BioInvasions Records (2025) Volume 14, Issue 1: 183–196

Research Article

First record of the marine alien bryozoan *Amathia verticillata* (delle Chiaje, 1822) in South Africa

Sarah Jane Ackland[1], Miranda Nicole Andersen[1], Alison Kock[2,3], Daniel van Blerk[4], Rushdi Ariefdien[2] and Tamara Bridgett Robinson[4]

[1]*Department of Botany and Zoology, Centre for Invasion Biology, Stellenbosch University, Matieland, 7602, South Africa*
[2]*South African National Parks, Scientific Services, Cape Town, 7701, South Africa*
[3]*South African Institute for Aquatic Biodiversity (SAIAB), Private Bag 1015, Makhanda, 6140, South Africa*
[4]*Centre for Invasion Biology, Stellenbosch University, Matieland, 7602, South Africa*

Corresponding author: Tamara Bridgett Robinson (trobins@sun.ac.za)

Citation: Ackland SJ, Andersen MN, Kock A, van Blerk D, Ariefdien R, Robinson TB (2025) First record of the marine alien bryozoan *Amathia verticillata* (delle Chiaje, 1822) in South Africa. *BioInvasions Records* 14(1): 183–196, https://doi.org/10.3391/bir.2025.14.1.15

Received: 16 August 2024
Accepted: 4 December 2024
Published: 17 February 2025

Handling editor: Kevin C.K. Ma
Thematic editor: April Blakeslee

Abstract

This study reports on the first discovery of the marine bryozoan *Amathia verticillata* (delle Chiaje, 1822) from South Africa. In November 2023, an unusual soft-bodied bryozoan was observed within the Langebaan Lagoon Marine Protected Area on the west coast of South Africa. Taxonomic investigations confirmed it to be *A. verticillata*. In response, surveys were conducted to assess its abundance and distribution within the MPA. The tidal estuarine lagoon was divided into 15 sampling areas, with each searched for *A. verticillata* colonies. Additionally, colonies were collected to identify associated epifaunal assemblages. *Amathia verticillata* was detected in 60% of areas, with a total of 2333 colonies recorded. Colonies varied greatly in size, with some more than two meters long. Most concerning was the presence of *A. verticillata* within meadows of the regionally endangered seagrass *Zostera capensis*. A total of 33 epifaunal species were recorded within the stolonal matrices, of which three were alien and one was cryptogenic. This highlights the role that *A. verticillata* may play in habitat provisioning. *Amathia verticillata* was most likely introduced to the system via biofouling, with spread facilitated by local tidal flow regimes. It is recommended that a seasonal monitoring plan be implemented to track the spread and density of the species within the lagoon. Given the potential impacts that *A. verticillata* may have on vulnerable native species, it is recommended that best practice to prevent spread be established, and that areas susceptible to secondary spread be monitored, to support rapid response to additional incursions by this invader.

Key words: Bryozoa, epifauna, Langebaan Lagoon, marine bioinvasions, Marine Protected Area

Introduction

The bryozoan *Amathia verticillata* (delle Chiaje, 1822), formerly known as *Zoobotryon verticillatum*, is a marine ctenostome bryozoan first described in 1822 in Naples, Italy (Marchini et al. 2015). The origin of this species has long been debated (Nascimento et al. 2021); however evidence suggests that its native range is within the Caribbean Sea (Winston 1995; Galil and Gevili 2014). *Amathia verticillata* has been recorded as invasive in numerous regions (i.e. the United States (Williams 2007), Galápagos (McCann et al.

2019), Mexico (Humara-Gil and Cruz-Gómez 2019), Brazil (Miranda et al. 2018), Argentina (López-Gappa and Liuzzi 2016), Portugal (Gestoso et al. 2017), the Mediterranean Sea (Marchini et al. 2015), Angola (Pestana et al. 2020), India (Jebakumar et al. 2017), Pakistan (Aslam et al. 2019), Taiwan (Minchin et al. 2016), Australia (Tilbrook 2012) and New Zealand (Gordon and Mawatari 1992)). Despite its broad geographic distribution, recent molecular work suggests that *A. verticillata* is a single widely distributed species and not a complex cryptogenic species (Nascimento et al. 2021).

Amathia verticillata is described as a eurytopic species as it occurs in many different habitats, including mangroves, oyster reefs, rocky shores, seagrass meadows (Marchini et al. 2015) and on artificial substrata (Nascimento et al. 2021). This species has been recorded mostly within enclosed and sheltered areas (e.g. coastal lagoons and bays) and has established in artificial equivalents (e.g. marinas and harbours) (Marchini et al. 2015; López-Gappa and Liuzzi 2016; Jebakumar et al. 2017; McCann et al. 2019). Long distance spread of this bryozoan likely occurs through hull fouling (McCann et al. 2015), with a very short larval stage thought to exclude dispersal via ballast water (Minchin 2012; Marchini et al. 2015; McCann et al. 2015; Miranda et al. 2018).

The success of this species in its invaded ranges can be attributed to its euryoecious nature and its reproductive strategies (Vieira et al. 2014; Marchini et al. 2015). Colonies of *A. verticillata* can develop through budding and fragmentation (Marchini et al. 2015) and are able to attach to substrata following local spread (McCann et al. 2015). Drifting colonies also have the potential to release viable larvae, further amplifying its ability to colonise new areas (McCann et al. 2015). In regions with favourable environmental conditions, *A. verticillata* has the ability to reproduce sexually year-round (e.g. Azores Archipelago (Micael et al. 2018)). Other physiological characteristics that contribute to its success include rapid growth, regeneration potential after periods of dormancy, hermaphroditism, and tolerance to variable salinities and temperature conditions (Nascimento et al. 2021). Colonies vary greatly in size and shape, with elongated or hanging colonies reaching lengths of two metres (Minchin 2012), while short, bushy colonies can remain as small as two centimetres (Marchini et al. 2015).

The environmental and socio-economic impacts of *A. verticillata* have been well-documented. It is known to cause extensive fouling in artificial habitats, resulting in economic loss through vessel hull fouling (Minchin 2012; Galil and Gevili 2014), blocking of intake pipes for industrial plants and vessels (Coleman 1999) and fouling of commercial fishing gear (Jebakumar et al. 2017). From an environmental perspective, *A. verticillata* colonies have the potential to rapidly proliferate and cover benthic areas, which can result in shading of native algae (e.g. shading of *Zostera marina* (Linnaeus, 1753) seagrass meadows leading to mass mortality and canopy collapse (Williams 2007)), spatial dominance (e.g. forming large mats draped over mangrove limbs in Tortuga Bay, Santa Cruz Island (McCann et al. 2015))

and modification of trophic dynamics (e.g. the removal of large volumes of planktonic material through suspension feeding, affecting food web dynamics (Amat and Tempera 2009)). Due to its structural complexity, this bryozoan also offers habitat to other biota (Guerra-García et al. 2024) and has been known to facilitate the introduction and establishment of other alien species (Marchini et al. 2015).

The present study documents the first record of *A. verticillata* in South African waters and assesses the abundance and distribution of this bryozoan within Langebaan Lagoon Marine Protected Area (MPA), a sheltered MPA along the west coast of South Africa. Additionally, epifauna associated with *A. verticillata* stolonal matrices were investigated.

Materials and methods

Langebaan Lagoon Marine Protected Area (MPA) falls within the West Coast National Park (WCNP) and the larger Saldanha Bay system. This lagoon is the only estuarine tidal lagoon and one of the few sheltered bays along South Africa's west coast (Figure 1). Composed primarily of intertidal sandflats and marshland, this tidal lagoon serves as an important refuge for a diverse suite of marine organisms, coastal birds, and at-risk species (Hanekom et al. 2009), including the critically endangered endemic limpet *Siphonaria compressa* (Allanson, 1958) (Angel et al. 2006) and the regionally endangered Cape dwarf seagrass *Zostera capensis* (Setchell, 1933) (Adams and van der Colff 2018). During spring tides, the lagoon experiences a tidal range of 1.8 m at the mouth to 1–1.5 m at the head (Day 1959).

In November 2023, an unusual bryozoan was observed on the jetty at Kraalbaai (Figure 2A). The identification of this species was confirmed as *Amathia verticillata* in December 2023 (see results below). To assess the extent of the invasion, field surveys took place during spring low tide in austral summer, February 2024. Following the design of previous surveys for alien species within the MPA (Robinson et al. 2004; Robinson and Swart 2015), the estuarine tidal lagoon was divided into 15 areas, each 3 km in length (Figure 1). In each area, three researchers spent one hour searching the intertidal and shallow subtidal (0–1 m) zones for *A. verticillata*. Search areas were stratified to ensure that colonies could not be counted by more than one researcher. The number of colonies detected were summed to provide a total count per tidal zone in each area. The number of colonies greater than 0.2 m^2 were also noted. When abundance allowed, three colonies were randomly collected from each zone and returned to the laboratory. All associated epifauna were identified using Griffiths (1976), Kensley (1978), Samaai and Gibbons (2005), Schwindt et al. (2018), Conlan et al. (2021) and Branch et al. (2022). In addition to the above surveys, subtidal artificial habitats (i.e. houseboats in Kraalbaai (Area 13) and a shipwreck in Zone B (Area 5)), were checked by two researchers for the presence of the bryozoan while snorkelling.

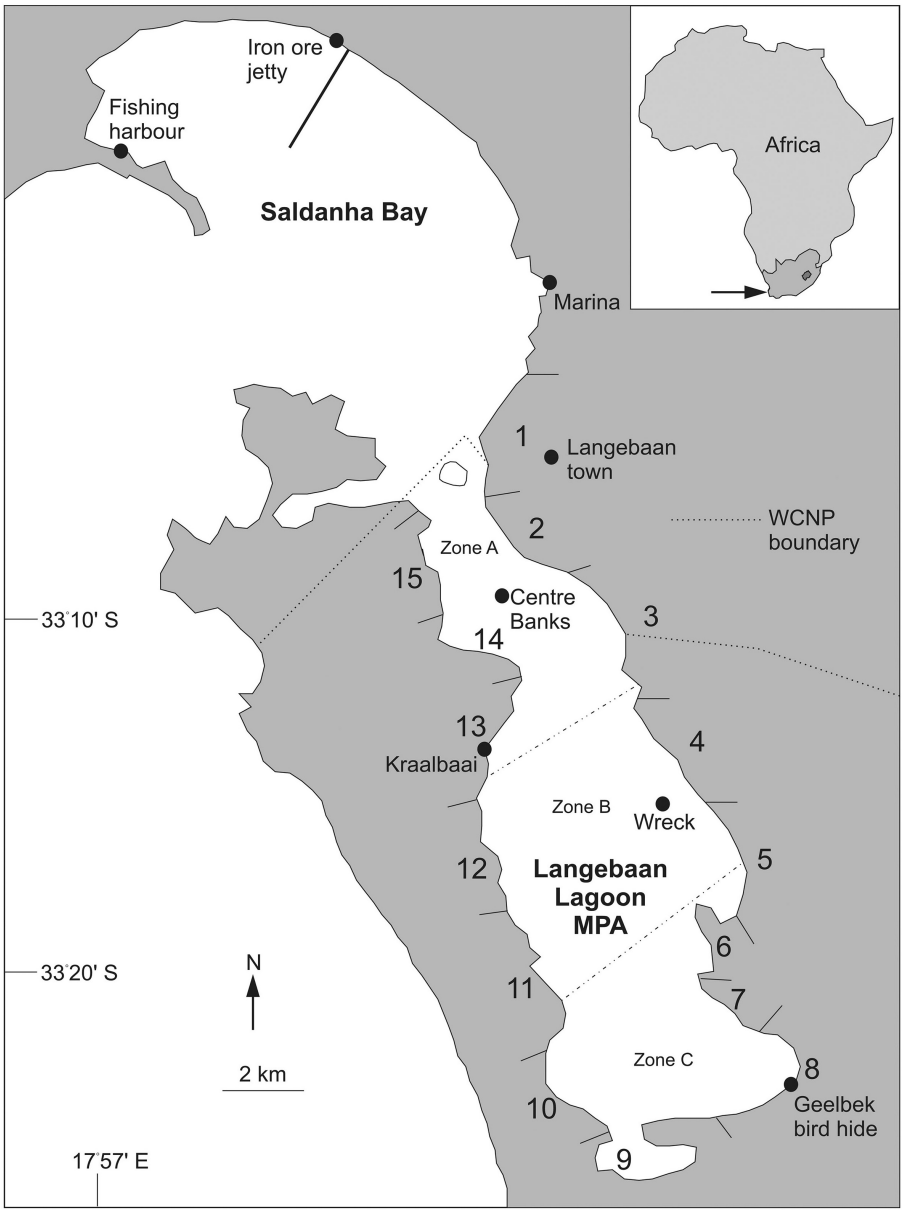

Figure 1. Map of the West Coast National Park (WCNP) showing Langebaan Lagoon Marine Protected Area and the 15 areas searched for *Amathia verticillata*. Other locations mentioned in the text are also indicated.

Results

Following the descriptions of Osburn and Soule (1953), Winston (2004) and Vieira et al. (2014), the specimens found in Kraalbaai were identified as *Amathia verticillata* (Figure 2B). The morphology of this species is distinct from that of the three congeners previously reported from South Africa (i.e. *Amathia gracilis* (Leidy, 1855), *Amathia lendigera* (Linnaeus, 1758) and *Amathia populea* (d'Hondt, 1983) (Boonzaaier 2017)) as none of these taxa have zooecium in two rows along the stolon. Additionally, another important diagnostic feature of *A. verticillata* is the presence of trifurcating branches.

Amathia verticillata was detected within nine of the fifteen sampled areas, with a total of 2333 colonies recorded (Figure 3; Supplementary material Table S1). The majority of colonies were recorded in areas ten (1021 colonies;

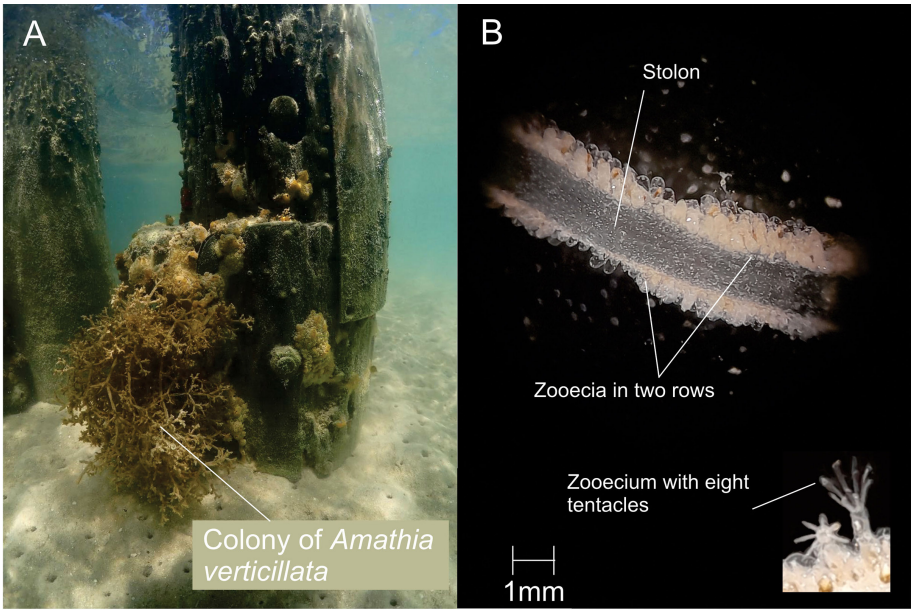

Figure 2. (A) A colony of *Amathia verticillata* attached to the jetty at Kraalbaai where the species was first detected in November 2023 (photo by Sarah Jane Ackland). (B) Some of the defining taxonomic characters used to identify *A. verticillata* (photo by Tammy Robinson).

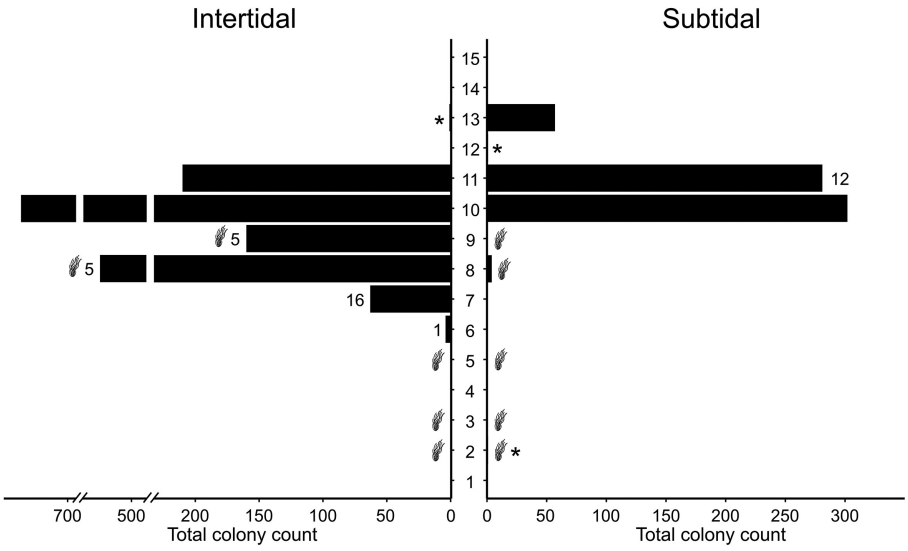

Figure 3. The total number of *Amathia verticillata* colonies recorded from the intertidal and subtidal zones in Langebaan Lagoon Marine Protected Area. Note: asterisks identify zones in which single colonies were recorded, numbers next to bars indicate the number of colonies greater than 0.2 m^2 and the illustration represents areas in which *Zostera capensis* meadows are present.

43.8%), eight (534 colonies; 22.9%) and eleven (491 colonies; 21%). These areas are located in the restricted and sanctuary areas of the Langebaan Lagoon. A total of 39 colonies were greater than 0.2 m^2 in size (Figure 4A). Overall, a higher number of colonies were detected within the intertidal zone (72.3%) than in the shallow subtidal (27.7%) (Figure 3). While some colonies were attached to artificial structures, including the support beams of bird hides and jetties, others were anchored into sand prawn (*Kraussillichirus kraussi* (Stebbing, 1900)) holes and thus occurred on the sandflats (Figure 4B). Dense subtidal populations were detected on the houseboats and the wreck. In both

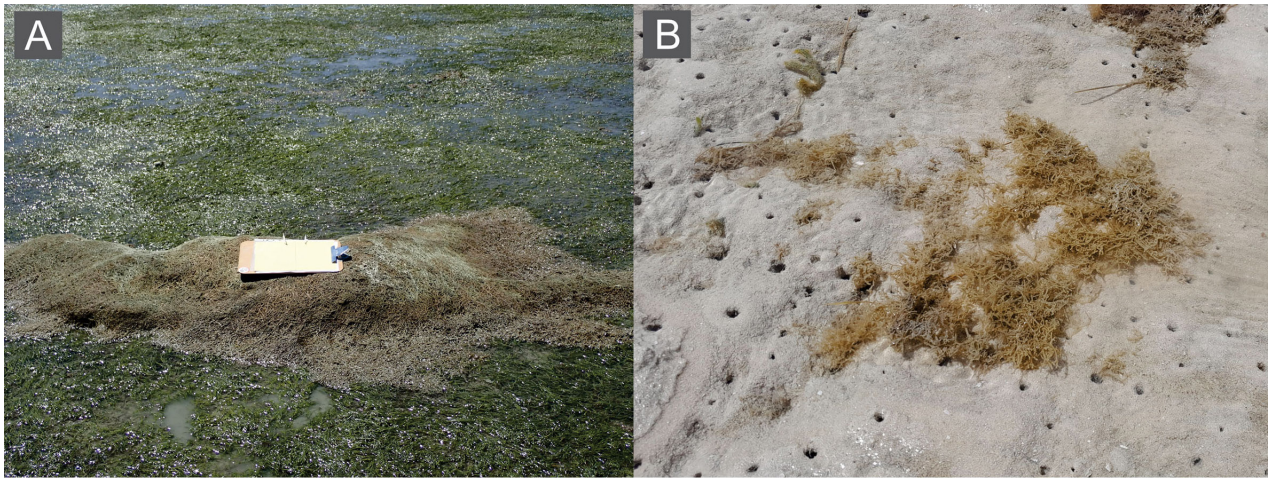

Figure 4. (A) A large colony of *Amathia verticillata* smothering *Zosteria capensis* seagrass at low tide. (photo by Alison Kock). (B) *A. verticillata* colonies anchored to sand prawn (*Kraussillichirus kraussi)* holes (photo by Tammy Robinson).

Table 1. Epifaunal taxa detected on *Amathia verticillata* colonies within Langebaan Lagoon Marine Protected Area. For each species, status (following Robinson et al. 2016; Robinson et al. 2020; Robinson *unpublished data*) and typical habitat are indicated (rocky (R) and/or sandy shores (S) following Branch et al. (2022)).

Taxon	Status	Habitat	Taxon	Status	Habitat
PORIFERA			MOLLUSCA		
Hymeniacidon perlevis	Cryptogenic	R	Assiminea globulus	Native	S
CNIDARIA			Burnupena lagenaria	Native	R
Actiniaria spp	–	R,S	Carditella capensis	Native	S
NEMERTEA			Clionella sinuata	Native	R,S
Nemertea spp	–	R,S	Crepidula porcellana	Native	R
ANNELIDA			Dendrofissurella scutellum	Native	R,S
Platynereis spp	–	R,S	Hydrobia spp	Native	S
ARTHROPODA			Nassarius capensis	Native	R,S
Cymadusa filosa	Native	R	Nassarius kraussianus	Native	S
Danielella edwardsii	Native	S	Oxystele antoni	Native	R
Exosphaeroma kraussi	Native	R	Tellimya trigona	Native	S
Exosphaeroma truncatitelson	Native	S	Sepia spp eggs	Native	R,S
Hymenosoma orbiculare	Native	S	ECHINODERMATA		
Jassa slatteryi	Invasive	R	Amphipholis squamata	Native	S
Mysid spp	–	S	Parvulastra exigua	Native	R
Paridotea reticulata	Native	R	CHORDATA		
Pilumnus minutus	Native	R	Ascidiacea spp 1	–	R
BRYOZOA			Ascidiacea spp 2	–	R
Bugula neritina	Invasive	R	Clinus heterodon	Native	R
Watersipora subtorquata	Invasive	R	RHODOPHYTA		
			Ceramium atrorubescens	Native	R

instances, the percentage cover of the bryozoan exceeded 65% of the hard substrate present. Additionally, colonies were found attached to algal wrack, dead sponges, solitary ascidians (*Pyura herdmani* (Drasche, 1884)) and fossilised oyster beds.

A total of 33 epifaunal species were recorded within the *A. verticillata* colonies (Table 1). The majority of these were native taxa, with three alien (i.e. the amphipod *Jassa slatteryi* (Conlan, 1990) and two bryozoans *Bugula neritina* (Linnaeus, 1758) and *Watersipora subtorquata* (d'Orbigny, 1852)) and one cryptogenic (i.e. the sponge *Hymeniacidon perlevis* (Montagu, 1814)) species detected. Almost half of the species recorded typically occur

on rocky shores and are thus not normally found on the sandflats of the lagoon. The most abundant taxonomic groups found inhabiting *A. verticillata* were amphipods and gastropods, accounting for 25% and 64% of all individuals respectively. The specimens that could not be identified to species level were all juveniles.

Discussion

The west coast is the most invaded region of the South African coastline (Robinson et al. 2020), with the highest number of alien species known from Saldanha Bay (Peters and Robinson 2018). This likely reflects the confluence of many introduction pathways, including an international port, a regional fishing harbour, multiple marinas and mariculture operations (Haupt et al. 2010; Faulkner et al. 2017; Peters and Robinson 2017, 2018). As such, it has been suggested that Saldanha Bay could seed alien species to the surrounding areas, including Langebaan Lagoon and the West Coast National Park (Peters and Robinson 2017). The detection of *Amathia verticillata* takes the number of alien species known from this system to 29 (Mead et al. 2011; Robinson et al. 2016; Peters and Robinson 2018). *Amathia verticillata* was found to be most abundant at the head of the tidal lagoon and occurred in meadows of the endangered seagrass *Zostera capensis*. Notably, this species provided a complex habitat for several rocky shore species within a dominantly sandy environment, with three alien species and one cryptogenic species associated with the bryozoan.

Amathia verticillata is likely to have arrived within Saldanha Bay via biofouling and then spread via fragmentation. After the initial introduction of *A. verticillata*, colonies were most likely dispersed short distances by drifting as rafted masses (Winston 2004) or attached to floating debris (Farrapeira 2011). *Amathia verticillata* colonies were detected almost exclusively within the southern portion of the lagoon (Areas 6 to 13), with a single detached colony detected in area two. This localised distribution is likely driven by flow regimes, in which strong tidal flow through the mouth of the lagoon (Day 1959) carried *A. verticillata* larvae and/or fragments from the bay to shallower areas at the head, where particles are deposited by reduced water flow (Day 1959). Additionally, numerous large colonies were found attached to the hulls of houseboats moored at Kraalbaai (Area 13) and a shallow shipwreck (Area 5). Hard substrata like these and the wooden support beams of bird hides may act as stepping stones for spread within the lagoon by providing a permanent habitat in an otherwise unsuitable environment (Bieler et al. 2017; de Oliveira Soares et al. 2020; Hoeksema et al. 2023). Reports of biofouling on environmental monitoring devices within the lagoon (K. Hutchings *pers. comm.*) and the presence of *A. verticillata* in the background of bird images taken from the Geelbek bird hide and uploaded to the citizen science platform, iNaturalist (S.J. Ackland *pers. obs.*),

suggest that *A. verticillata* has been present in the lagoon since at least 2021. Since then, this invader has become abundant at the head of the lagoon, with most colonies unattached and drifting among *Z. capensis* seagrass meadows or entangled in *Spartina maritima* (Curtis) cordgrass.

The epifauna collected from the stolonal matrices of *A. verticillata* colonies revealed a diversity of associated fauna. This observation is consistent with other studies that have found a range of macrofauna associated with *A. verticillata* (e.g. Farrapeira 2011; Ferrario et al. 2014), including alien invertebrates (Marchini et al. 2015; Guerra-García et al. 2024). The presence of *A. verticillata* within the lagoon may affect the structure of the communities that naturally occur within the area by providing a complex habitat for sessile benthic species that are generally not supported by the adjacent sandy areas of the lagoon. The microhabitats within the stolon matrices of the bryozoan could offer a substrate for settlement while providing protection from predators and fluctuating environmental conditions (Zavacki et al. 2025). A similar outcome was recorded in the lagoon when the Mediterranean mussel *Mytilus galloprovincialis* (Lamarck, 1819) invaded Centre Banks (Robinson and Griffiths 2002) with the complex mussel matrix increasing diversity and abundance of biota, primarily by offering a suitable substratum for rocky shore species that do not normally occur on sandflats (Robinson et al. 2007).

The overlapping distribution of *A. verticillata* and *Z. capensis* within Langebaan Lagoon may be a cause for concern. Langebaan Lagoon is one of the few sheltered areas on the South African coast that supports *Z. capensis* (Adams 2016). This species is considered "Vulnerable" by the IUCN (Short et al. 2010) but "Endangered" within South Africa (Adams and van der Colff 2018). As such, there are active efforts to experiment with restoration to conserve meadows in Langebaan Lagoon (Watson et al. 2023). This seagrass is an important habitat for macrofauna (Barnes 2013; Lawrence 2024) and meaningfully contributes to blue carbon storage (Wasserman et al. 2023). Additionally, this macrophyte supports South Africa's most endangered marine mollusc, the pulmonated limpet *Siphonaria compressa,* which is endemic to just two localities (i.e. Langebaan Lagoon and the Knysna Estuary (Angel et al. 2006)). *Amathia verticillata* is known to occur in seagrass beds in many invaded regions (e.g., Camps-Castellà et al. 2020; El Zrelli et al. 2021; Kumar et al. 2022), with the species causing mass mortality by shading and fouling meadows (Williams 2007). In this study, *A. verticillata* was found in two of the five main seagrass meadows, raising concerns about the potential impacts on the limpet and seagrass. Especially worrisome was numerous large (± 2 m long) colonies in the meadow in Area 8. It should be noted that the largest seagrass meadow within the lagoon (i.e. Centre Banks) was not sampled in this study. While greater water flow in this area, when compared to the meadows at the head of the lagoon (Day 1959), may

prevent the accumulation of *A. verticillata* on Centre Banks, future work should consider the distribution of *A. verticillata* within this seagrass meadow and assess the implications for *Z. capensis*.

The growth and sexual reproduction of *A. verticillata* has been linked to temperature (Bullivant 1968), with abundance following a clear seasonal pattern in many invaded regions (e.g. Winston 1995; Coleman 1999; Micael et al. 2018; Guerra-García et al. 2024; Zavacki et al. 2025). *Amathia verticillata* has been reported to reach maximum biomass during the warmest months of the year. For example, in Mission Bay, USA, cover of this bryozoan is known to increase rapidly from ~ 20% to greater than 80% in less than a month during summer (Zavacki et al. 2025). As temperature declines in autumn, this species begins to enter a senescence period (Guerra-García et al. 2024), during which branches fall off and biomass declines (Micael et al. 2018). In winter, a complete absence of the species has been noted in some regions (e.g. Guerra-García et al. 2024; Zavacki et al. 2025), while sexually reproducing colonies have still been found in others (Micael et al. 2018). The cycle completes when temperatures rise in the spring and biomass increases (Zavacki et al. 2025). While the mechanism behind the apparent disappearance and the reemergence of *A. verticillata* in some regions remains unknown, it has been suggested that the benthos may act as a repository for *A. verticillata*, allowing the species to survive and resettle once temperatures begin to rise (Zavacki et al. 2025).

Given the variability in the temporal abundance of this species in its invaded range, together with a lack of understanding of how it might affect vulnerable species, there is a need to quantify these aspects in the context of Langebaan Lagoon. To achieve this, it is recommended that seasonal monitoring of *A. verticillata* be instituted to assess abundance; colony characteristics that might provide insight into variability in abundance (e.g. size and biomass, strength of branches, presence of reproductive ovicells, changes in colouration); and environmental conditions that may drive temporal abundance patterns (e.g. temperature and salinity (Guerra-García et al. 2024; Zavacki et al. 2025)). This monitoring should be prioritised in key seagrass meadows such as Geelbek and Centre Banks, given the importance of preserving these habitats (Barnes 2013; Wasserman et al. 2023; Lawrence 2024). Additionally, the potential impacts of *A. verticillata* on *Z. capensis* and the abundance of the endemic and endangered *S. compressa* should be assessed. This information can then be used to inform evidence-based management of *A. verticillata* within Langebaan Lagoon MPA. Eradication of marine invasive species is seldom feasible (Roy et al. 2024) and not a viable option for managing *A. verticillata* in Langebaan Lagoon. However, impacts of *A. verticillata* could be mitigated if removal strategies are implemented around target areas and seasons to suppress the population. For example, if abundance is found to vary seasonally as in other locations (Guerra-García et al. 2024; Zavacki et al. 2025) and large mats are found to smother seagrass

beds in late summer, a feasible approach may be simply to remove the large mats from meadows at this time of the year and institute no interventions through the rest of the year when the risk of smothering is reduced.

Potential secondary dispersal of *A. verticillata* from Langebaan Lagoon to other suitable areas along the South African coast via fouling on small vessels (Ulman et al. 2019; Ashton et al. 2022), commercial fishing gear (Jebakumar et al. 2017), drifting (Marchini et al. 2015) or floating debris (Farrapeira 2011; García-Gómez et al. 2021) is a cause for concern. Given that successful eradication is unlikely once *A. verticillata* is established (Amat and Tempera 2009; McCann et al. 2015), it is important that management authorities evaluate and refine guidelines for vessels moving in and out of the lagoon (e.g. visiting yachts and houseboats) and for activities like hull cleaning within the MPA. Additionally, locations within the region of Saldanha Bay that may offer suitable habitat for *A. verticillata*, especially those with seagrass (e.g. Berg River Estuary and Olifants River Estuary (Adams 2016)), should be closely monitored to allow for early detection and rapid response to *A. verticillata* before it becomes established (Reaser et al. 2020). In order to facilitate such monitoring, it is paramount that regional rangers are trained to identify *A. verticillata*.

To ensure a coordinated response to the discovery of this species, it is crucial to communicate with government agencies, local communities (such as fishing and aquaculture groups), and other stakeholders (like yacht clubs and research institutes) using established working groups and coastal committees. This will facilitate the flow of information about measures aiming to prevent spread and new detections. This is particularly important as *A. verticillata* poses a threat not only to the MPA, but also to local industries in Saldanha Bay, including aquaculture and shipping.

This study documents the first occurrence of *A. verticillata* in South Africa, providing foundational knowledge on this globally invasive species within Langebaan Lagoon MPA. Considering the high abundance and wide distribution of this bryozoan within the lagoon, together with the likelihood of the species being present within the greater Saldanha Bay system, eradication is unfeasible. Nonetheless, monitoring locations that may be vulnerable to secondary spread coupled with rapid response to new detections will likely offer the most effective approach to preventing spread and ultimately minimising impacts on native taxa.

Authors' contribution

TBR conceptualised the study. All authors were involved in data collection and contributed to the written manuscript. Submission of the manuscript was approved by all.

Authors' ORCIDs

Sarah Jane Ackland: 0009-0009-0503-107X; Miranda Nicole Andersen: 0009-0009-3525-176X; Alison Kock: 0000-0001-9981-1652; Daniel van Blerk: 0000-0003-0069-3364; Tamara Bridgett Robinson: 0000-0001-5515-1445

Acknowledgements

Sandra Ackland and Inge Raubenheimer are thanked for their assistance in the field when this unusual species was first detected in the West Coast National Park. The researchers would like to thank the West Coast National Park management, Cape Research Centre (SANParks) staff and Groen Sebenza interns for their support and assistance during fieldwork, notably Emma Wright, Kylen Brown and Monray Thorne. Two anonymous reviewers are thanked for their constructive comments during the review process.

Funding declaration

This research was supported through the Research Chair "Managing Invasions in Protected Areas" held by TBR.

Ethics and permits

No ethical approval was required for this study. Fieldwork was undertaken under the authorization of agency scientists at South African National Parks (SANParks) in accordance with the National Environmental Management: Protected Areas Act 57 of 2003.

References

Adams JB (2016) Distribution and status of *Zostera capensis* in South African estuaries. A review. *South African Journal of Botany* 107: 63–73, https://doi.org/10.1016/j.sajb.2016.07.007

Amat JN, Tempera F (2009) *Zoobotryon verticillatum* Della Chiaje, 1822 (Bryozoa), a new occurrence in the archipelago of the Azores (North-Eastern Atlantic). *Marine Pollution Bulletin* 58: 761–764, https://doi.org/10.1016/j.marpolbul.2009.02.019

Angel A, Branch GM, Wanless RM, Siebert T (2006) Causes of rarity and range restriction of an endangered, endemic limpet, *Siphonaria compressa*. *Journal of Experimental Marine Biology and Ecology* 330: 245–260, https://doi.org/10.1016/j.jembe.2005.12.031

Ashton GV, Zabin CJ, Davidson IC, Ruiz GM (2022) Recreational boats routinely transfer organisms and promote marine bioinvasions. *Biological Invasions* 24: 1083–1096, https://doi.org/10.1007/s10530-021-02699-x

Aslam S, Siddiqui G, Kazmi SJH, Moura CJ (2019) First occurrence of the non-indigenous bryozoan *Amathia verticillata* (della Chiaje, 1882) at the Hab river mouth in Pakistan. *Regional Studies in Marine Science* 30: 1–5, https://doi.org/10.1016/j.rsma.2019.100706

Barnes RSK (2013) Distribution patterns of macrobenthic biodiversity in the intertidal seagrass beds of an estuarine system, and their conservation significance. *Biodiversity and Conservation* 22: 357–372, https://doi.org/10.1007/s10531-012-0414-z

Bieler R, Granados-Cifuentes C, Rawlings TA, Sierwald P, Collins TM (2017) Non-native molluscan colonizers on deliberately placed shipwrecks in the Florida Keys, with description of a new species of potentially invasive worm-snail (Gastropoda: Vermetidae). *PeerJ* 5: e3158, https://doi.org/10.7717/peerj.3158

Boonzaaier MK (2017) Diversity and zooeography of South African Bryozoa. PhD thesis, University of the Western Cape, South Africa, 339 pp

Branch GM, Griffiths CL, Branch M, Beckley L (2022) Two Oceans. A guide to the marine life of southern Africa. Struik, Cape Town, South Africa, 464 pp

Bullivant JS (1968) Attachment and growth of the stoloniferous ctenostome bryozoan, *Zoobotryon verticillatum*. *Bulletin of the Southern California Academy of Sciences* 67: 199–202

Camps-Castellà J, Ballesteros M, Trobajo R, Pontes M, Prado P (2020) Not all nudibranchs are carnivorous: trophic ecology of *Polycerella emertoni* in the Ebro Delta. *Marine Ecology Progress Series* 645: 67–82, https://doi.org/10.3354/meps13379

Coleman FS (1999) Note on *Zoobotryon verticillatum* (Bryozoa) in a solar salt field. *International Journal of Salt Lake Research* 8: 71–74, https://doi.org/10.1007/BF02442138

Conlan KE, Desiderato A, Beermann J (2021) *Jassa* (Crustacea: Amphipoda): a new morphological and molecular assessment of the genus. *Zootaxa* 4939: 1–191, https://doi.org/10.11646/zootaxa.4939.1

Day JH (1959) The biology of Langebaan Lagoon: a study of the effect of shelter from wave action. *Transactions of the Royal Society of South Africa* 35: 475–547, https://doi.org/10.1080/00359195909519025

de Oliveira Soares M, Salani S, Paiva SV, Braga MDA (2020) Shipwrecks help invasive coral to expand range in the Atlantic Ocean. *Marine Pollution Bulletin* 158: 111394, https://doi.org/10.1016/j.marpolbul.2020.111394

El Zrelli R, Mansour L, Crocetta F, Rabaoui L (2021) The macroalgae *Lophocladia lallemandii* and *Sarconema filiforme* and the spaghetti bryozoan *Amathia verticillata* in native seagrass beds in the Gulf of Gabès (southeastern Tunisia, Mediterranean Sea). *BioInvasions Records* 10: 103–108, https://doi.org/10.3391/bir.2021.10.1.12

Farrapeira CMR (2011) The introduction of the bryozoan *Zoobotryon verticillatum* (Della Chiaje, 1822) in northeast of Brazil: a cause for concern. *Biological Invasions* 13: 13–16, https://doi.org/10.1007/s10530-010-9788-6

Faulkner KT, Robertson MP, Rouget M, Wilson JRU (2017) Prioritising surveillance for alien organisms transported as stowaways on ships travelling to South Africa. *PLoS ONE* 12: e0173340, https://doi.org/10.1371/journal.pone.0173340

Ferrario J, Marchini A, Lodola A, Occhipinti Ambrogi A (2014) The pseudoindigenous bryozoan *Zoobotryon verticillatum* along the Mediterranean and Atlantic European coasts. *Biologia Marina Mediterranea* 21: 117–118

Galil BS, Gevili R (2014) *Zoobotryon verticillatum* (Bryozoa: Ctenostomatida: Vesiculariidae), a new occurrence on the Mediterranean coast of Israel. *Marine Biodiversity Records* 7: 1–4, https://doi.org/10.1017/S1755267214000086

García-Gómez JC, Garrigós M, Garrigós J (2021) Plastic as a vector of dispersion for marine species with invasive potential. A review. *Frontiers in Ecology and Evolution* 9: 629756, https://doi.org/10.3389/fevo.2021.629756

Gestoso I, Ramalhosa P, Oliveira P, Canning-Clode J (2017) Marine protected communities against biological invasions: a case study from an offshore island. *Marine Pollution Bulletin* 119: 72–80, https://doi.org/10.1016/j.marpolbul.2017.03.017

Gordon DP, Mawatari SF (1992) Atlas of marine-fouling bryozoa of New Zealand ports and harbours. *Miscellaneous Publications of the New Zealand Oceanographic Institute* 107: 1–52

Griffiths CL (1976) Guide to the benthic marine amphipods of southern Africa. South African Museum, Cape Town, South Africa, 106 pp

Guerra-García JM, Ruiz-Velasco S, Navarro-Barranco C, Moreira J, Angulo G, García-Domínguez R, Amengual J, Saenz-Arias P, López-Fé CM, Martínez-Pita I, García-García FJ, Ros M (2024) Facilitation of macrofaunal assemblages in marinas by the habitat-forming invader *Amathia verticillata* (Bryozoa: Gymnolaemata) across spatiotemporal scale. *Marine Environmental Research* 193: 106256, https://doi.org/10.1016/j.marenvres.2023.106256

Hanekom N, Randall RM, Nel P, Kruger N (2009) West Coast National Park - State of Knowledge. South African National Parks (SANParks), February 2009, 65 pp

Haupt TM, Griffiths CL, Robinson TB (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

Hoeksema BW, Meijer zu Schlochtern MP, Samimi-Namin K, McFadden CS (2023) In the aftermath of Hurricane Irma: Colonization of a 4-year-old shipwreck by native and non-native corals, including a new cryptogenic species for the Caribbean. *Marine Pollution Bulletin* 188: 114649, https://doi.org/10.1016/j.marpolbul.2023.114649

Humara-Gil KJ, Cruz-Gómez (2019) First record of the non-indigenous bryozoan *Amathia verticillata* (delle Chiaje, 1822) (Bryozoa, Vesiculariidae) in the southern Mexican Pacific. *Check List* 15: 515–522, https://doi.org/10.15560/15.3.515

Jebakumar JPP, Nandhagopal G, Rajan Babu B, Ragumaram S, Ravichandran V, Marchini A, Minchin D (2017) The bryozoan *Amathia verticillata* (delle Chiaje, 1822) fouling harbours of the southeast coast of India: re-evaluating its status. *Bioinvasions Records* 6: 211–216, https://doi.org/10.3391/bir.2017.6.3.05

Kensley B (1978) Guide to the marine isopods of southern Africa. South African Museum, Cape Town, South Africa, 173 pp

Kumar JPPJ, Nandhagopal G, Babu BR, Ragumarn S, Jha DK, Kumar JS, Dharani G, Ravichandran V (2022) A looming chance of bio invasion by a bryozoan *Amathia verticillata* among the sea fan and seagrass population along Tamil Nadu coast: a case study. *Proceedings of the Zoological Society* 75: 173–180, https://doi.org/10.1007/s12595-021-00387-1

Lawrence CM (2024) Quantifying direct and indirect linkages between seagrasses, environment and associated macrofauna in a temperate lagoon. *Marine Ecology* e12804, https://doi.org/10.1111/maec.12804

López-Gappa J, Liuzzi MG (2016) Recent discovery of non-indigenous bryozoans in the fouling assemblage of Quequén Harbour (Argentina, Southwest Atlantic). *Marine Biodiversity* 48: 1159–1167, https://doi.org/10.1007/s12526-016-0561-7

Marchini A, Ferrario J, Minchin D (2015) Marinas may act as hubs for the spread of the pseudo-indigenous bryozoan *Amathia verticillata* (delle Chiaje, 1882) and its associates. *Scientia Marina* 79: 355–365, https://doi.org/10.3989/scimar.04238.03A

McCann LD, Keith I, Carlton JT, Ruiz GM, Dawson TP, Collins K (2015) First record of the non-native bryozoan *Amathia* (=*Zoobotryon) verticillata* (delle Chiaje, 1822) (Ctenostomata) in the Galápagos Islands. *BioInvasions Records* 4: 255–260, https://doi.org/10.3391/bir.2015.4.4.04

McCann LD, McCuller MI, Carlton JT, Keith I, Geller JB, Ruiz GM (2019) Bryozoa (Cheilostomata, Ctenostomata, and Cyclostomata) in Galapagos Island fouling communities. *Aquatic Invasions* 14: 85–131, https://doi.org/10.3391/ai.2019.14.1.04

Mead A, Carlton JT, Griffiths CL, Rius M (2011) 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

Micael J, Gillon A, Jardim N, Rodrigues P, Costa AC (2018) Sexual reproduction in the invasive bryozoan *Amathia verticillata* (Ctenostomatida: Vesiculariidae). *Journal Coastal Conservation* 22: 305–314, https://doi.org/10.1007/s11852-017-0577-6

Minchin D (2012) Rapid assessment of the bryozoan, *Zoobotryon verticillatum* (Delle Chiaje, 1822) in marinas, Canary Islands. *Marine Pollution Bulletin* 64: 2146–2150, https://doi.org/10.1016/j.marpolbul.2012.07.041

Minchin D, Liu T, Cheng M (2016) First record of Bryozoan *Amathia* (*Zoobotryon*) *verticillata* (Bryozoan: Vesiculariidae) from Taiwan. *Pacific Science* 70: 509–517, https://doi.org/10.2984/70.4.9

Miranda AA, Almeida ACS, Vieira LM (2018) Non-native marine bryozoans (Bryozoa: Gymnolaemata) in Brazilian waters: assessment, dispersal and impacts. *Marine Pollution Bulletin* 130: 184–191, https://doi.org/10.1016/j.marpolbul.2018.03.023

Nascimento KB, Migotto AE, Fehlauer-Ale KH (2021) Molecular data suggests the worldwide introduction of the bryozoan *Amathia verticillata* (Ctenostomata, Vesiculariidae). *Marine Biology* 168: 33, https://doi.org/10.1007/s00227-021-03837-8

Osburn RC, Soule JD (1953) Order Ectoprocta, Suborder Ctenostomata. In: Bryozoa of the Pacific coast of America. Part 3, Cyclostomata, Ctenostomata, Entoprocta, and Addenda. Allan Hancock Pacific Expeditions 14, pp 726–758

Pestana LB, Dias GM, Marques AC (2020) Spatial and temporal diversity of biofouling species associated with Angolan bays. *African Journal of Marine Science* 42: 413–422, https://doi.org/10.2989/1814232X.2020.1831954

Peters K, Robinson TB (2017) First record of the marine alien amphipod *Caprella mutica* (Schurin, 1935) in South Africa. *BioInvasions Records* 6: 61–66, https://doi.org/10.3391/bir.2017.6.1.10

Peters K, Robinson TB (2018) From Chile to the South African west coast: first reports of the Chilean stone crab *Homalaspis plana* (H. Milne Edwards, 1834) and the South American sunstar *Heliaster helianthus* (Lamarck, 1816) outside their natural ranges. *BioInvasions Records* 7: 421–426, https://doi.org/10.3391/bir.2018.7.4.11

Reaser JK, Burgiel SW, Kirkey J, Brantley KA, Veatch SD, Burgos-Rodriguez J (2020) The early detection of and rapid response (EDRR) to invasive species: a conceptual framework and federal capacities assessment. *Biological Invasions* 22: 1–19, https://doi.org/10.1007/s10530-019-02156-w

Robinson TB, Griffiths CL (2002) Invasion of Langebaan Lagoon, South Africa, by *Mytilus galloprovincialis* – effects on natural communities. *African Zoology* 37: 151–158, https://doi.org/10.1080/15627020.2002.11657170

Robinson TB, Swart C (2015) Distribution and impact of the alien anemone *Sagartia ornata* in the West Coast National Park. *Koedoe* 57: a1246, https://doi.org/10.4102/koedoe.v57i1.1246

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

Robinson TB, Branch GM, Griffiths CL, Govender A (2007) The invasion and subsequent die-off of *Mytilus galloprovincialis* in Langebaan Lagoon, South Africa: effects on natural communities. *Marine Biology* 152: 225–232, https://doi.org/10.1007/s00227-007-0697-x

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, Peters K, Brooker B (2020) Coastal invasions: The South African context. In: Van Wilgen BW, Measey J, Richardson DM, Wilson JR, Zengeya TA (eds), Biological Invasions in South Africa. Springer International Publishing, pp 229–247, https://doi.org/10.1007/978-3-030-32394-3_9

Roy HE, Pauchard A, Stoett PJ, Truong TR, Meyerson LA, Bacher S, Galil BS, Hulme PE, Ikeda T, Kavileveettil S, McGeoch MA, Nuñez MA, Ordonez 16, Rahlao SJ, Schwindt E, Seebens H, Sheppard AW, Vandvik V, Aleksanyan A, Ansong M, August T, Blanchard R, Brugnoli E, Bukombe JK, Bwalya B, Byun C, Camacho-Cervantes M, Cassey P, Castillo ML, Courchamp F, Dehnen-Schmutz K, Zenni RD, Egawa C, Essl F, Fayvush G, Fernandez RD, Fernandez M, Foxcroft LC, Genovesi P, Groom QJ, González AI, Helm A, Herrera I, Hiremath AJ, Howard PL, Hui C, Ikegami M, Keskin E, Koyama A, Ksenofontov S, Lenzner B, Lipinskaya T, Lockwood JL, Mangwa DC, Martinou AF, McDermott SM, Morales CL, Müllerov J, Mungi NA, Munishi LK, Ojaveer H, Pagad SN, Pallewatta NPKTS, Peacock LR, Per EP, Pergl J, Preda C, Pyšek P, Rai RK, Ricciardi A, Richardson DM, Riley S, Rono BJ, Ryan-Colton E, Saeedi H, Shrestha BB, Simberloff D, Tawake A, Tricarico E, Vanderhoeven S, Vicente J, Vilà M, Wanzala W, Werenkraut V, Weyl OLF, Wilson JRU, Xavier RO, Ziller SR (2024) Curbing the major and growing threats from invasive alien species is urgent and achievable. *Nature Ecology and Evolution* 8: 1216–1223, https://doi.org/10.1038/s41559-024-02412-w

Samaai T, Gibbons MJ (2005) Demospongiae taxonomy and biodiversity of the Benguela region on the west coast of South Africa. *African Natural History* 1: 1–96, https://hdl.handle.net/10520/EJC17340

Schwindt E, Battini N, Giachetti CB, Castro KL, Bortolus A (2018) Marine-coastal exotic species of Argentina. Vazquez Mazzini, Puerto Madryn, Argentina, 165 pp

Short FT, Coles R, Waycott M, Bujang JS, Fortes M, Prathep A, Kamal AHM, Jagtap TG, Bandeira S, Freeman A, Erftemeijer P, La Nafie YA, Vergara S, Calumpong HP, Makm I (2010) *Zostera capensis*. *The IUCN Red List of Threatened Species* 2010: e.T173370A7001305, https://doi.org/10.2305/IUCN.UK.2010-3.RLTS.T173370A7001305.en

Tilbrook KJ (2012) Bryozoa, Cheilostomata: first records of two invasive species in Australia and the northerly range extension for a third. *Check List* 8: 181–183, https://doi.org/10.15560/8.1.181

Ulman A, Ferrario J, Forcada A, Seebens H, Arvanitidis C, Occhipinti-Ambrogi A, Marchini A (2019) Alien species spreading via biofouling on recreational vessels in the Mediterranean Sea. *Journal of Applied Ecology* 56: 2620–2629, https://doi.org/10.1111/1365-2664.13502

Vieira LM, Migotto AE, Winston JE (2014) Ctenostomatous Bryozoa from São Paulo, Brazil, with descriptions of twelve new species. *Zootaxa* 3889: 485–524, https://doi.org/10.11646/zootaxa.3889.4.2

Wasserman J, Human LR, Adams JB (2023) Blue carbon stocks in southern Africa's Endangered seagrass *Zostera capensis*. *Estuarine, Coastal and Shelf Science* 284: 108296, https://doi.org/10.1016/j.ecss.2023.108296

Watson KM, Pillay D, von der Heyden S (2023) Using transplantation to restore seagrass meadows in a protected South African lagoon. *PeerJ* 11: e16500, https://doi.org/10.7717/peerj.16500

Williams SL (2007) Introduced species in seagrass ecosystems: status and concerns. *Journal of Experimental Marine Biology and Ecology* 350: 89–110, https://doi.org/10.1016/j.jembe.2007.05.032

Winston JE (1995) Ectoproct diversity of the Indian River coastal lagoon. *Bulletin of Marine Science* 57: 84–93

Winston JE (2004) Bryozoans from Belize. *Atoll Research Bulletin* 523: 1–14, https://doi.org/10.5479/si.00775630.523.1

Zavacki EM, Reyns NB, Crooks JA, Boudrias MA (2025) The influence of biogenic habitat created by non-indigenous bryozoan, *Amathia verticillata*, on the resident marine invertebrate community in San Diego, California. *Aquatic Invasions* 20 *(in press)*

Web sites, online databases and software

Adams J, van der Colff D (2018) *Zostera capensis*. National Assessment: Red List of South African Plants version. http://redlist.sanbi.org/species.php?species=4111-1 (accessed 18 April 2024)

Supplementary material

The following supplementary material is available for this article:

Table S1. Sampling sites and geo-referenced records of *Amathia verticillata*.

This material is available as part of online article from:
http://www.reabic.net/journals/bir/2025/Supplements/BIR_2025_Ackland_etal_SupplementaryMaterial.xlsx