

Rapid Communication

The porcelain crab *Porcellana africana* Chace, 1956 (Decapoda: Porcellanidae) introduced into Saldanha Bay, South Africa

Charles L. Griffiths^{1,*}, Selwyn Roberts¹, George M. Branch¹, Korbinian Eckel²,
Christoph D. Schubart² and Rafael Lemaitre³

¹Centre for Invasion Biology and Department of Biological Sciences, University of Cape Town, Rondebosch 7700, South Africa

²Zoology and Evolution, University of Regensburg, D-93040 Regensburg, Germany

³Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, 4210 Silver Hill Road, Suitland, MD 20746, USA

Author e-mails: Charles.griffiths@uct.ac.za (CLG), selwyn.roberts@ymail.com (SR), mbranch@mweb.co.za (GMB), korbinian.e@web.de (KE), Christoph.Schubart@biologie.uni-regensburg.de (CDS), lemaitrr@si.edu (RL)

*Corresponding author

Received: 10 January 2018 / Accepted: 3 April 2018 / Published online: 26 April 2018

Handling editor: April Blakeslee

Abstract

The porcelain crab *Porcellana africana* Chace, 1956, a species native to NW Africa, between Western Sahara and Senegal, is reported from Saldanha Bay, South Africa, and both morphological evidence and DNA analysis are used to confirm its identity. The taxonomic history of *P. africana* is summarized, and the taxonomic implications of the DNA analysis are discussed. The observations that the South African population appeared suddenly and that it is located in and around a major international harbour, strongly suggest that it represents a recent shipping introduction. *Porcellana africana* was first detected at a single site within Saldanha Bay in 2012, but by 2016 was abundant under intertidal boulders and within beds of the invasive mussel *Mytilus galloprovincialis* across most of the Bay. It remains absent along the adjacent oceanic coastline and in other regional harbours, but these should be monitored to detect any subsequent range expansion.

Key words: Anomura, invasive species, rocky shores, taxonomy, DNA analysis

Introduction

Several fairly recent reviews have outlined the history of marine bioinvasions in South Africa (Griffiths et al. 2009), or have listed the introduced marine species reported from the region and discussed various aspects of their status, distribution patterns, areas of origin, and/or possible impacts (Mead et al. 2011a, b; Robinson et al. 2016). The most recent regional listing by Robinson et al. (2016) recognises 53 marine species as invasive (those that have spread significantly from their initial points of introduction), plus 36 additional species as alien (those that have not yet spread significantly). Three decapod crustaceans are among the listed introductions. Two of these are considered invasive, these being the European shore crab *Carcinus maenas* (Linnaeus, 1758), which has

spread between (but remains almost entirely confined to) two harbours in the Cape Town area (Hampton and Griffiths 2007; Mabin et al. 2017) and the pea crab *Pinnixa occidentalis* Rathbun, 1894, which is spreading within the Saldanha Bay system (Clark and Griffiths 2012). The third introduced decapod, the furrowed crab *Xantho hydrophilus* (Herbst, 1790) (reported as *X. incisus*), is categorised as alien, as it is known only from a single record within an onshore oyster culture facility at Kleinzee, on the Atlantic coastline of the Northern Cape province (Haupt et al. 2010).

Prior to this study, the only anomuran crustacean reported as introduced in South Africa was a checklist entry by Emmerson (2016: 446) of the European porcelain crab *Porcellana platycheles* (Pennant, 1777), which he listed, without further comment, as a “new

invasive alien". Emmerson's report was in fact based on specimens collected by one of us (GMB) from Saldanha Bay in 2012 (as detailed further below). Based on this same record, and on early drafts of this paper, the species is also reported, now correctly as *P. africana* Chace, 1956, in the most recent edition of a regional field guide (Branch et al. 2016), but again without supporting evidence. Subsequent surveys of Saldanha Bay have revealed that this population is now abundant and well established. The aim of this paper is thus to report in more detail on the true identity and likely origins of this non-native porcelain crab, and to benchmark the current distribution, density and structure of the introduced population in South Africa.

Taxonomic background

Prior to the discovery documented here, only five other species from the family Porcellanidae had been reported in South Africa (Emmerson 2016), but most of these have subtropical distributions and only one, *Pisidia streptocheles* (Stimpson, 1858), is known from temperate regions of the country, including the cool-temperate west coast (see Barnard 1950; Kensley 1981, both as *Porcellana streptocheles*). *Pisidia streptocheles* is, however, unlikely to be confused with species in the genus *Porcellana*, as its body is not pubescent, the chelae are not strongly flattened, and the inner apex of the merus is produced into a distinctive, strong, square-truncated tooth.

The porcelain crab, *Porcellana platycheles* is a small, pubescent anomuran with large, flattened chelae and is usually found clinging to the underside of rocks in the intertidal zone. Its range has historically been considered to include the European Atlantic shores and Mediterranean Sea, with an extralimital occurrence in the Canary Islands (e.g., Bouvier 1940 and references therein). Chace (1956), however, subdivided *P. platycheles* into two subspecies, a northern subspecies *P. platycheles platycheles*, distributed on the European coasts and the Canary Islands, and a new, southern subspecies, which he described as *P. p. africana*, and which was distributed intertidally to a depth of 22 m along the coast of northwestern Africa, from Western Sahara to Senegal. Chace examined only two specimens of what he considered *P. p. platycheles* from the Canary Islands. Chace (1956: 24–30, Figure 7) differentiated the two subspecies primarily based upon the presence of three distinct spines on the outer margin of the carpus (in addition to a distal spine) of the major cheliped in *P. p. platycheles*, whereas no such spines (other than the outer distal spine) were present on the outer margin of the carpus in *P. p. africana*. He also noted

that the southern subspecies was less spinose and more tuberculate and rugose beneath the hairy covering than was the northern subspecies. Chace's southern subspecies has not been reported since his original description. The subspecific division of *P. platycheles*, however, has seldom been used, as most taxonomic and other works continued to report the European and Mediterranean taxon using the specific rank, *P. platycheles* (e.g., Zariquiey 1968; Davenport 1972; Türkay et al. 1987; García-Raso 1990; Hayward and Ryland 1990; López de la Rosa and García Raso 1992; González-Gordillo et al. 1996). Even reports of new specimens from the Canary Islands used that same species rank (Fransen 1991; González Pérez 1995). It was d'Udekem d'Acoz (1999) who considered the two subspecies of *P. platycheles* proposed by Chace (1956) to be sufficiently distinct to justify elevating them to specific rank, and that ranking has been accepted since (Osawa and McLaughlin 2010; WoRMS Editorial Board 2017). A single specimen described from the coast of Brazil, as *P. paivacarvalhoi* Rodrigues da Costa, 1968, was also considered by Veloso and de Melo (1993) and subsequent Brazilian catalogues (Young 1998; Melo 1999) as a junior synonym of *P. platycheles*. However, Rodríguez et al. (2005) questioned the single Brazilian record of this European species from the western Atlantic, and thus excluded it as a component of the porcellanid fauna from that region. This record might, however, represent another introduction and merits further investigation. In summary, it seems that both *P. platycheles* and *P. africana* should be considered as valid species and we treat them as such in this paper.

Methods

Identification and DNA analyses

Two males and two female specimens collected in Saldanha Bay were preserved in ethanol and sent to one of us (RL) for more thorough identification and comparison with paratypes of *P. platycheles africana* (Figure 1), and these have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington DC, USA (USNM 1292094). Two additional specimens were also sent to CDS and KE at the University of Regensburg, Germany, where they were sequenced and compared with samples of *P. platycheles* from both the Mediterranean Sea and the European coast of the Northern Atlantic.

The sequenced samples have been deposited in the Senckenberg Museum, Frankfurt under catalogue number SMF-50858. Representative samples of the material collected in Saldanha Bay have also been deposited in the Iziko South African Museum, Cape



Figure 1. Left: dorsal and ventral views of male paratype of *Porcellana platycheles africana* (partially denuded), carapace width 8.9 mm, Western Sahara, collected 2 Nov 1935, USNM 98968. Right: dorsal and ventral views of male specimens 8 mm carapace width, collected from Saldanha Bay, May 2016. Photos by Amanda Wilson (left) and Charles Griffiths (right).

Table 1. Data for specimens of *Porcellana platycheles* and *P. africana* used for genetic analysis.

| Locality/species | Specimens examined | Geographic coordinates | Collection date |
|--|--------------------|------------------------|-----------------|
| <i>P. platycheles</i> Spain, Alicante | 16 | 38.686389; 0.1475 | 2011 and 2015 |
| Turkey, Izmir | 10 | 38.328611; 26.295694 | 2015 |
| France, Normandy | 11 | 48.910167; -1.570367 | 2012 |
| <i>P. africana</i> Spain, Gran Canaria | 18 | 27.907; -15.38 | 2015 |
| Saldanha Bay, South Africa | 2 | 33.61962; 18.15709 | 2016 |

Town, South Africa (SAMC) under catalogue numbers MB-A067556 (preliminary August 2015 sample) and MB-A067557-60 (main May 2016 survey samples).

DNA analyses were undertaken for material listed in Table 1. DNA-extraction was performed with a Puregene Kit (Gentra Systems: Minneapolis, MN55447, USA), using muscle tissue from walking legs or chelae. The selective amplification of an approximately 850 basepair fragment from the cytochrome oxidase

subunit I (COI) gene was carried out by polymerase chain reaction (PCR) (40 cycles; 45 s 95 °C / 60–90 s 45–48 °C / 90 s 72 °C; denaturing/annealing/extension temperatures) with the forward-degenerate primer COL6b (Schubart and Huber 2006; ACAATCATAA AGATATYGG) and the reverse degenerate primers COH1b (Schubart 2009; TGTATARGCRTCTGG RTARTC) or COH3 (Reuschel and Schubart 2006; AATCARTGDGCAATWCCRSCRAAT). DNA

sequencing was carried out as EZ-sequencing by MacroGen Europe, Inc. (The Netherlands). Sequences were edited manually with the program Chromas Lite Version 2.1.1 (Technelysium Pty Ltd) and aligned without gaps in BioEdit version 7.2.5 (Hall 1999). Haplotype networks were created with the TCS-method (Clement et al. 2002) and saved as graphics with the program PopART (Leigh and Bryant 2015). Accession numbers for these samples are GenBank MH045618–MH045674.

Distribution, density and population structure

The distribution pattern, abundance and sex and size distributions of the intertidal *P. africana* population in Saldanha Bay were assessed based on a suite of intertidal samples collected between May and July 2016, following the methods detailed by Robinson et al. (2004), who surveyed this same area for alien species in 2003. In summary, the coastline of Saldanha Bay and Langebaan Lagoon was divided into 2-km sections and one intertidal transect was carried out randomly within those sections that contained suitable rocky shore habitat and that could be accessed. Many of the 2-km sections within the Langebaan Lagoon section consist exclusively of soft mud, which is not a suitable habitat for *P. africana*, and these sites were not surveyed, while a few sections could not be sampled, as they house military or port facilities to which we were denied security access.

To assess whether *P. africana* was present at other sites in the region, additional surveys were carried out at nearby locations on the open coast outside the Bay, as well as around the Cape Peninsula, about 100 km to the south, and in Table Bay Harbour, Cape Town, which is the closest other major international harbour.

Surveys were conducted at Low Water of Spring Tides (LWS). At each transect site the intertidal zone between the drift-line and LWS was divided into 20-cm height strata and, if present, any boulders within an area of 1 m² were turned over and inspected for porcelain crabs. If there were no boulders, three 0.1 m² quadrats were placed on the rock and any attached fauna (principally mussels and barnacles) that could be concealing crabs was scraped off and searched. All porcelain crabs found were placed in labelled jars and subsequently counted, sexed (on the basis of pleopod structure and position), and their carapace widths measured using Vernier callipers. Based on the width of each intertidal stratum in metres, we subsequently calculated the total numbers of porcelain crabs per linear metre of rocky shoreline within each coastal section.

Results

Identification and origin

Figure 1 shows a male specimen of *Porcellana africana* from Saldanha Bay alongside a largely denuded paratype of Chace's (1956) *P. platycheles africana*. A comparison of our specimens from Saldanha Bay with Chace's (1956) paratypes of *P. p. africana*, showed that they agree morphologically and thus we believe represent what is currently considered a full species, *P. africana*.

Identification based on morphological characteristics was supported by genetic evidence. A TCS network based on an 850 bp long alignment (Figure 2) shows the two South African individuals (green) examined as fitting most closely to those from the Canary Islands (white), and differing considerably from individuals of *P. platycheles* from the Mediterranean Sea and the European coast of the Northern Atlantic (red, blue and yellow). This supports the morphological comparisons and suggests that the specimens from South Africa and the Canary Islands both represent *P. africana*, while the other specimens in the network from Europe, including the Mediterranean Sea, correspond to *P. platycheles*. The large number of mutational steps between the two validates their distinction as separate species.

Distribution, density and population structure

Porcellana africana specimens were found at eight sites around the perimeter of Saldanha Bay (Figure 3), but were absent from Langebaan Lagoon, most likely due to lack of suitable rocky shore habitat in this sheltered, muddy lagoon. The sites where populations were established were distributed around the northern, eastern and western shores of the Bay, but excluded the site closest to the mouth of the Bay and that furthest into the Lagoon, although both of these sites appeared to contain ample suitable boulder habitat. Populations were present not only on boulder shores, where the crabs congregated under loose rocks, but also in areas where the shore comprised large, smooth granite boulders and platforms devoid of loose rocks. There the crabs were found sheltering within dense beds of the introduced mussel *Mytilus galloprovincialis*, which is abundant on rocky shores throughout this region (Robinson et al. 2004) and greatly increase habitat complexity, providing habitat for multiple species (Sadchatheeswaran et al. 2015).

Additional surveys were undertaken on the open coast at Tsaarsbank, just to the south of Saldanha Bay and at Jacob's Bay and Paternoster, about 10 and 25 km north of the entrance to the Bay respectively,

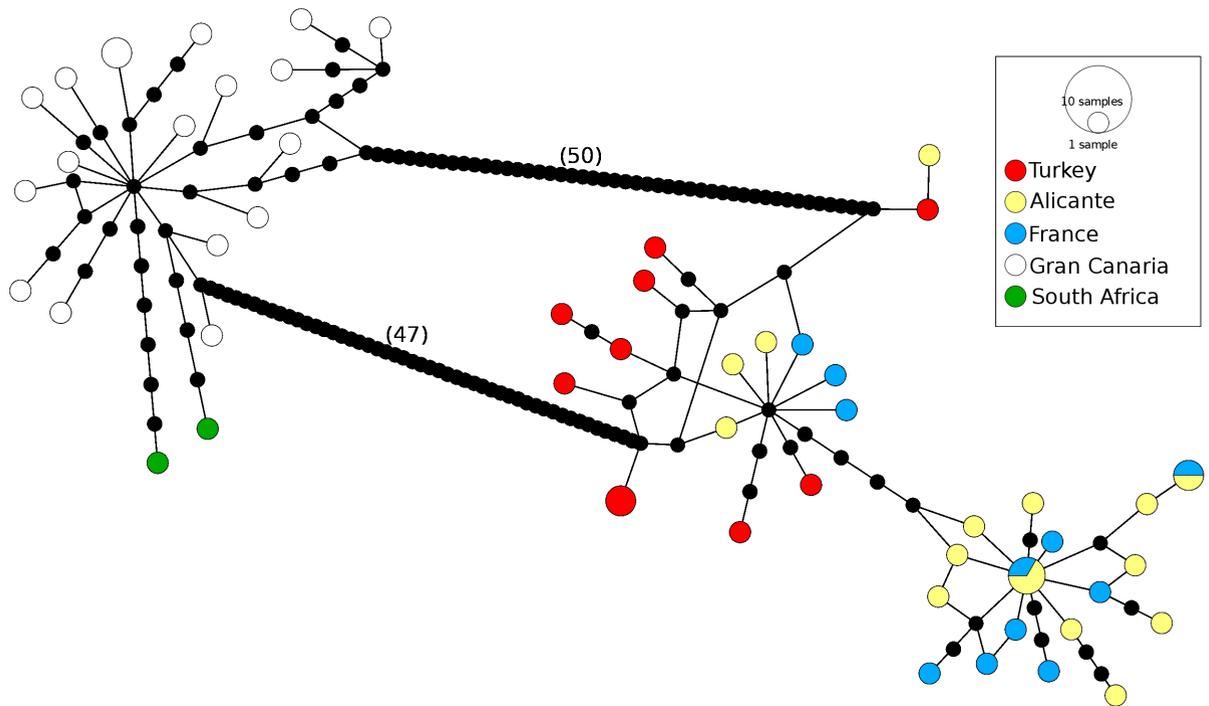


Figure 2. COI haplotype network based on an 850 bp alignment, highlighting that specimens from Saldanha Bay (South Africa, green dots) correspond most closely to specimens of *P. africana* from the Canary Islands (white dots) rather than to *P. platycheles* from Turkey and the European mainland. Black dots symbolize mutational steps in undetected haplotypes. Numbers in brackets indicate numbers of mutational steps between specimens from South Africa and the Canary Islands, and those from the European mainland.

but no *Porcellana* specimens were found at any of these sites, nor were any seen during numerous recent collecting trips by CLG to the open coastlines of Table Bay and False Bay, or along the shores of the Cape Peninsula, some 100 km to the south, nor in Table Bay Harbour.

The size composition of the sample of 100 individuals at Schaapen Island in 2012 was bimodal, with a large peak at 3 mm and a much smaller one at 10 mm and a full range of size classes present, the smallest being 1 mm carapace width, and the largest a single exceptionally large male of 14 mm. Of the total of 223 individuals collected in 2016, 110 were males and 113 were females, giving a sex ratio of 1:1. The size distribution of the sampled population (Figure 4) was unimodal and showed males to be on average about 1 mm larger than females, the largest male being 10 mm and the largest female 9 mm. The most abundant size classes were 6–7 mm for males and 5–6 mm for females. Only three of the sampled females (of 6, 7 and 7 mm carapace width respectively) were ovigerous at the time of sampling.

Extrapolating from the densities in these subsamples, total population densities on rocky shores

within Saldanha Bay in 2016 were estimated as ranging from 15 to as many as 976 crabs per linear metre of rocky shoreline. In terms of intertidal distribution, crabs were widely distributed across the intertidal zone from 20 cm below LWS (the lowest level sampled) to 60–80 cm above LWS, approximately representing mid-tide level. Maximum densities occurred in the zone 20–40 cm above LWS and dropped evenly both above and below this zone.

Discussion

Identification, origin, and taxonomic implications

The genetic evidence presented in this study clearly points to the existence of two distinct species, *P. platycheles* and *P. africana*. The morphological evidence, although valid, is less conclusive, as considerable variation and overlap is now known to occur in the characters proposed by Chace (1956) to separate the two taxa. In fact, Chace's report of *P. platycheles* (as subspecies *P. p. platycheles*) from the Canary Islands needs reevaluation in light of our finding that the specimens analysed herein from the Canary Islands

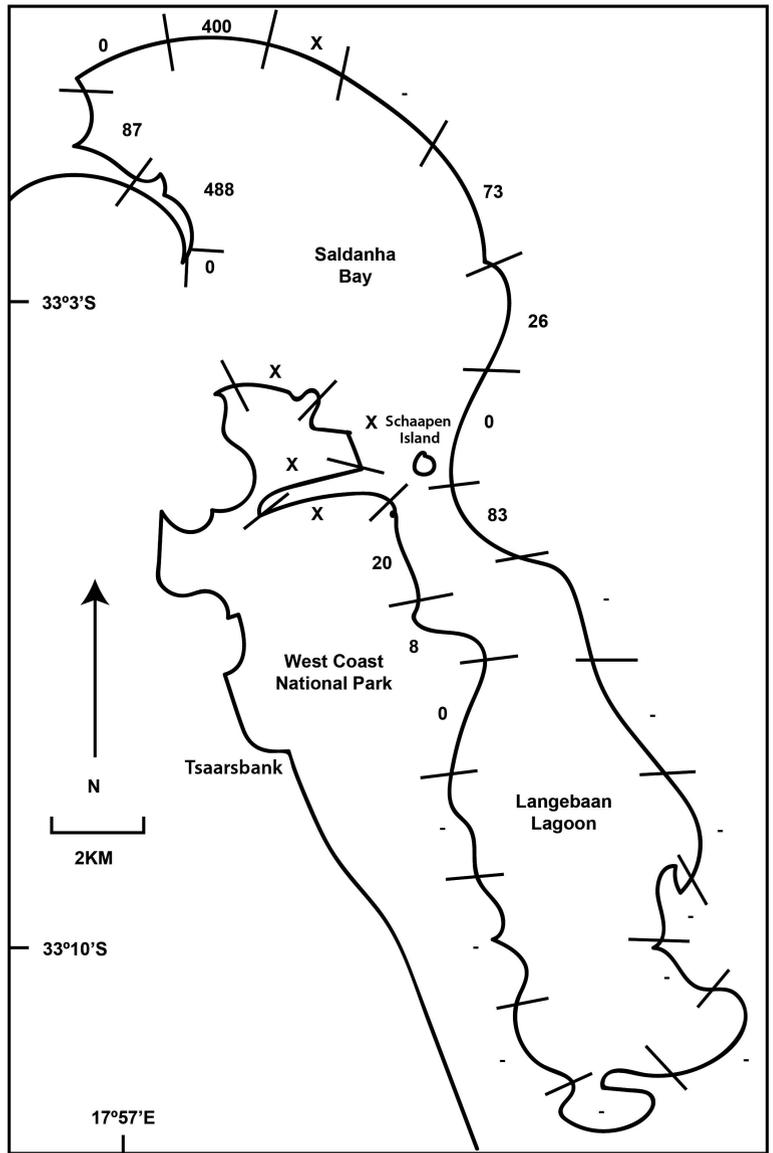


Figure 3. Saldanha Bay and Langebaan Lagoon with coastline divided into 2-km sections assessed for *Porcellana africana* abundance. Sections marked with a dash contained no suitable rocky substrata. Those with numbers indicate average densities of *P. africana* per linear m rocky shoreline. Those marked X are security areas to which we were unable to gain access.

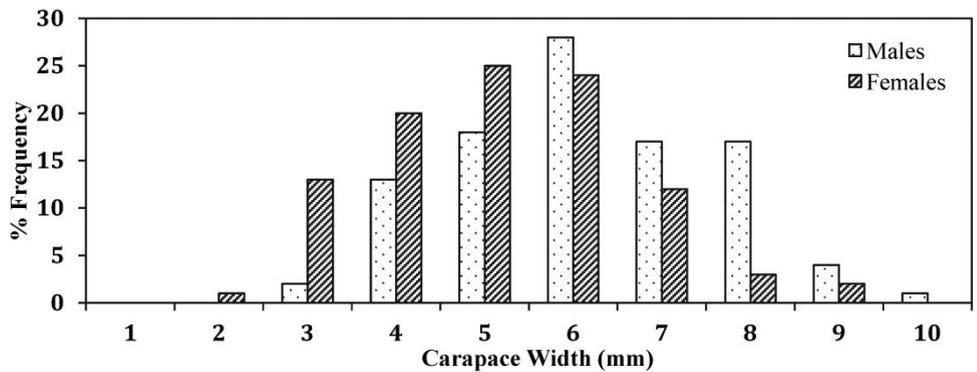


Figure 4. Size-frequency distribution of 233 *Porcellana africana* sampled from Saldanha Bay in 2016.

are genetically different from European and Mediterranean specimens, and instead are conspecific with the South African specimens of *P. africana* from Saldanha Bay. The fact that the South African specimens differ by several mutational steps from the Canary Island specimens also suggests that the source population for the South African invasion may have originated from another (unsampled) location, possibly on the west African mainland, or that we missed populations in our sampling of the genetically diverse Canary Islands that are more genetically similar to the individuals we detected in South Africa.

Since the marine fauna of West Africa remains very poorly sampled, it could be argued that the arrival of *P. africana* in South Africa might represent a natural range extension of a widespread tropical African population. However, this seems highly unlikely, as (a) this would represent a range expansion of some 6,300 km from the nearest known populations, (b) the species has not been detected during other rocky intertidal surveys along the coasts of southern Angola (Kensley and Penrith 1973), Namibia (Penrith and Kensley 1970a, b), or along the west coast of South Africa (e.g. Hammond and Griffiths 2006; Robinson et al. 2007; Tucker et al. 2017), and (c) the current records are restricted to a major international bulk cargo port. Saldanha Bay is also home to numerous other marine invasive species (Robinson et al. 2004; Mead et al. 2011a, b), including the brachyuran crab *Pinnixa occidentalis*, recently recorded as being introduced to just this one bay (Clark and Griffiths 2012).

The most probable mode of introduction of *P. africana* seems to be shipping, in particular introduction of larvae via ballast water, or of adults in niche areas on the hulls of vessels, as the introduction site is a major international harbour, frequented mostly by bulk carriers. These vessels were reported to discharge nearly 20 million tonnes of ballast water into the harbour between January 1999 and June 2002 (Awad et al. 2003). The discharging vessels at that time originated from no less than 131 source ports, the largest number of these being in Europe and Asia, but including Las Palmas (Canary Islands) and several ports in West Africa (Awad et al. 2003), one of more of which could have served as source for this species.

The date of introduction of *P. africana* can also be estimated, based on the date of first discovery and that of earlier surveys. The first specimens were collected in South Africa by one of us (GMB) on Schaapen Island, Saldanha Bay in April 2012. At that time the population was already well established

($n = 100$ were collected) and comprised animals of a range of sizes up to 14 mm carapace width, indicating that the population must have been extant for at least 2–3 years. Prior to that sample, a previous survey of alien marine species of Saldanha Bay had been undertaken by Robinson et al. (2004). They sampled intertidal sites all around the Bay during 2003 and it would have been most unlikely that they would have failed to detect this unusual and easily recognised species, had it been present at that time. The date of first successful establishment can thus be confidently estimated as being between 2003 and 2009.

Local distribution, density and population structure

Although *Porcellana africana* was first found in the study area in 2012, no attempt to quantify density or distributional range was made until 2016. By that time the species was found living in considerable densities of up to nearly 1000 individuals per linear metre of shore on suitable sites around Saldanha Bay (the equivalent of > 100 per m^2 at some sites). Interestingly though, it was absent nearest the mouth of the Bay and at sites along the open coastline both north and south of the Bay (Figure 3). Neither has it been recorded in recent surveys of invasive species in other harbours around the region (Peters et al. 2014), nor in recent surveys of boulder shores (its favoured habitat) undertaken by Tucker et al. (2017) at several sites along the SW coastline of South Africa. Also none were seen on the open coastline during recent (2016–2018) survey work at numerous sites in both False Bay and Table Bay (CLG, pers. obs.). We thus deduce that this invasive species is currently restricted to Saldanha Bay.

Measures of population density and of size structure indicate that the invasion is well established, comprising a dense population containing a full range of size-classes. In addition, the occurrence of many individuals in the size class 1–2 mm and the bimodality of samples taken at Schaapen Island in 2012 suggest that reproduction and recruitment was already taking place in the area at that date. By 2016, this species had become one of the more abundant and conspicuous intertidal crustaceans in Saldanha Bay. We did not extend our survey significantly into the subtidal, for logistical reasons, but consider *P. africana* to be primarily intertidal, although the known depth range extends to 22 m (Chace 1956). According to field guides, the ecologically equivalent European species, *P. platycheles*, is also “primarily intertidal” (e.g. Gibson et al. 2001). Our own observations for *P. africana* in Saldanha Bay and from the Canary Islands confirm this, and show

maximum densities to occur 20–40 cm above LWS with a sharp decline in densities occurring at the lowest level sampled, which was from LWS to 20 cm below LWS.

This is the first recorded occurrence of an invasive porcelain crab in South Africa (Robinson et al. 2016), and indeed, this group is poorly represented among the numerous marine crustaceans reported as being alien or invasive globally (Galil et al. 2011). The only porcelain crabs we are aware of as being invasive are *Petrolisthes elongatus* in Australia and *P. armatus* (Gibbes, 1850) in the southern USA.

Petrolisthes elongatus (Milne-Edwards, 1837) is native to New Zealand, but has been introduced to Tasmania and Victoria, Australia, where it occurs under stones in the low intertidal and on shallow reefs. Little appears to be known about the impacts of this invasion, although invasive populations attain higher abundances in the mid-low intertidal, and attain higher male (but not female) biomass than that reported in the native range (Gribben et al. 2013).

Petrolisthes armatus appears to have a broad native range in both tropical Atlantic and Pacific Oceans (Hiller and Lessios 2017), but has recently expanded into Georgia and South Carolina, where it has become extremely abundant, reaching densities of 4 000–11 000 crabs m⁻² in some locations (Hollebone and Hay 2007). At these high densities, both mesocosm and field experiments have shown that the species may have numerous ecological impacts, including suppressing the growth of small oysters, the biomass of benthic microalgae and recruitment of mud crabs (Hollebone and Hay 2008). It also has a variety of impacts on trophic relationships, including acting as prey for native crabs (Wassick et al. 2017).

Ecological impacts of the invasion of *Porcellana africana* in Saldanha Bay, South Africa, as reported here, remain unquantified. Members of this genus are cryptic filter feeders that may also pick up detrital particles (Stevcic 1988) and it thus seems unlikely that the current population would have dramatic impacts on other benthic invertebrates, or in terms of forming a major prey item for predatory fish. However, the current density remains more than an order of magnitude lower than that reported for invasive *Petrolisthes armatus* in the southern USA (Hollebone and Hay 2007), and may thus still be well below saturation level. The population should thus be monitored to assess whether it is increasing in density, as well as to determine whether the species expands onto the open coastline, or colonises other suitable harbours in the region. Experimental studies could also be undertaken to determine its impacts on other invertebrates with which it shares

habitat, and stomach contents analysis could determine whether it is being consumed by predators such as intertidal fish or shore birds.

Acknowledgements

Financial support for this study was provided by a grant to CLG from the NRF/DST Centre of Excellence for Invasion Biology. A permit for collection of these specimens was issued jointly by the South African Department of Environmental Affairs and Department of Agriculture, Forestry and Fisheries and collection procedures were approved by the University of Cape Town Animal Ethics Committee. We thank SANParks for permission to sample in the West Coast National Park and Pierre Nel for facilitating access to the study sites. Donia Wozniak and Kim-Kelly Hunt kindly assisted us with field surveys. RL thanks CHJM Fransen (Naturalis Biodiversity Center, Leiden), for his help in obtaining important information on Dutch expeditions that included the Canary Islands, and cruise reports and A. Wildson for helping taking photographs of the paratype of *P. p. africana*. Our sincere thanks also to the three anonymous reviewers whose insightful suggestions greatly improved the final published version of this paper.

References

- Awad A, Clarke C, Greyling L, Hillard R, Polglaze J, Raaymakers S (2003) Ballast Water Risk Assessment: Port of Saldanha Bay, Republic of South Africa. Globallast Monograph Series No. 13. IMO, London, 131 pp
- Barnard KH (1950) Descriptive catalogue of South African decapod Crustacea (crabs and shrimps). *Annals of the South African Museum* 38: 1–837
- Bouvier E-L (1940) Décapodes marcheurs. Faune de France, Paris 37: 1–399, pls 1–14
- Branch GM, Griffiths CL, Branch ML, Beckley LE (2016) Two Oceans: A Guide to the Marine Life of southern Africa, 4th edition. Struik Nature, Cape Town, 446 pp
- Chace FA (1956) Expédition océanographique Belge dans les eaux côtières africaines de l'Atlantique Sud (1948–1949). *Résultats scientifiques* 3(5): 17–43
- Clark BM, Griffiths CL (2012) Western Pea Crabs *Pinnixa occidentalis* Rathbun 1894 (Brachyura: Thoracotremata: Pinnotheroidea) invade Saldanha Bay, South Africa. *African Journal of Marine Science* 34: 153–156, <https://doi.org/10.2989/1814232X.2012.675128>
- Clement M, Snell Q, Walke P, Posada D, Crandall K (2002) TCS: estimating gene genealogies. Proceeding 16th International Parallel Distributed Processing Symposium, IEEE: 184, <https://doi.org/10.1109/IPDPS.2002.1016585>
- Davenport J (1972) Salinity tolerance and preference in the porcelain crabs, *Porcellana platycheles* and *Porcellana longicornis*. *Marine Behaviour and Physiology* 1: 123–138, <https://doi.org/10.1080/10236247209386893>
- D'Udekem d'Acoz C (1999) Inventaire et distribution des crustacés décapodes de l'Atlantique nord-oriental, de la Méditerranée et des eaux continentales adjacentes au nord de 25°N. *Patrimoines naturels (MNHN/SPN)* 40: i–x, 1–383 pp
- Emmerson WD (2016) A Guide to, and Checklist for, the Decapoda of Namibia, South Africa and Mozambique (Volume 3). Cambridge Scholars Publishing, Newcastle upon Tyne, 711 pp
- Fransen CHJM (1991) Crustacea of the CANCAP and MAURITANIA expeditions. Nationaal Natuurhistorisch Museum, Leiden: 1–200
- Galil BS, Clark PF, Carlton JT (2011) In the Wrong Place - Alien Marine Crustaceans: Distribution, Biology and Impacts. Springer, Dordrecht, 716 pp, <https://doi.org/10.1007/978-94-007-0591-3>
- García-Raso JE (1990) Study of Crustacea Decapoda taxocoenosis of *Posidonia oceanica* beds from the southeast of Spain. *Marine Ecology* 11: 309–326, <https://doi.org/10.1111/j.1439-0485.1990.tb00386.x>

- Gibson R, Hextall B, Rogers A (2001) *Photographic Guide to the Sea and Shore of Britain and North-west Europe*. Oxford University Press, Oxford, 436 pp
- González-Gordillo JI, Cuesta JA, Rodríguez A (1996) Studies on the larval development of northeastern Atlantic and Mediterranean Porcellanidae (Decapoda, Anomura). I – Redescription of the larval stages of *Porcellana platycheles* (Pennant, 1777) reared under laboratory conditions. *Helgoländer Meeresunters* 50: 517–531, <https://doi.org/10.1007/BF02367164>
- González Pérez JA (1995) Catálogo de los crustáceos decápodos de las Islas Canarias: gambas, langostas, cangrejos. Publicaciones Turquesas, 281 pp
- Gribben PE, l'Ons S, Phillips NE, Geange SW, Wright JT, Murray BR (2013) Biogeographic comparisons of the traits and abundance of an invasive crab throughout its native and invasive ranges. *Biological Invasions* 15: 1877–1885, <https://doi.org/10.1007/s10530-013-0416-0>
- Griffiths CL, Mead A, Robinson TB (2009) A brief history of marine bio-invasions in South Africa. *African Zoology* 44: 241–247, <https://doi.org/10.3377/004.044.0212>
- Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98
- Hammond W, Griffiths CL (2006) Biogeographical variation in community composition of mussel-bed infauna along the southern African coastline. *African Zoology* 41: 123–130, <https://doi.org/10.1080/15627020.2006.11407342>
- Hampton SL, Griffiths CL (2007) Why *Carcinus maenas* cannot get a grip on South Africa's wave-exposed coastline. *African Journal of Marine Science* 29: 123–126, <https://doi.org/10.2989/AJMS.2007.29.1.11.76>
- Haupt TM, Griffiths CL, Robinson TB, Tonin AFG (2010) Oysters as vectors of marine aliens, with notes on four introduced species associated with oyster farming in South Africa. *African Zoology* 45: 52–62, <https://doi.org/10.3377/004.045.0101>
- Hayward PJ, Ryland JS (1990) *The marine fauna of the British Isles and North-West Europe*: 1. Introduction and protozoans to arthropods. Clarendon Press: Oxford, UK, 627 pp
- Herbst JFW (1782–1804) Versuch einer Naturgeschichte der Krabben und Krebse nebst einer Systematischen Beschreibung ihrer Verschieden Arten. Gottlieb August Lange, Berlin & Stralsund, Volumes 1–3, 515 pp, 62 pls
- Hiller A, Lessios HA (2017) Phylogeography of *Petrolisthes armatus*, an invasive species with low dispersal ability. *Scientific Reports* 7: 3359, <https://doi.org/10.1038/s41598-017-03410-8>
- Hollebone AL, Hay ME (2007) Population dynamics of the non-native crab *Petrolisthes armatus* invading the South Atlantic Bight at densities of thousands m². *Marine Ecology Progress Series* 336: 211–223, <https://doi.org/10.3354/meps336211>
- Hollebone AL, Hay ME (2008) An invasive crab alters interaction webs in a marine community. *Biological Invasions* 10: 347–358, <https://doi.org/10.1007/s10530-007-9134-9>
- Kensley B (1981) On the zoogeography of Southern African decapod Crustacea, with a distributional checklist of species. *Smithsonian Contributions to Zoology* 338: 1–64, <https://doi.org/10.5479/si.00810282.338>
- Kensley BF, Penrith ML (1973) The constitution of the intertidal fauna of rocky shores of Moçamedes, southern Angola. *Cimbebasia* 2: 113–123
- Leigh JW, Bryant D (2015) PopART: Full-feature software for haplotype network construction. *Methods in Ecology and Evolution* 6: 1110–1116, <https://doi.org/10.1111/2041-210X.12410>
- Linnaeus C (1758) *Systema naturae per Regna Truia Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. Edition 10, 1: i–iii, 1–824
- López de la Rosa I, García Raso JE (1992) Crustáceos decápodos de fondos de concrecionamientos calcáreos asociados a *Posidonia oceanica* del sur de España (Almería). *Cahiers de Biologie Marine* 33: 55–74
- Mabin CA, Wilson JR, Le Roux JJ, Robinson TB (2017) Reassessing the invasion of South African waters by the European shore-crab *Carcinus maenas*. *African Journal of Marine Science* 39: 259–267, <https://doi.org/10.2989/1814232X.2017.1363818>
- Mead A, Carlton JT, Griffiths CL, Rius M (2011a) Introduced and cryptogenic marine and estuarine species of South Africa. *Journal of Natural History* 45: 2463–2524, <https://doi.org/10.1080/00222933.2011.595836>
- Mead A, Carlton JT, Griffiths CL, Rius M (2011b) Revealing the scale of marine bioinvasions in developing regions. *Biological Invasions* 13: 1991–2008, <https://doi.org/10.1007/s10530-011-0016-9>
- Melo GAS (1999) *Manual de Identificação dos Crustacea Decapoda do litoral brasileiro: Anomura, Thalassinidea, Palinuridea, Astacidea*. Editora Plêiade, São Paulo, 551 pp
- Osawa M, McLaughlin PA (2010) Annotated checklist of anomuran decapod crustaceans of the world (exclusive of the Kiwaioidea and families Chirostyliidae and Galatheidae of the Galatheoidea). Part 2 – Porcellanidae. *The Raffles Bulletin of Zoology Suppl.* 23: 109–129
- Pennant T (1777) *British Zoology*. Volume 4, Crustacea Mollusca Testacea. London: B. White, pp. i–viii+10+1–157+2+93 pls
- Penrith ML, Kensley BF (1970a) The constitution of the intertidal fauna of rocky shores of South West Africa Part 1. Luderitzbucht. *Cimbebasia* 1: 191–239
- Penrith ML, Kensley BF (1970b) The constitution of the fauna of rocky intertidal shores of South West Africa. Part 2. Rocky Point. *Cimbebasia* 1: 243–268
- Peters K, Griffiths C, Robinson TB (2014) Patterns and drivers of marine bioinvasions in eight Western Cape harbours, South Africa. *African Journal of Marine Science* 36: 49–57, <https://doi.org/10.2989/1814232X.2014.890669>
- Rathbun MJ (1894) *Scientific Results of Explorations by the U. S. Fish Commission Steamer Albatross*. 24. Descriptions of new genera and species of crabs from the west coast of North America and the Sandwich Islands. *Proceedings of the United States National Museum* [1893], 16(933): 223–260
- Reuschel S, Schubart CD (2006) Phylogeny and geographic differentiation of Atlanto-Mediterranean species of the genus *Xantho* (Crustacea: Brachyura: Xanthidae) based on genetic and morphometric analyses. *Marine Biology* 148: 853–866, <https://doi.org/10.1007/s00227-005-0095-1>
- Robinson TB, Alexander ME, Simon CA, Griffiths CL, Peters K, Sibanda S, Miza S, Groenewald B, Majiedt P, Sink KJ (2016) Lost in translation? Standardising the terminology used in marine invasion biology and updating South African alien species lists. *African Journal of Marine Science* 38: 129–140, <https://doi.org/10.2989/1814232X.2016.1163292>
- Robinson TB, Branch GM, Griffiths CL, Govender A, Hockey PAR (2007) Changes in South African rocky intertidal invertebrate community structure associated with the invasion of the mussel *Mytilus galloprovincialis*. *Marine Ecology Progress Series* 340: 163–171, <https://doi.org/10.3354/meps340163>
- Robinson TB, Griffiths CL, Kruger N (2004) Distribution and status of marine invasive species in and bordering the West Coast National Park. *Koedoe* 47: 79–87, <https://doi.org/10.4102/koedoe.v47i1.73>
- Rodríguez IT, Hernández G, Felder DL (2005) Review of the western Atlantic Porcellanidae (Crustacea: Decapoda: Anomura) with new records, systematic observations, and comments on biogeography. *Caribbean Journal of Science* 41(3): 544–582
- Rodrigues da Costa H (1968) Novas espécies de Porcellanidae brasileiras (Crustacea, Anomura). *Annuaire de l'Academia Brasileira de Ciências* 40(3): 405–406
- Sadchatheeswaran S, Branch GM, Robinson TB (2015) Changes in habitat complexity resulting from sequential invasions of a rocky shore: implications for community structure. *Biological Invasions* 17: 1799–1816, <https://doi.org/10.1007/s10530-014-0837-4>
- Schubart CD (2009) Mitochondrial DNA and decapod phylogenies: the importance of pseudogenes and primer optimization. In:

- Martin JW, Crandall KA, Felder DL (eds), Crustacean Issues 18. Decapod Crustacean Phylogenetics. CRC Press, Taylor & Francis Group, Boca Raton, pp 47–65, <https://doi.org/10.1201/9781420092592-c4>
- Schubart CD, Huber MGJ (2006) Genetic comparisons of German populations of the stone crayfish, *Austropotamobius torrentium* (Crustacea: Astacidae). *Bulletin Français de la Pêche et de la Pisciculture* 380–381: 1019–1028, <https://doi.org/10.1051/kmae:2006008>
- Stevčić Z (1988) Autecological investigations of the porcelain crab *Porcellana platycheles* (Pennant) (Decapoda, Anomura) in the Rovinj area (Northern Adriatic). *Crustaceana* 55: 242–252, <https://doi.org/10.1163/156854088X00339>
- Tucker L, Griffiths CL, Schroeter F, Vetter HD (2017) Boulder shores in South Africa - a distinct but poorly documented coastal habitat type. *African Journal of Marine Science* 39: 193–202, <https://doi.org/10.2989/1814232X.2017.1329167>
- Türkay M, Fischer G, Neumann V (1987) List of the marine Crustacea of the Northern Sporades (Aegean Sea) with systematic and zoogeographic remarks. *Investigación Pesquera* 51 (Suppl 1): 87–109
- Veloso VG, de Melo GAS (1993) Taxonomia e distribuição da família Porcellanidae (Crustacea, Decapoda, Anomura) no litoral brasileiro. *Iheringia, Série Zoologia* 75: 171–186
- Wassick A, Hughes M, Baeza A, Fowler A, Wilber D (2017) Spacing and movement of the green porcelain crab *Petrolisthes armatus*: evidence for male competition and mate guarding. *Marine and Freshwater Behaviour and Physiology* 50: 165–177, <https://doi.org/10.1080/10236244.2017.1347020>
- WoRMS Editorial Board (2017) World Register of Marine Species. Available from <http://www.marinespecies.org> at VLIZ. Accessed 2017-10-19, <https://doi.org/10.14284/170>
- Young PS (1998) Catalogue of Crustacea of Brazil. Rio de Janeiro: Museu Nacional, Série Livros 6, i–xvii, 717 pp
- Zariquiey ÁR (1968) Crustáceos decápodos Ibéricos. *Investigación Pesquera*, 32, i–xv, 1–510