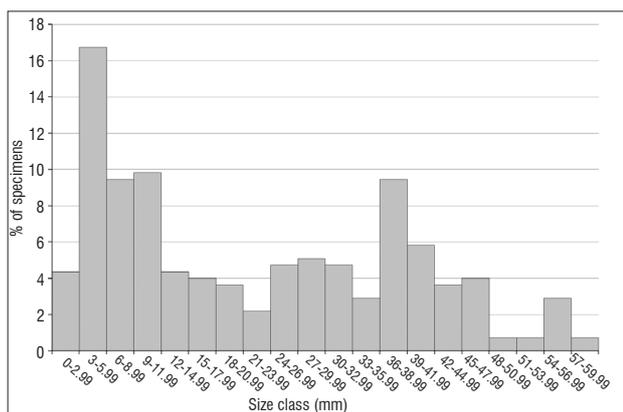


Figure 3: Size class distribution (n=275) of *Meretrix morphina* in Lake St Lucia in November 2015.

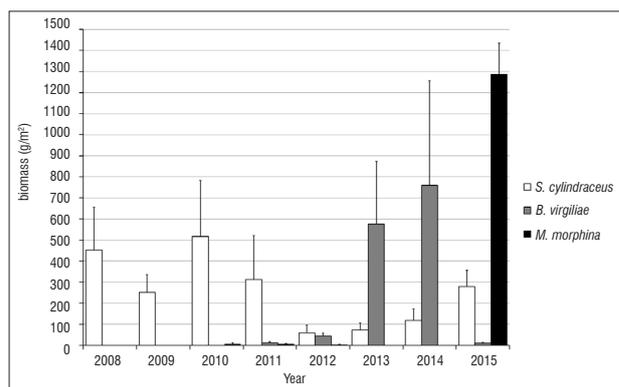


Figure 4: Estimated average biomass (fresh weight, g/m²) of *Solen cylindraceus*, *Brachidontes virgilliae* and *Meretrix morphina* in Lake St Lucia between 2008 and 2015. Error bars show s.e.



Photo: Lynette Clennell

Figure 5: Dense aggregations of exposed and dying *Meretrix morphina* clams, while water levels receded and hypersaline conditions became re-established around Catalina Bay, Lake St Lucia, in November 2015.

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Authors' contributions

N.A.F.M., N.P., R.P. and N.K.C. were the project initiators and coordinators and were responsible for sampling design, compilation of data and the manuscript write-up; R.P., N.A.F.M., N.P., N.K.C., S.J., R.H.T. and C.F. were responsible for sample collection and analysis and the manuscript write-up.

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