Rapid Communication

Giants and titans: first records of the invasive acorn barnacles *Megabalanus tintinnabulum* (Linnaeus, 1758) and *Megabalanus coccopoma* (Darwin, 1854) on intertidal rocky shores of South Africa

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Citation: Pfaff MC, Biccard A, Mvula PE, Olbers J, Mushanganyisi K, Macdonald A, Samaai T (2022) Giants and titans: first records of the invasive acorn barnacles *Megabalanus tintinnabulum* (Linnaeus, 1758) and *Megabalanus coccopoma* (Darwin, 1854) on intertidal rocky shores of South Africa. *BioInvasions Records* 11(3): 721–737, https://doi.org/10.3391/bir.2022.11.3.14

Received: 26 October 2021
Accepted: 13 January 2022
Published: 27 June 2022

Handling editor: Jasmine Ferrario
Thematic editor: April Blakeslee

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Abstract

During intertidal rocky shore surveys on the east coast of South Africa in 2018, the non-indigenous giant purple barnacle *Megabalanus tintinnabulum* (Linnaeus, 1758), a well-known fouling and globally-invasive species, was discovered. This motivated a survey of the entire South African east coast at 31 rocky shore sites, which confirmed that breeding populations of this barnacle have been established in most wave-exposed low-shore intertidal habitats between the Mozambique border and Mkambati Nature Reserve and that its current South African distribution spans 725 km of coastline. Another non-indigenous and common fouling species, the titan acorn barnacle *M. coccopoma* (Darwin, 1854), was discovered at three of the sites, its local distribution spanning 370 km of coastline. While currently uncommon, this species is known to reach high densities in other non-native regions. Both *Megabalanus* species are large and conspicuous and were not found during extensive surveys in the 1990s and early 2000s, suggesting that their introduction and spread occurred within the past two decades. Their establishment on subtidal reefs remains to be confirmed but is likely, based on frequent encounters of empty shells washed up on beaches or on buoys. Prior to this, no non-indigenous invasive species have been reported to occur on intertidal rocky shores of the subtropical South African east coast, while the country's south and west coasts have experienced severe ecological impacts from invasive mussels and barnacles since the 1970s. Two alternative processes have likely led to the introduction and spread of the two species: (i) their dispersal from ship fouling communities and spread along the coast from focal points, such as local ports and harbours; or (ii) their arrival by southward range expansions of tropical populations concurrent with recent climate-mediated thermal shifts in the region. The supporting evidence of both are discussed, as well as management implications.

Key words: invasive species, introduced species, climate change, range expansion, fouling species, Cirripedia

Introduction

Coastal marine ecosystems are particularly prone to species introductions, since organisms that travel on hulls or in ballast water of ships, or escape from aquaculture industries may have repeated opportunities to establish in non-native shallow-water habitats. Intertidal rocky shores around the world have thus been severely impacted by invasive species, most commonly mussels and barnacles. A well-known example is the world-wide dispersal of the Mediterranean mussel *Mytilus galloprovincialis* (Lamarck, 1819) from its native range in the Mediterranean, Adriatic and Black Seas to Japan, South Africa, China, the USA, Canada, Korea, Australia and Mexico (Lee and Morton 1985; McDonald et al. 1991; Anderson et al. 2002; Branch and Steffani 2004). Another prominent example is the introduction of the barnacle *Astrominius modestus* (Darwin, 1854) from New Zealand to Europe in 1943, where it has become spatially dominant in intertidal communities (Bishop 1947; Crisp 1958; Harms 1998; Lawson et al. 2004). Furthermore, poleward range shifts, e.g. of tropical species that move into subtropical and temperate regions, have become increasingly common (Carlton et al. 2011; Crickenberger and Moran 2013), which has facilitated a further suite of new invasions through climate-mediated thermal shifts.

In South Africa, several introduced species have had severe impacts on intertidal rocky shore communities, primarily along the cool-temperate west coast and the warm-temperate south coast (Robinson and Griffiths 2002; Robinson et al. 2005; Branch et al. 2008, 2010; Laird and Griffiths 2008; Mead et al. 2011; De Greef et al. 2013). The most prominent examples are *M. galloprovincialis*, which was deliberately introduced to an aquaculture farm in Saldanha Bay in the 1970s and has since invaded the entire west and south coasts (Branch and Steffani 2004; Robinson et al. 2007; Mead et al. 2011); the Pacific north-western barnacle *Balanus glandula* (Darwin, 1854), which has become the most dominant barnacle on the west coast (Mead et al. 2011; Robinson et al. 2015); and the bisexual mussel *Semimytilus algosus* (Gould, 1850), native to the Pacific coast of South America, which is currently spreading eastward from the west coast of South Africa (Skein et al. 2018; Pfaff et al. 2019). Thus far, no invasive species have been reported on the rocky shores of the subtropical east coast of South Africa (Mead et al. 2013). This may be a result of limited search effort in this region (Bailey et al. 2020) but likely also reflects the difficulty to establish in these oligotrophic and predominantly wave-exposed systems, where competition with native species and disturbance is fierce (Branch and Steffani 2004; Pfaff et al. 2010; Mead et al. 2011). However, with a widening of the tropical belt (Lu et al. 2009), warm-water species (including introduced or cryptogenic species) are increasingly moving poleward (Booth et al. 2007; Rahel and Olden 2008; Figueira and Booth 2010; Canning-Clode et al. 2011), making biogeographic transition zones in subtropical regions, such as the east coast of South Africa, particularly vulnerable to the introduction of new species. This concern was confirmed in 2018, when we discovered a specimen of the well-known invasive giant purple barnacle *Megabalanus tintinnabulum* (Linnaeus, 1758) in the iSimangaliso Wetland Park, KwaZulu-Natal (KZN) on the east coast of South Africa. During follow-up surveys, the results of which are reported here, we found a second notorious invasive, the titan acorn barnacle *M. coccopoma* (Darwin, 1854).

Megabalanus tintinnabulum and *M. coccopoma* are among the longest known and most frequently reported fouling species, with their first records dating back to Darwin's pioneering work on barnacles (Darwin 1854; Pilsbry 1907; Hentschel 1923; Visscher 1928; Allen 1953; Yan and Huang 1993; Zvyagintsev 2000; Farrapeira 2006), where he notes that *M. tintinnabulum* "is attached in wonderful numbers to ships' bottoms arriving at our ports, from West Africa, the West Indies, the East Indian Archipelago, and China". *Megabalanus tintinnabulum* is commonly reported to have a cosmopolitan distribution. Given its propensity to hitchhike on ship hulls (Ashton et al. 2016), it is possible that it was dispersed around the globe by early ship farers, and its native range is in fact cryptogenic (Carlton et al. 2011). *Megabalanus coccopoma* is native to the tropical eastern Pacific coasts of Central and South America (Newman and McConnaughey 1987). Being a well-known fouling species (Kerckhof and Cattrijsse 2001), it has been introduced to many locations around the world (Carlton et al. 2011), where, similar to *M. tintinnabulum*, it inhabits lower intertidal and shallow subtidal habitats up to ca. 40 m depth (Richmond 2002; Biccard and Griffiths 2016). The first collection of this species outside its native range dates back to 1875 when it was found in Mauritius in the Western Indian Ocean (Innocenti 2006). Since then, it has successfully invaded Brazil and the Atlantic coasts of Mexico and southern USA, Europe, Great Britain, Japan, Australia, and tropical west Africa (Lacombe and Monteiro 1974; Young 1994; Kerckhof and Cattrijsse 2001; Richmond 2002; Perreault 2004; Celis et al. 2007; Yamaguchi et al. 2009; Kerckhof et al. 2010; Knott 2010; Carlton et al. 2011).

Megabalanus coccopoma is known to have expanded its native and non-native ranges in the western Atlantic in concert with climatic episodes and warming periods (Carlton et al. 2011). During the El Niño event of 1982–83, it temporarily expanded its natural range northward and colonised Southern California (Newman and McConnaughey 1987). Furthermore, while a non-native population has been establishing in Brazil since the 1970s (Lacombe and Monteiro 1974), it was only recorded spreading northwards into coastal waters of the USA from 2005 during an ocean warming event, reaching a remarkable expansion rate of 794 km/yr in 2011 (Crickenberger and Moran 2013).

Biccard (2012) identified museum specimens of *M. tintinnabulum* that were collected from ship hulls in South African harbours as early as 1946

(Table Bay) and 1950 (Knysna). In 2010, established populations of both *M. tintinnabulum* and *M. coccopoma* were collected from wave-rider buoys off Richard's Bay and a barge off Cape Vidal, KZN, indicating the first known record of autochthonous recruitment of these non-native species on artificial substrata (A. Biccard *unpublished data*). Here, we provide the first intertidal records and current distributions of the two non-native barnacles in natural habitats of South Africa, documenting their establishment and spread along large portions of the country's subtropical east coast. While processes of their introduction and spread are at this stage speculative, we discuss the two most likely scenarios and their associated management implications.

Materials and methods

Following the inadvertent discovery of *M. tintinnabulum* at a single site (Crayfish Point; 28.42°S; 32.43°E) in the iSimangaliso Wetland Park in northern KZN in September 2018, we first conducted intertidal rocky shore surveys northward of this point at the majority of (accessible) rock ledges in the Park (in May 2019). Once we had confirmed their presence along the entire northern coastline, we continued surveys of the remainder of the subtropical portion of the South African east coast between June 2019 and November 2019. The 31 sampling sites spanned ca. 750 km of coastline between Kosi Bay in the north and Nqabara in the south (Figure 1; Supplementary material Table S1). In addition to these specimens, incidental encounters—primarily of empty shells that washed up on beaches or were found on buoys—were recorded from nine locations within the sampling area (Table S1).

At each site, focused searches for non-indigenous adult barnacles were undertaken in the low- and mid-intertidal zones of wave-exposed rock ledges, where the target species were known to occur from our first collections in 2018 and the literature (Richmond 2002; Biccard 2012; Biccard and Griffiths 2016). Where present, up to 20 specimens were collected and stored in 96% ethanol. In the laboratory, specimens were dissected under a stereo microscope to verify correct identifications according to internal characters listed under *Descriptions* in the Results.

Field identifications of acorn barnacles can be challenging due to their significant phenotypic plasticity, which is augmented by the effects of erosion and cramming on the shape and texture of barnacle shells and their frequent overgrowth by epibionts. To aid future field identification and the monitoring of these non-native species on the east coast of South Africa, we collated the main distinguishing characters for their field identification in the context of the other four acorn barnacle species that co-occur on this coast.

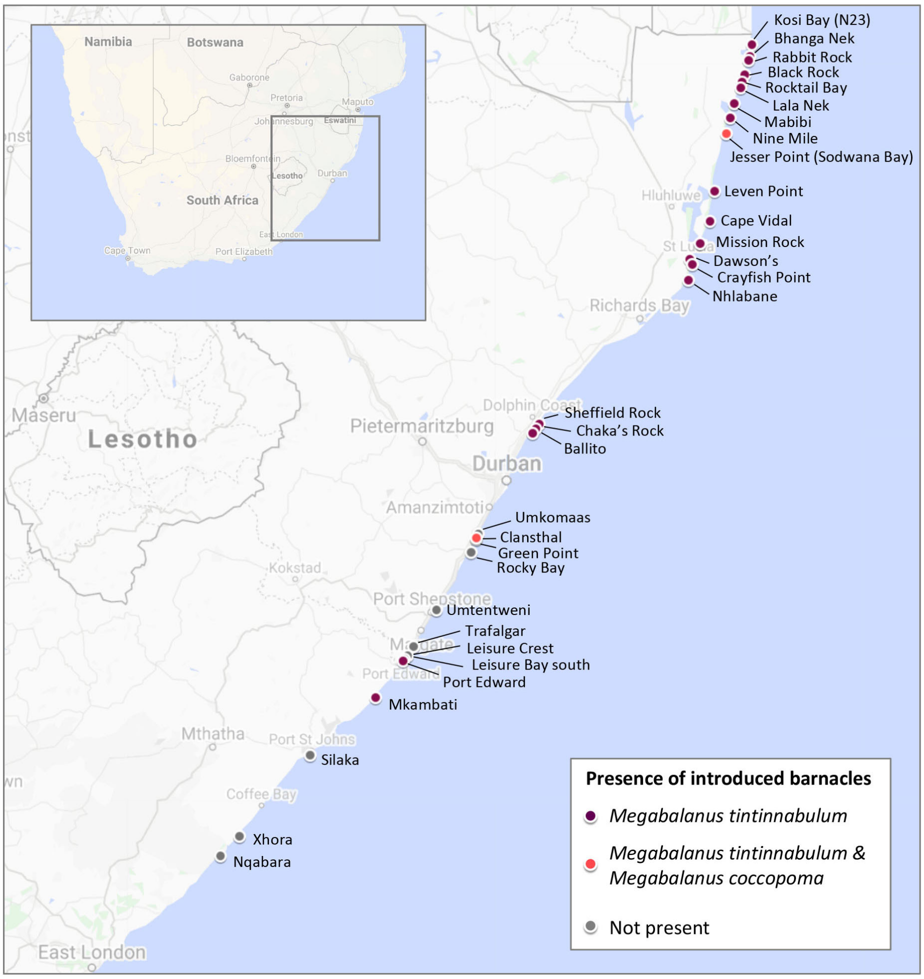

Figure 1. Study area on the east coast of South Africa (see insert), showing the 31 intertidal survey sites (circles) and presence of the two new records of alien barnacles, *Megabalanus tintinnabulum* and *M. coccopoma*.

Due to the patchy occurrence of the *Megabalanus* species, the initial attempt to determine densities from counts in randomly-placed quadrats was deemed inappropriate, rendering extremely low average densities for all sites while densities in selected patches were high. This study is thus focused on presence/absence data.

Results

First records and current distributions

We discovered and collected the first specimens for taxonomic identification of *M. tintinnabulum* (Figure 2A, C) in September 2018 in the low intertidal zone at Crayfish Point in the iSimangaliso Wetland Park (Figure 1). This marked the first confirmed record of this species in natural habitats on the South African coast. During follow-up surveys in 2019, a second sizeable non-indigenous barnacle species, *M. coccopoma* (Figure 2B, D) was recorded for the first time.

Follow-up surveys of rocky shores on the South African east coast confirmed that *M. tintinnabulum* was well established, reaching dense patches

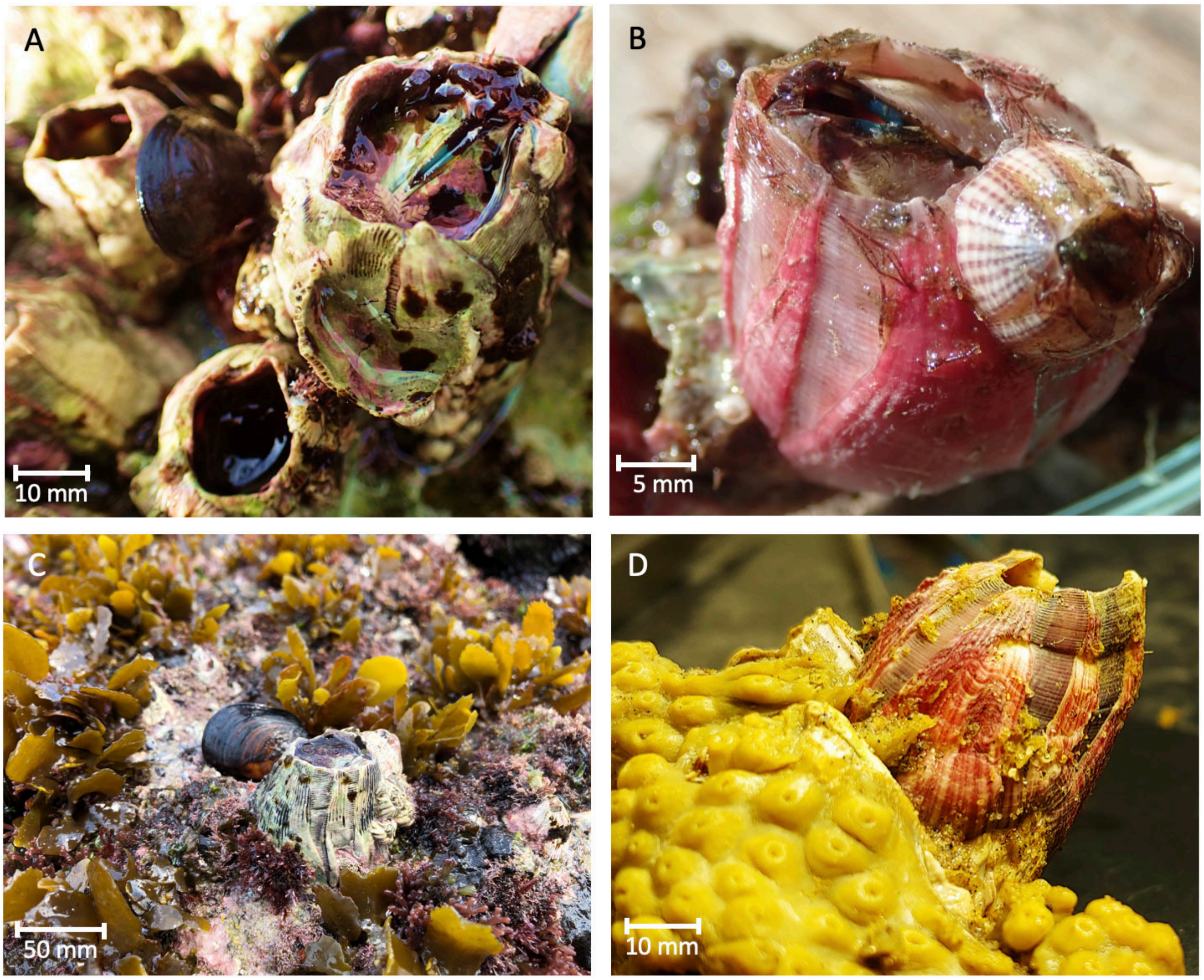

Figure 2. The first records of invasive species on the subtropical east coast of South Africa include (A, C) the giant purple barnacle *Megabalanus tintinnabulum* and (B, D) the titan acorn barnacle *M. coccopoma*. As their names indicate, they are large and conspicuous, with basal diameters and heights reaching >50 mm. (Photographs by M. Pfaff (A, D), J. Olbers (B, C)).

at the majority of the surveyed intertidal sites north of (and including) Mkambati (Figure 1, Table S1). It was not present at the three southernmost sites, suggesting that Mkambati is the current southern distribution limit for this non-indigenous species, at least in the intertidal zone. The fact that populations comprised multiple age cohorts, including smaller individuals living epibiotically on larger ones (Figure 2A), suggests that a breeding population has established along this coast.

By contrast, *M. coccopoma* was only present at two of the 31 sampling sites, at Jesser Point in northern KZN (Delagoa ecoregion) and at Clansthal in southern KZN (Natal ecoregion), across a range of ca. 370 km. It was only found sporadically and solitary at these sites, not forming clusters. The shells of *M. coccopoma* were however commonly found along beaches of the Natal ecoregion (Table S1) suggesting that it might indeed be well established subtidally.

Field identifications and taxonomic descriptions

Since no indigenous barnacle species on the KZN coast reach the adult sizes of the two introduced *Megabalanus* species (with basal diameters and heights

Table 1. Selected characteristics for the field identification of the most common intertidal acorn barnacles on the South African east coast that co-occur with the recently introduced *Megabalanus tintinnabulum* and *M. coccopoma*. Combinations of distinguishing features are shown in bold font.

	Megabalanus tintinnabulum	*Megabalanus coccopoma*	*Tetraclita rufotincta*	*Tetraclita serrata*	*Octomeris angulosa*	*Chthamalus dentatus*
Basal / carino-rostral diameter*	**Up to 75 mm / 35 mm**	50 mm / 30 mm	30 mm / 20 mm	28 mm / 17 mm	**38 / 25 mm**	20 mm / 10 mm
Height*	**70 mm**	55 mm	30 mm	28 mm	23 mm	4 mm
Shape of shell*	Tubolo-conical or conical	**Globulo-conical or cylindrical**	Conical	Conical	Depressed, tubulo-conical	**Star-shaped outline**
Orifice	Moderate to large	Moderately small, < 1/2 of basal diameter, subtriangular to subovate	Circular, small or moderate size	Circular, small	**Very large**	Large
Number of wall plates	6	6	4	4	**8**	6
Basal plate or basis	Calcareous, porose	Calcareous	Calcareous	Calcareous	Membranous	Membranous
Wall plates	Reddish purple/purplish pink/blackish purple often with darker or lighter longitudinal striae; radii with dark horizontal striae and horizontal summits, summits of alae oblique.	**Bright pink**, smooth, sometimes finely ribbed. Radii with horizontal summits.	Dirty purple/pink. Fine, short longitudinal ribs.	**Dark grey (never pink)**. Unworn specimens with longitudinal serrated ribs.	Dirty white to brown.	White, dirty white, fawn or marbeled brown
Colour of tergo-scutal flaps (see Figure 3)	**Three transverse dark brown/maroon bands interspersed with bright iridescent blue-green patches**	**Predominantly brown, with one bright blue-green iridescent band**	Mostly brown with cream patches and rim	Cream-colored centre, dark brown edges	Cream-coloured edges	White, cream or light grey
Tergum beaked	Bluntly beaked	Yes	Yes, **sharply pointed pink tips**	Yes	No	No
Rostrum with radii/alae	Rostrum with radii overlapping the alae of contiguous plates	Rostrum with radii overlapping the alae of contiguous plates	Rostrum with radii overlapping the alae of contiguous plates	Rostrum with radii overlapping the alae of contiguous plates	Rostrum with alae **overlapped by** the radii of contiguous plates	Rostrum with alae **overlapped by** the radii of contiguous plates
Position on the shore	Lower intertidal on exposed ledges extending to subtidal	Mid to low intertidal and subtidal	Mid to lower intertidal	Mid to lower intertidal	Mid to low intertidal on exposed ledges	Upper to mid intertidal

* typical of fully-grown free-standing individuals; shape and dimensions differ when growing in clusters.

of > 50 mm), their size was initially considered the most reliable characteristic for field identifications. A compilation of characters (Table 1) identified the shape and colour of the wall plates and the colour of tergo-scutal flaps, a fleshy lining of the orifice observed in living specimens (Figure 3), as other distinguishing features. Final confirmation of field identifications does, however, require the assessment of internal taxonomic characters through dissections of collected specimens (Figures 4, 5). The following section provides taxonomic descriptions for the two introduced *Megabalanus* species.

Phylum Arthropoda
Class Hexanauplia
Order Sessilia
Family Balanidae
Genus *Megabalanus*

Megabalanus coccopoma **(Darwin, 1854)**

(Figure 4)

Description: Shell large and bright pink, scutum with broad, obtusely inflected tergal part and strongly toothed occludent margin; 6 smooth

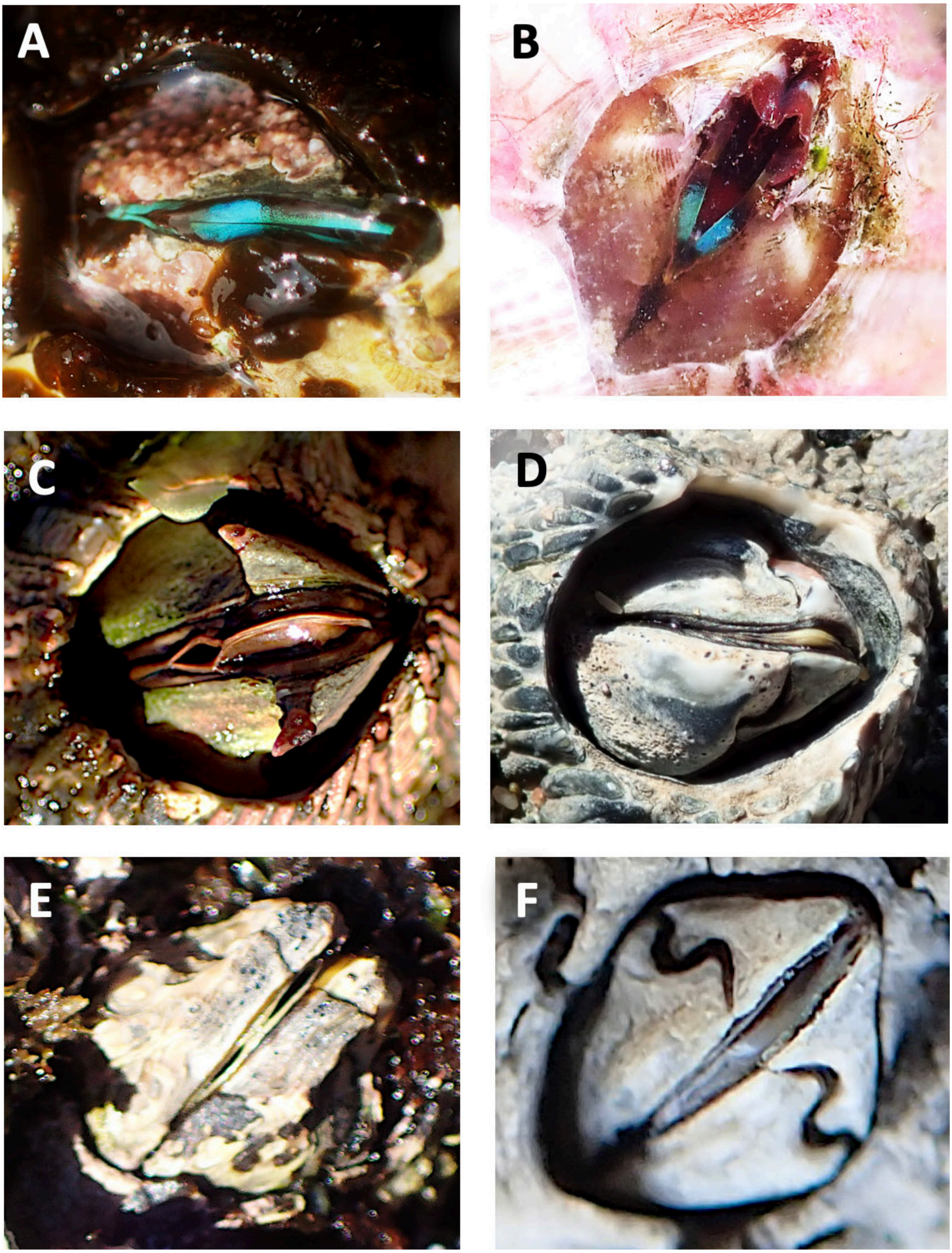

Figure 3. One of the most characteristic features for field identification of live specimens is the colour of the tergo-scutal flaps that line the an acorn barnacle's orifice, here shown for the non-native barnacles (A) *Megabalanus tintinnabulum* and (B) *M. coccopoma* in context of the native barnacles (C) *Tetraclita rufotincta*, (D) *T. serrata*, (E) *Octomeris angulosa* and (F) *Chthamalus dentatus.* (Photographs by M. Pfaff (A, C, E), J. Olbers (B, D, F)).

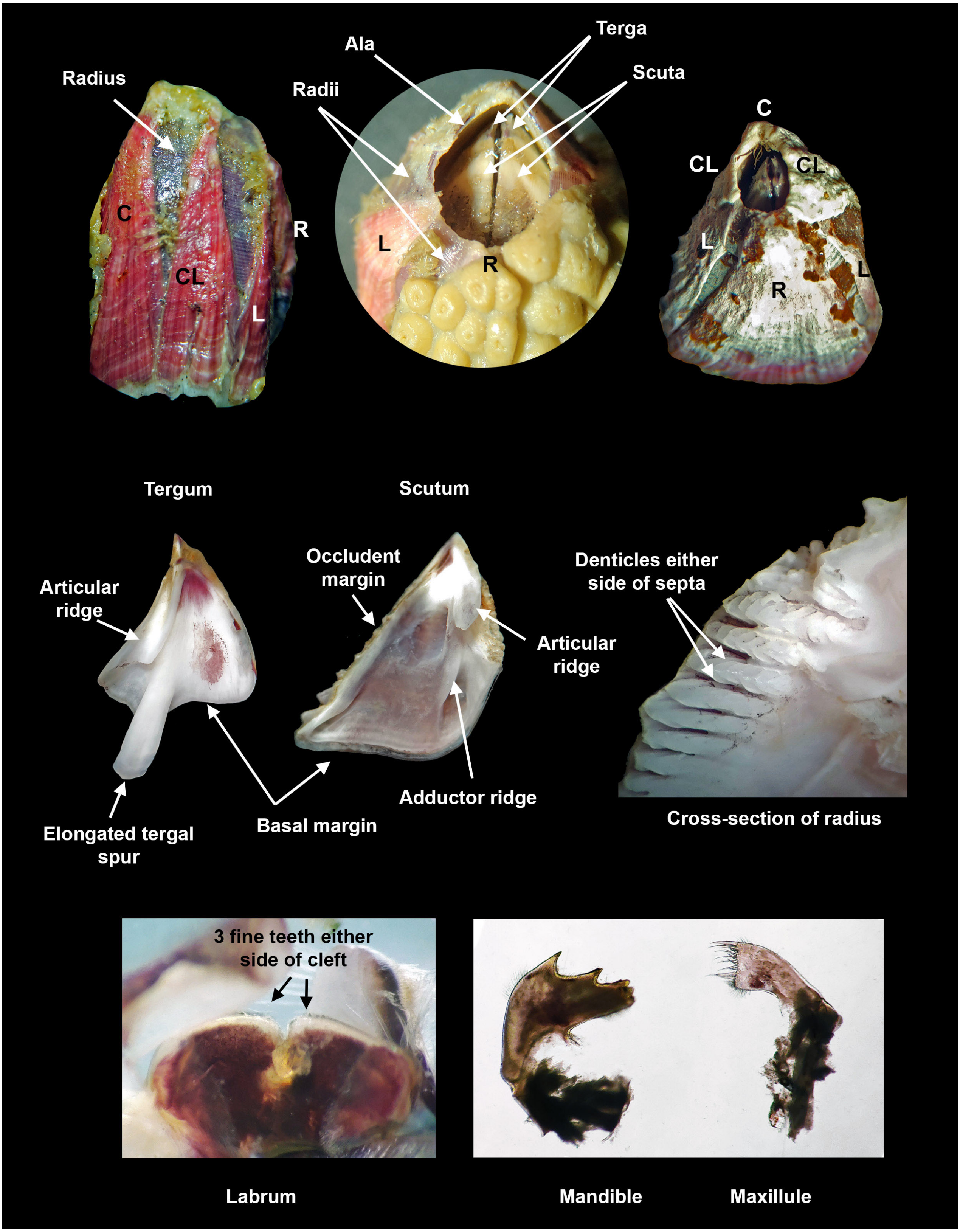

Figure 4. Taxonomic characters from the dissection of *Megabalanus coccopoma*. Morphological terms for shell plates (parietes) are indicated with letters as follows: C = carina, CL = carinal latus, L = latus, R = rostrum. (Photographs by A. Biccard).

parietes, rugose, sometimes finely ribbed, intense rose colour with occasional fine, light-pink longitudinal lines. Radii tinged with purple, moderately wide with horizontal summits, orifice half width of basal diameter. Articular ridge of scutum about four-fifths length of tergal margin, adductor ridge well-developed and separated from articular ridge. Tergum with spur furrow infolded, almost closed, apex beaked, spur long and narrow, occupying about one-sixth of the basal margin, separated by 1.5 times its width from basiscutal angle, basal margin usually sloping to spur on both sides, occasionally straight on one or both sides, protuberant near carinal margin. Cirrus I, outer ramus with 15 articles, longer than inner ramus, which has 14 articles. Mandible with 4 teeth, labrum straight with 3 fine teeth either side of notch, maxilla I with 3 large upper spines separated from 9 spines on lower margin by distinct, shallow notch.

***Megabalanus tintinnabulum* (Linnaeus, 1758)**
(Figure 5)

Description: Shell tall and cylindrical varying to conical, parietes without spines or projections, smooth, sometimes roughened, reddish purple/purplish pink/blackish purple often with darker or lighter longitudinal striae. Radii wide, horizontally striate, summits horizontal, summits of alae oblique. Orifice one to two-thirds of basal diameter. Scutum with narrow to broad tergal segment, ranging from obtusely inflicted in conical specimens to not obtusely inflicted in cylindrical specimens, growth ridges not scalloped by longitudinal striae, basal margin straight, occludent margin toothed, articular ridge one-half to two-thirds length of tergal margin. Tergum with spur furrow closed, spur moderately long occupying slightly less than a quarter of the basal margin, separated from basiscutal angle by one and a half times its own width, scutal margin denticulate, articular ridge about two-thirds of scutal margin, crests for depressor muscles weak to moderately developed – more prominent in younger specimens. Mouthparts: labrum with 3 teeth either side of deep cleft, mandible with 5 teeth excluding inferior angle, maxilla I slightly notched. Size: carino-rostral diameter 50 mm; height 50 mm.

Discussion

First arrival and possible impacts

This study documents the first records of the well-known invasive acorn barnacles *M. tintinnabulum* and *M. coccopoma* on South African rocky shores. We found that *Megabalanus tintinnabulum* is well established in low intertidal habitats along the entire KwaZulu-Natal (KZN) coast, forming dense clusters that contain multiple cohorts at all sampled sites within its distribution range, including smaller individuals living epibiotically on larger ones. By contrast, solitary individuals of *M. coccopoma* were found sporadically at two of the sampling sites. This study exclusively focused on their intertidal distributions, but it is possible that populations have also established in adjacent shallow-subtidal habitats, as suggested by frequent

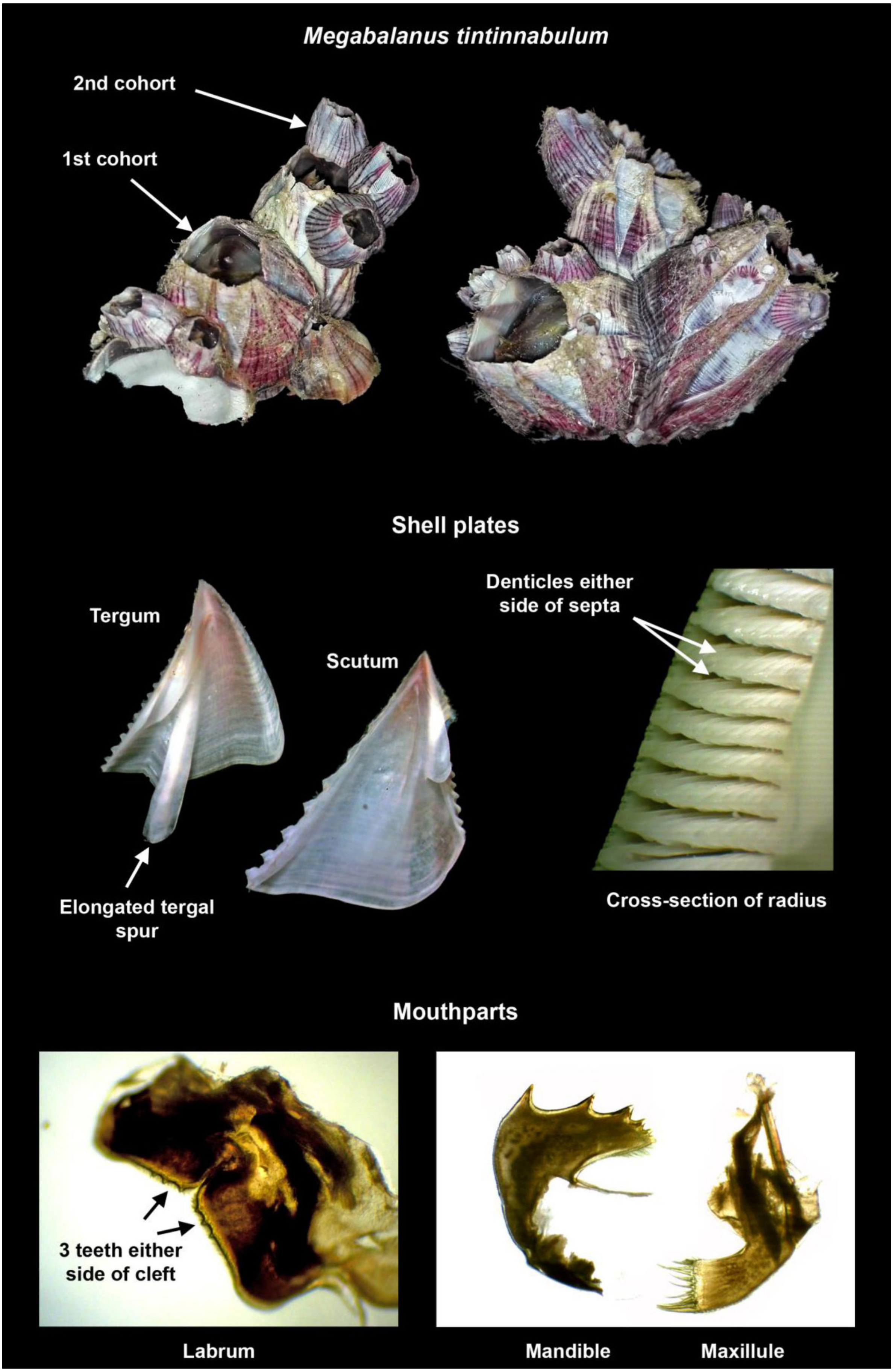

Figure 5. Taxonomic characters from the dissection of *Megabalanus tintinnabulum* (Photographs by A. Biccard).

incidents of shells of both species that are washed up on KZN beaches. Neither of the two species were found in the late 1990s and early 2000s, when comprehensive intertidal rocky shore biodiversity surveys were conducted in this region (Bustamante et al. 1997; Sink 2001), indicating that their arrival and spread along the South African coast occurred within the past 20 years.

Megabalanus tintinnabulum has become an established member of wave-exposed intertidal communities along the KZN coast, where it is most frequently found in very turbulent low-shore conditions among mixed algal turfs and crusts, articulated coralline and other upright algae (e.g. *Arthrocardia* spp., *Sargassum* spp.), mussels (*Perna perna* Linnaeus, 1758), red bait (*Pyura stolonifera* Heller, 1878), other indigenous barnacles (e.g. *Tetraclita serrata* Darwin, 1954, *T. rufotincta* Pilsbry, 1916), and zooanthids (e.g. *Palythoa* spp., *Zooanthus* spp.). It occurs as an epibiont on mussels and barnacles, and as basibiont of conspecifics, other indigenous barnacle species, various species of algae, and a suite of mobile taxa (e.g. limpets, periwinkles, polychaetes, amphipods, and isopods). The large size of this species, which reaches basal diameters of up to 75 mm and heights of 70 mm, suggests that it significantly alters the physical structure of low intertidal shores by increasing habitat complexity. While adverse effects through competitive displacement of indigenous species, such as mussels and barnacles, are a likely impact of the invasion of *M. tintinnabulum*, we observed that some species appear to benefit from the increased wave shelter provided by its shells. Although barnacles are not commonly consumed by people in South Africa, we observed during our survey that fishers were harvesting large individuals, possibly as bait, reducing their densities at some locations (M. Pfaff *personal observations*). *Megabalanus coccopoma* is, at this stage, too rare on South African rocky shores to predict its ecological impacts, but has been observed to reach high densities, outcompeting *M. tintinnabulum*, in other non-native populations in west Africa (Kerckhof et al. 2010). Given that *M. coccopoma* has expanded its native and non-native ranges in several other regions during warming periods (Newman and McConnaughey 1987; Carlton et al. 2011; Crickenberger and Moran 2013), it is likely that this species will become increasingly well-established on the South African east coast and, given appropriate environmental conditions, will continue spreading poleward along the east coast.

Alternative hypotheses regarding the introduction and spread of the two species

At least two alternative dispersal pathways might have led to the arrival and spread of the two new invasive barnacles along the South African coast. One scenario involves (likely multiple) introductions from fouling populations associated with commercial shipping and yacht traffic.

Alternatively, a progressive southward range expansion from tropical East African populations could have occurred due to the significant warming of coastal KZN waters (of up to 0.25 °C per decade in summer months) associated with an intensification of the Agulhas Current that has taken place since the 1980s (Rouault et al. 2009, 2010), in concert with a global widening of the tropical belt (Seidel et al. 2008). External fouling on ship hulls and other mobile man-made structures is considered one of the most common vectors for the introduction of barnacles (Ashton et al. 2016), while others include the transport of larvae in ballast tanks or cargo holds, buoys, commercial seafood and mariculture industries, habitat restoration projects, drifting anthropogenic debris, and marker tags on marine animals (Carlton et al. 2011). Biccard and Griffiths (2016) reported the presence of both *M. tintinnabulum* and *M. coccopoma* in the fouling communities on buoys outside the commercial ports of Richards Bay and Durban (Natal ecoregion) in 2010, suggesting that the dispersal from artificial substrata is a likely mechanism for the introduction of these species. However, species range expansions could have alternatively led to the introductions and spread, in particular of the more commonly found *M. tintinnabulum*, as reported for barnacles from other parts of the world (Carlton et al. 2011). Given that both *Megabalanus* species are well-established in tropical east Africa (Richmond 2002; Innocenti 2006; Carlton et al. 2011) and that a suite of tropical species, including reef-fish (Lloyd et al. 2012; Vergés et al. 2014), brachyuran crabs (Ma and McQuaid 2021) and the intertidal barnacle *Tetraclita rufotincta* (Biccard 2012), have recently expanded their ranges southward (i.e. poleward) towards temperate regions of the South African east coast, a climate-mediated range expansion of *Megabalanus* is also not unlikely. Several introduced barnacle species have experienced similar range expansions related to warming events, including *M. coccopoma* itself (in North America), the native north-eastern Pacific *T. rubescens* and the native western Atlantic *Chthamalus fragilis* Darwin, 1754 (Carlton et al. 2011).

Conclusions

This survey first confirmed the arrival and establishment of the two globally-invasive barnacle species *M. tintinnabulum* and *M. coccopoma* in natural intertidal benthic habitats of South Africa. *M. tintinnabulum* has spread and become a relatively common member of low-shore intertidal rocky shore communities along the entire subtropical east coast, where it provides a habitat for numerous other species that colonise its shell plates and potentially displaces native species, such as the mussel *Perna perna*. *Megabalanus coccopoma* was only sporadically encountered alive in the intertidal zone, but the frequency of empty shells found washed up on KZN beaches suggests that well-established subtidal populations exist, which have not yet been assessed. Two alternative processes could have led to the introduction and spread of the two species on the South African coast: their introduction via fouling communities on vessels that frequently arrive in the region at the two large shipping ports of Richard's Bay and Durban or at small harbours; or the southward (i.e. poleward) range expansion of previously established tropical populations facilitated by recent warming conditions of KZN coastal waters. While introductions from fouling communities on vessels can be mitigated by more stringent regulations regarding vessel maintenance and cleaning protocols in harbours and ports, species range expansions due to changing climate are beyond mitigation on a national scale. In order to recommend appropriate management measures and avoid future species invasions, it is therefore desirable to determine the recent dispersal histories of these newly arrived barnacle species on the South African coast. This can be achieved by the use of molecular genomic tools that provide high-resolution data for assessing population structure. Subtidal surveys would also determine if densities are higher in the subtidal zones in comparison to the intertidal zones, which would give a better indication of the severity of the invasion.

Acknowledgements

We thank Knowledge Mondli Dlamini and Nicolette Naidoo for their assistance during field work, and Anchor Environmental Consultants for the use of their laboratory for dissections. We are grateful for the comments and valuable suggestions of two anonymous reviewers.

Funding declaration

This study was funded by the South African National Department of Forestry, Fisheries and the Environment, Oceans and Coasts Research and forms part of the National Rocky Shore Monitoring and Marine Biodiversity Programmes. The funders supported the study design, data collection and analysis, decision to publish, and preparation of the manuscript. The co-authors received funding for their time to contribute to this work from their respective institutions.

Ethics and permits

We acknowledge that it is understood that with the submission of this article the authors have complied with the institutional and/or national policies governing the humane and ethical treatment of the experimental subjects and that we are willing to share the original data and materials if so requested. No ethics clearance was required for the survey and collection of invasive barnacles. Sampling within the iSimangaliso Wetland Park was authorised through a Research Agreement between MCP and the iSimangaliso Wetland Park Authority entitled "National Rocky Shore Monitoring Programme in the KZN province: decadal changes in rocky shore community structure due to climate change and other anthropogenic impacts", signed on 13 September 2018. Collection permits were obtained prior to the study from the Department of Environment, Fisheries and Forestry and the iSimangaliso Wetland Park.

Authors' contribution

MCP: research conceptualisation; sample design and methodology; investigation and data collection; data analysis and interpretation; permit approval; funding provision; writing of the original draft, review and editing; AB: research conceptualisation; sample design and methodology; data analysis and interpretation; writing of the original draft, review and editing; PEM: research conceptualisation; investigation and data collection; writing of the original draft, review and editing; JMO: sample design and methodology; investigation and data collection; data analysis and interpretation; permit approval; writing of the original draft, review and editing; KM: sample design and methodology; investigation and data collection; writing of the original draft, review and editing; AM: research conceptualisation; investigation and data collection; writing of the original draft, review and editing; TS: research conceptualisation; sample design and methodology; investigation and data collection; funding provision; writing of the original draft, review and editing.

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Supplementary material

The following supplementary material is available for this article:

Table S1. First records of the invasive barnacles *Megabalanus tintinnabulum* and *M. coccopoma* at 37 locations along the South African east coast.

This material is available as part of online article from:
http://www.reabic.net/journals/bir/2022/Supplements/BIR_2022_Pfaff_etal_SupplementaryMaterial.xlsx