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Research Article

To South Africa and beyond: Local distribution and global invasion potential of the alien anemone *Cereus pedunculatus*

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Abstract

Effective management of invasive alien species relies on spatial and temporal data. Yet, such information is scarce in the marine realm due to challenges associated with monitoring in highly connected environments that can be difficult to observe. As a result, many marine invasions remain poorly documented, hindering management. One such case is that of the European daisy anemone *Cereus pedunculatus* Pennant, 1777 in its invaded range of South Africa. Until recently, this alien anemone was thought to be restricted to the Langebaan Lagoon marine protected area (MPA), where occurrence records are seldom updated. The recent detection of *C. pedunculatus* in a distant estuary highlights the potential for further spread. To inform the management of this species, this study updated occurrence and abundance records in Langebaan Lagoon MPA and identified potential invasion hotspots using an ensemble-based species distribution model. Field surveys revealed that the anemone has expanded into six new areas of the lagoon since 2013. Modelling results indicate highly suitable conditions for the anemone at 31 sheltered sites along the coast of South Africa, including four sites within MPAs (i.e. Namaqua National Park MPA, Betty's Bay MPA, Stilbaai MPA, and Goukamma MPA). Given this invasion risk, management agencies should employ routine monitoring and develop contingency plans for these sites to ensure adequate preparedness for future incursions of the species. Additionally, countries with climatically suitable regions, including Argentina, Australia, Denmark, New Zealand, Norway, and the United States, may consider including *C. pedunculatus* on national watchlists.

Key words: Anthozoa, daisy anemone, ensemble model, Knysna Estuary, Langebaan Lagoon, marine bioinvasions, species distribution

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Introduction

In recognition of the global scale of biological invasions (Sardain et al. 2019; Bailey et al. 2020) and the impacts they have (Anton et al. 2019; Dueñas et al. 2021; Cuthbert et al. 2022), there is increasing emphasis on the prevention and management of invasive alien species. Target 6 of the Kunming-Montreal Global Biodiversity Framework (CBD/COP/DEC/15/4) directly addresses

this imperative. To support progress towards this ambitious target and comply with national legislative directives, comprehensive measures of spatial and temporal trends in alien species occurrences are needed (Lehtiniemi et al. 2015; McGeoch et al. 2023). Such data, obtained through consistent monitoring and surveillance (Loureiro et al. 2021), underpins risk assessments (Kumschick et al. 2020), management feasibility assessments (Booy et al. 2020), and contingency planning (Booy et al. 2017; Padayachee et al. 2019).

Despite their importance, invasion records and long-term survey data are largely incomplete in the marine realm due to challenges with monitoring in highly connected environments, limited search efforts, insufficient methodological standardization, ambiguous invasion histories, and declines in taxonomic expertise (Ojaveer et al. 2014; Bailey et al. 2020; Fowler et al. 2025). These gaps are particularly pronounced for smaller-bodied taxa (Galil et al. 2018) and understudied groups (e.g. Ascidians (Zhan et al. 2015) and Anthozoans (Glon et al. 2020)). The absence of such baseline occurrence data is especially problematic in the marine realm, where invasive species management is uniquely challenging. When a marine invader goes undetected in a region and becomes established, eradication becomes exceedingly challenging and is seldom feasible (Guastella et al. 2019; Simberloff 2020; Ribeiro et al. 2023). In such cases, containment of the invader and the identification of high-risk areas where proactive management might still be feasible, may be the only viable options (Giakoumi et al. 2019).

For these reasons, once a marine invader is identified within a country, understanding the extent of the invasion (e.g. Mabin et al. 2017; Bezuidenhout and Robinson 2020) is an essential first step for management intervention. Anticipating spread, particularly to nearby vulnerable areas, is the next step. Species distribution models are increasingly used to forecast suitable regions for marine invasions (e.g. Goldsmit et al. 2020; Blanco et al. 2021; Ohanna et al. 2025). These models can support the creation of watchlists and contingency plans (Jarnevich et al. 2023; Clarke et al. 2025), ultimately reducing invasion-related costs by guiding proactive management (Diagne et al. 2021; Cuthbert et al. 2022).

The alien anemone *Cereus pedunculatus* Pennant, 1777 is established and naturalized in Langebaan Lagoon marine protected area (MPA) on the west coast of South Africa (Robinson and Swart 2015; Fig. 1) and exemplifies the challenges posed by limited and outdated baseline data. This European species is native to northern Europe and the Mediterranean Sea (Schmidt 1972; Manuel 1981) and was first reported from Langebaan Lagoon in 2001 as *Sagartia* (now *Cylista*) *ornata* (Acuña et al. 2004), although recent work has clarified its identity as *Cereus pedunculatus* (Andersen et al. in press). The distribution of *C. pedunculatus* in Langebaan Lagoon changed considerably during the first 12 years after it was first detected (Robinson and Swart 2015). However, no subsequent monitoring has been conducted. This lack of up-to-date information limits our understanding of its invasion dynamics in this important MPA and hinders compliance with South Africa's National Environmental Management: Biodiversity Act 2004 (NEMBA Act No. 10 of 2004), which requires regular reporting on the status of biological invasions.

Historically, *C. pedunculatus* was thought to be restricted to Langebaan Lagoon (Robinson and Swart 2015), due to the deep waters and narrow intertidal zones of Saldanha Bay and the exposed nature of the open coast (Griffiths et al. 2010; Assis et al. 2015). Yet, in January 2025, a population of this anemone was detected over 650 km away in Knysna Estuary on the South African south

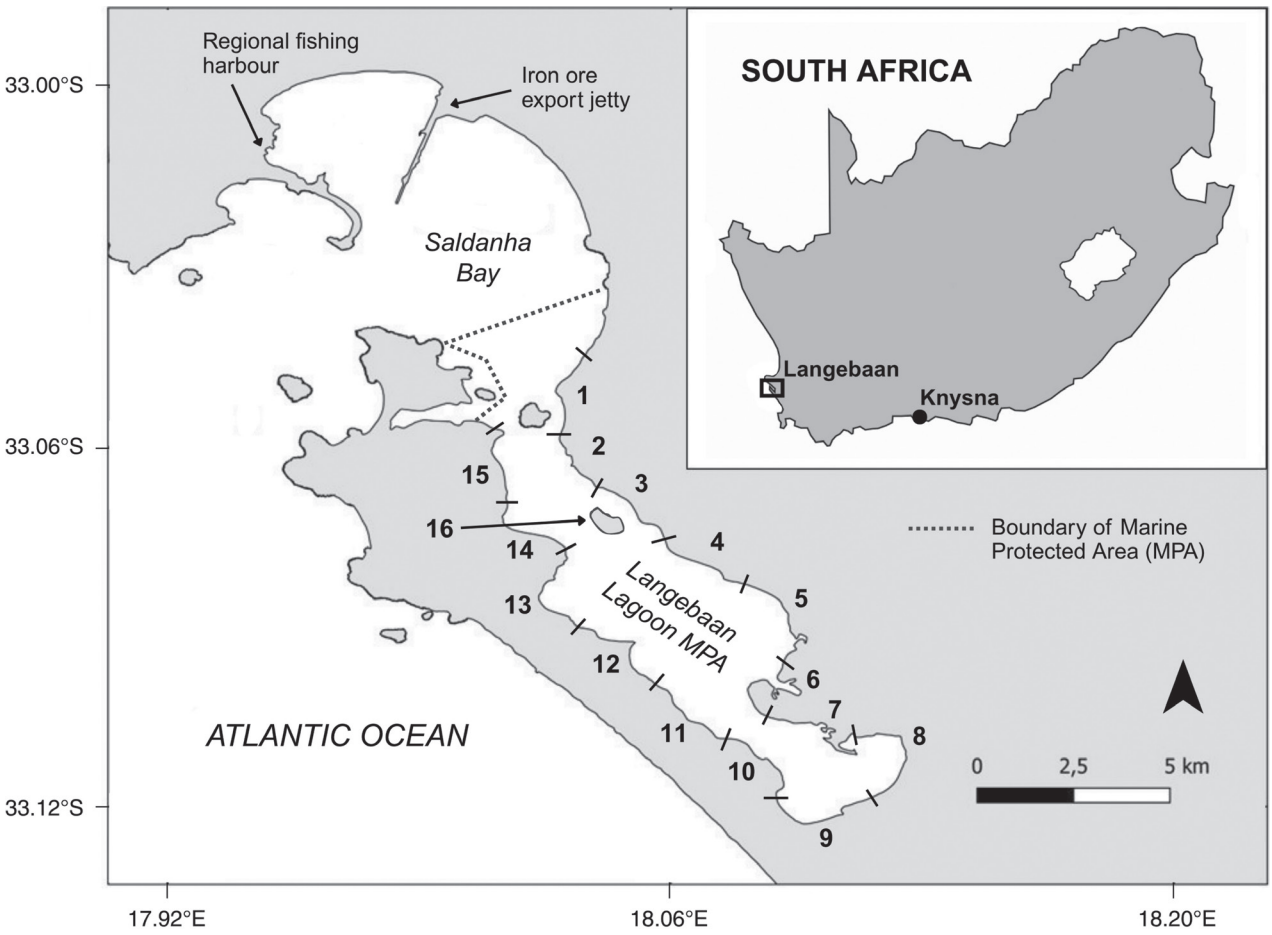

Figure 1. Map of Langebaan Lagoon marine protected area and Saldanha Bay in South Africa. Fifteen, 3 km long sampling areas are illustrated, as outlined by Robinson and Swart (2015). These areas and Centre Banks (Area 16), a sandflat exposed at low tide, were surveyed for *Cereus pedunculatus*. The locations of Langebaan (first reported occurrence) and Knysna (new introduction or secondary introduction) are indicated on the overview map.

coast (van Blerk unpublished data). Knysna Estuary is of particular conservation importance as it supports several at-risk species (e.g. the range-restricted endemic limpet *Siphonaria compressa* Allanson, 1958 (Angel et al. 2006), the endangered seahorse *Hippocampus capensis* Boulenger, 1900 (Lockyear et al. 2006), and the locally endangered seagrass *Zostera capensis* Setchell, 1933 (Adams 2016)). The estuary also shares faunal and environmental similarities with Langebaan Lagoon (Angel et al. 2006). This raises concerns about the potential vulnerability of other sheltered areas, such as Berg River Estuary, which is even closer to Langebaan Lagoon.

This study used the invasion of *C. pedunculatus* in South Africa as an example of maintaining baseline data on a marine alien species and assessing its potential for spread. Specifically, we pursued two complementary aims: (1) to update and extend the long-term dataset for *C. pedunculatus* in Langebaan Lagoon MPA by conducting the first surveys of its distribution and abundance since 2013; and (2) to identify potential invasion hotspots at national and global scales using ensemble-based species distribution modelling. Integrating field surveys with distribution modelling enhanced our current understanding of the *C. pedunculatus* invasion in South Africa and its potential for spread, elucidating priority areas where proactive management measures should be focused.

Methods

Study site

Field work was conducted in the Langebaan Lagoon marine protected area (MPA) (33°08'S, 18°03'E). This 6000-hectare protected area is approximately 15 km long and four km wide. The lagoon opens into Saldanha Bay, which is fed by the Atlantic Ocean. Composed primarily of intertidal sandflats and marshland, the lagoon serves as an important refuge for a diverse suite of marine organisms, coastal birds, and at-risk species, including *Siphonaria compressa* and *Zostera capensis* (Angel et al. 2006; Pillay et al. 2010; Adams 2016). 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).

Distribution and abundance surveys

The distribution and abundance of *Cereus pedunculatus* were surveyed in April 2025, during the same time of year and tidal phase as previous studies (Robinson et al. 2004; Robinson and Swart 2015). Following these studies, the shoreline of the lagoon was divided into 15 sampling areas, each 3 km in length (Fig. 1). Additionally, Centre Banks (Area 16) was surveyed to assess the density of *C. pedunculatus* in *Z. capensis* seagrass meadows, as the anemone was recently reported from this area (Lawrence 2024). Within each of the 16 sampling areas, habitats previously identified as suitable for this anemone (i.e. hard substrates, especially those partially buried in loose sediment, loose rocks on fossilized oyster beds, *Spatina maritima* (Curtis) Fernald cordgrass beds and *Z. capensis* seagrass beds (Robinson et al. 2004; Robinson and Swart 2015; Lawrence 2024)) were closely examined using standardized surveys. Geolocations of all populations were recorded for occurrence data and mapping. In areas where the anemone was detected, 10 quadrats of 0.25 m^2 were randomly placed in suitable habitats in each shore zone (high-, mid-, and low-shore zones). The habitat type and number of anemones within each of these quadrats were recorded.

Statistical analyses considered historical data from 2001 (Robinson et al. 2004) and 2013 (Robinson and Swart 2015), and data collected in 2025. After verifying statistical assumptions were met, a generalized least squares (GLS) model was used to examine how anemone density varied across areas over time in the mid-shore. Note that other shore zones were not considered, as this is the only zone in which the anemone has historically occurred. Additionally, areas in which the anemone has never been recorded were excluded from the analysis. The saturated model included both predictors and their interaction term, and best fit model was identified using the 'dredge' function from the MuMIn package (Bartoń 2025) and the lowest Akaike information criterion (AIC) value (Burnham and Anderson 2002). All analyses were carried out in R v.4.3.4 (R Core Team).

Species distribution modelling

Occurrence data cleaning and processing

Georeferenced global occurrence data for *C. pedunculatus* were obtained from the Global Biodiversity Information Facility (8203 records) and the Ocean Biodiversity Information System (5369 records) on December 5, 2024. Data quality control involved multiple steps. First, duplicate and invalid occurrences (those with missing, identical, or default 0.0 coordinates) were excluded using the CoordinateCleaner package v.3.0.1 (Zizka et al. 2019). Records with coordinates rounded

to fewer than three decimal places were removed due to low spatial resolution (Mancinelli et al. 2021). Finally, records with high temporal or taxonomic uncertainty were excluded, including those lacking a year of record (Mancinelli et al. 2021; Song et al. 2024) or catalogued under the unaccepted synonym *Sagartia* (now *Cylista*) *troglodytes* Price, 1847.

The cleaned occurrence dataset was supplemented with seven additional georeferenced records identified through literature searches in Scopus, Web of Science, and Google Scholar (December 26, 2024) using the keyword "*Cereus pedunculatus*". Given that global records are thought to more closely characterise the realized niche of an alien species than records from either it's native or non-native range alone (Jiménez-Valverde et al. 2011; Zhang et al. 2020), 14 records from preliminary field surveys conducted in Langebaan Lagoon during austral autumn and winter 2024 and one record from Knysna estuary (van Blerk unpublished dataset) were also included in the dataset. To reduce potential sampling biases and spatial autocorrelation effects on model overfitting (Boria et al. 2014), spatial thinning was then applied to the dataset. Records were thinned to the lowest resolution of environmental predictors (5 arc min or ~9.2 km at the Equator) and clipped to the predictors' extent (see below). After thinning, 716 occurrence records of *C. pedunculatus* were retained for model calibration and validation (Suppl. material 1, 2: table S1, fig. S1).

Environmental data selection

Candidate environmental predictors were selected based on their biological relevance to anemone invasions (Glon et al. 2020) and their established application in related studies focusing on intertidal alien species (e.g. Gimenez et al. 2022; Adamu and Hussaini 2024). These included sea surface temperature, salinity, primary productivity, and dissolved oxygen (Suppl. material 1: table S2) obtained from Bio-ORACLE v.2.2 (Assis et al. 2017). Environmental layers from 2000–2014 were used as opposed to those from 2010–2020 because they were found to have higher spatial accuracy in narrow waterways where the anemone occurs, and do not meaningfully vary from 2010–2020 data (linear regressions, $p < 0.001$ in all cases; Suppl. material 2: fig. S2). Additionally, bathymetry data from MARSPEC (Sbrocco and Barber 2013) were included to provide a comprehensive assessment of habitat suitability. Considering that *C. pedunculatus* is limited to intertidal and occasionally shallow subtidal (< 25 m) environments (Manuel 1981), only grid cells within 25 km of the coastline were retained (Samaai et al. 2022).

The collinearity of predictors was checked at 10000 randomly generated background points using Pearson's correlation in the covsel package v.1.0.0 (Adde et al. 2023). Two predictors were considered highly correlated when $|r| > 0.7$ (Dormann et al. 2012) (Suppl. material 2: fig. S3). In these instances, one of the two correlated predictors was manually selected based on biological relevance. This resulted in the exclusion of dissolved oxygen and the retention of four predictors: maximum sea surface temperature, maximum sea surface salinity, mean primary productivity, and bathymetry.

Ensemble modelling

This study opted for an ensemble approach using the biomod2 package v.4.2-6-2 (Thuiller et al. 2009), as ensembles are known to limit modelling bias and uncertainty (Dormann et al. 2018; Ramirez-Reyes et al. 2021). Pseudo-absences were randomly generated within 25 km of the coastline over ten runs at an equal weight

to the occurrence records (PAs = 716) to account for variance across sampling runs (Barbet-Massin et al. 2012). Eleven algorithms were considered: Artificial Neural Networks (ANN), Classification Tree Analysis (CTA), Flexible Discriminant Analysis (FDA), Generalised Additive Model (GAM), Gradient Boosting Machine (GBM), Generalised Linear Model (GLM), Multivariate Adaptive Regression Splines (MARS), Maximum Entropy (MaxEnt), Random Forest (RF), Species Range Envelope (SRE), and Extreme Gradient Boosting (XGBoost). To select the most accurate and least spatially biased model from each algorithm category (Suppl. material 1: table S3), five-fold spatial cross-validation along the y(latitudinal)-axis was used. This method reduces the effects of spatial autocorrelation and allows for consideration of spatial transferability in model selection (Roberts et al. 2016). Initial models were trained with default parameters, and the most accurate algorithms—ANN, CTA, GBM, GLM, MARS, and MaxEnt —were selected based on the validation True Test Statistic (TSS) (Suppl. material 2: fig. S4). For the most performant subset of algorithms, hyperparameters were tuned using spatial cross-validation, and optimal parameters were selected based on model sensitivity and specificity values (Suppl. material 1: table S3). The contribution of each model to the ensemble was weighed based on model accuracy.

Identification of potentially suitable sites

Sites along the South African coast that are potentially susceptible to the establishment of *C. pedunculatus* were identified using the ensemble model suitability scores and marine habitat shapefiles (South African National Biodiversity Institute 2011) overlaid in QGIS. This manual approach was chosen over incorporating habitat into the SDM to enable careful interrogation of each site. Sites were classified as highly suitable if they met two criteria: (1) a suitability score ≥ 0.75, and (2) the presence of one of three habitat types (i.e. sheltered rocky shore; lagoon; or estuarine shore near to mixed substrate). These habitat types were selected based on known habitat preferences of the species within South Africa (Robinson and Swart 2015) and its native range (Manuel 1981; Cognetti and Maltagliati 2000). In areas meeting both criteria, sites were identified as one geolocation point per pixel, at the resolution of the suitability model. To identify suitable sites within key conservation areas, a shapefile of South African Marine Protected Areas (Department of Environmental Affairs 2022) was overlaid.

Outside of South Africa, highly suitable global sites were identified using the suitability score threshold (≥ 0.75) alone, irrespective of habitat type, as the availability of high-resolution coastal habitat data is inconsistent across regions.

Results

Distribution and abundance

Cereus pedunculatus was recorded in six new areas of Langebaan Lagoon in 2025 (i.e. Areas 1, 4, 6, 8, 11, 15; Fig. 2), and surveyed at Centre Banks (Area 16, 140 ± 30.6 individuals/m^2) for the first time. Although the anemone was newly detected in the high- and low-shore zones in 2025, its highest densities remained in the mid-shore zone (Suppl. material 1: table S4). The best fit GLS model, based on AIC, included area, year, and their interaction. Anemone density differed significantly between areas (GLS, $F_{(13)} = 32.84$, $p < 0.001$) and years (GLS, $F_{(2)} = 28.68$, $p < 0.001$), while the interaction between these was also significant (GLS, $F_{(26)} = 18.86$, $p < 0.001$) (Fig.

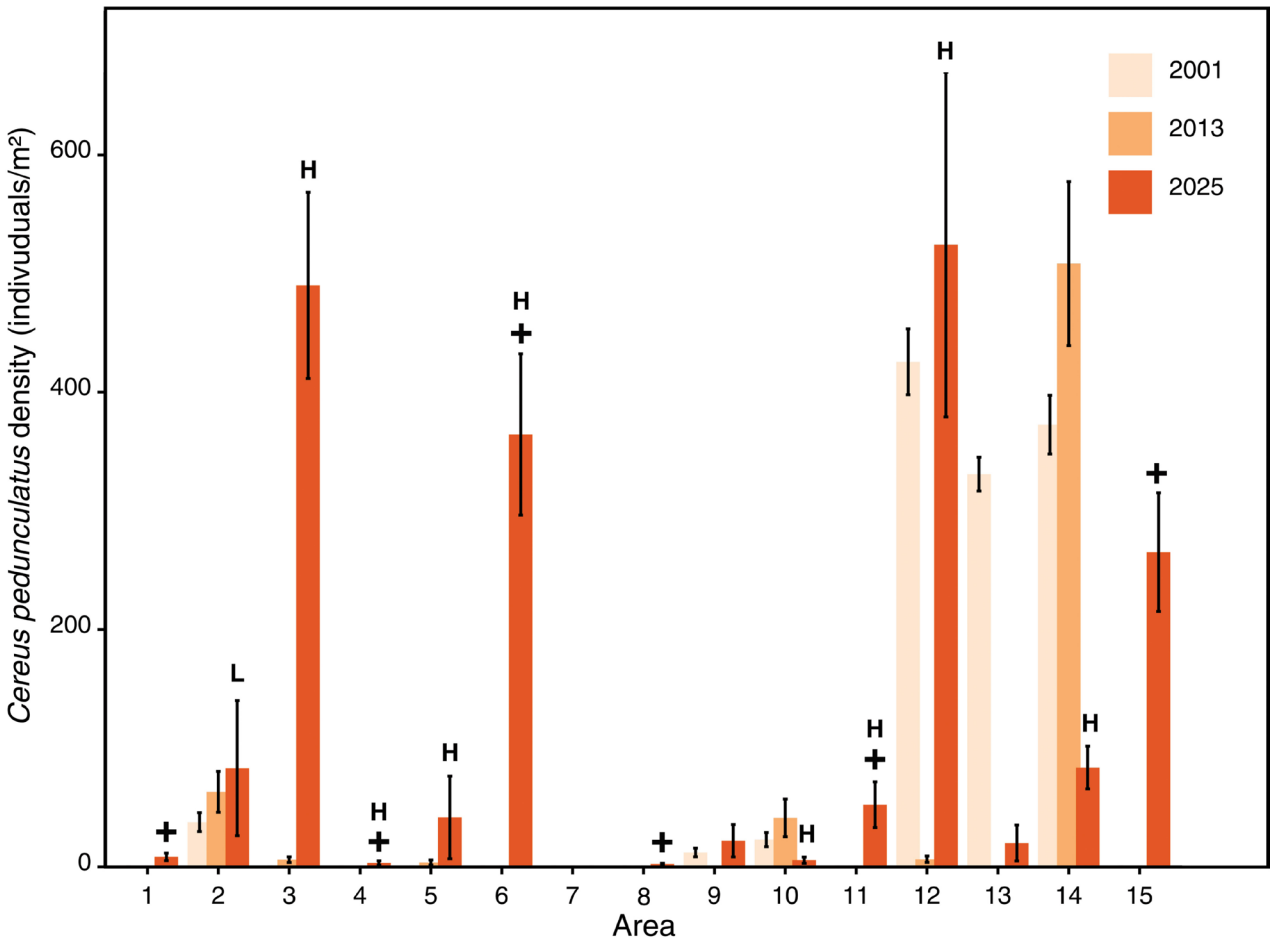

Figure 2. Abundance and distribution of *Cereus pedunculatus* through time in Langebaan Lagoon. Mean density per m^2 (± SE) of *C. pedunculatus* is shown for the mid-shore of survey areas in 2001, 2013, and 2025. (+) indicates areas where the anemone was documented for the first time in 2025. Letters indicate areas where the anemone was also detected in the high (H) or low (L) shore zones for the first time.

2). The high abundances recorded in Areas 3, 6, and 15 in 2025 were notable given that the anemone had previously been absent or occurred only in very low numbers in these areas. In addition to fossilized oyster beds and cordgrass beds, in 2025, *C. pedunculatus* was commonly found attached to *Zostera capensis* seagrass rhizomes (Areas 3–6, 8, and 9). Additionally, in Area 6, the anemone was found to be associated with the crumb-of-bread sponge *Hymeniacidon perlevis* Montagu, 1814 for the first time.

Although previously restricted to the mid-shore, the anemone was detected in the high- (Areas 3, 4, 5, 6, 10, 11, 12, and 14) and low-shore zones (Area 2) in 2025 (Fig. 2). The numerous high-shore records (Suppl. material 1: table S4) correspond with occurrences in cordgrass. While the relatively high *C. pedunculatus* densities in the low-shore of Area 2 (376.0 ± 170.0 individuals/m^2) coincided with observations of the native anemones *Anthopleura anneae* Carlgren, 1940 and *Anthopleura michaelensi* Pax, 1920 in the high- and mid-shore.

Species distribution modelling

The six individual models used in the ensemble performed well overall (TSS > 80%), resulting in a relatively high-performing ensemble model (sensitivity = 97.1%; specificity = 93.8%; Suppl. material 2: fig. S5). The projected ensemble closely aligns with *C. pedunculatus* occurrence records, showing high suitability in its native range of Europe (Fig. 3). The Gradient Boosting Machine (GBM) was the best-performing indi-

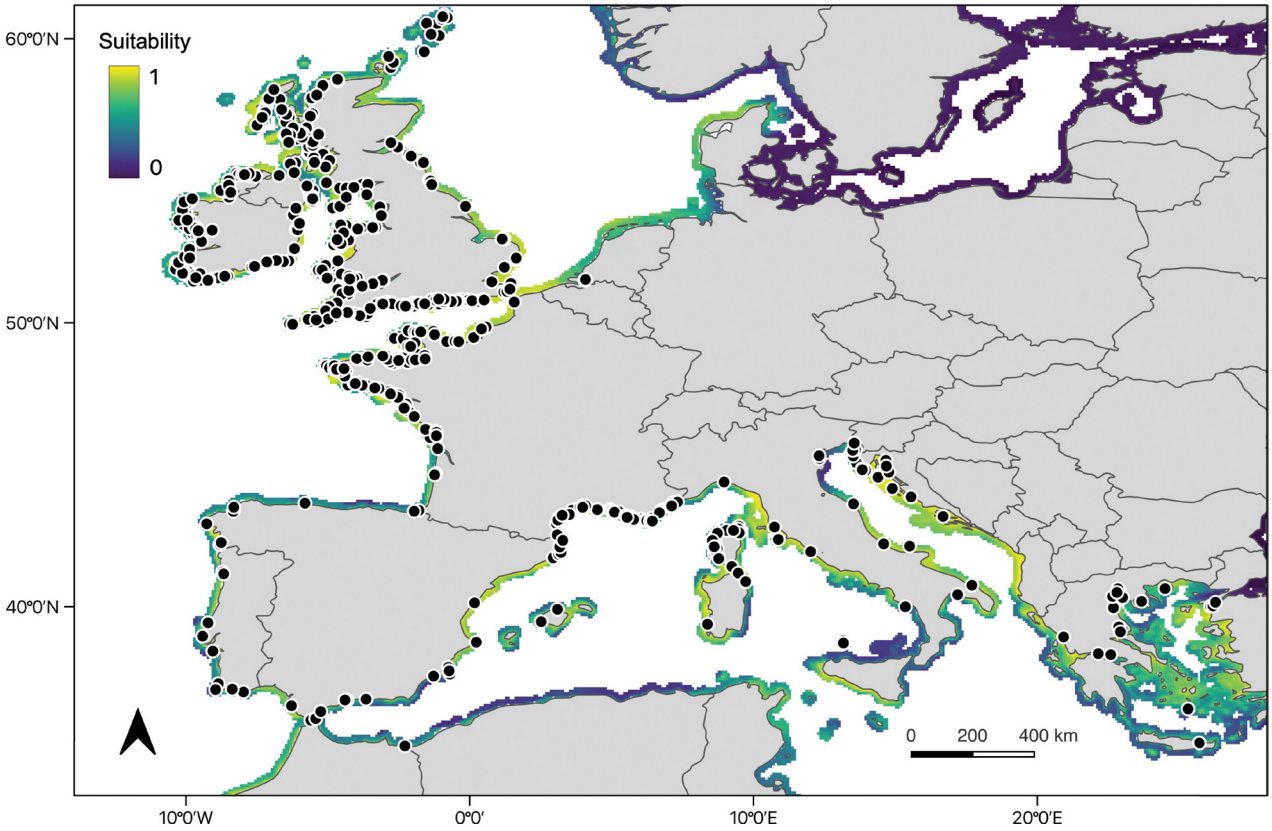

Figure 3. Habitat suitability for *Cereus pedunculatus* in its native range. Based on the projection of the ensemble model over Europe. Thinned occurrence records of *C. pedunculatus* are indicated with black dots. Additional records in the Azores Islands, the Sea of Marmara and Lebanon can be found in Suppl. material 2: fig. S8.

vidual model (sensitivity = 98.6% ± 0.09; specificity = 98.0% ± 0.17; Suppl. material 2: fig. S4). In contrast, MaxEnt performed most poorly (sensitivity = 90.7% ± 0.46; specificity = 81.0% ± 1.80) with greater variation between runs and the highest rate of false occurrences (Suppl. material 2: fig. S5). Among the predictor variables, maximum sea surface temperature (50.17%), maximum sea surface salinity (35.20%), and bathymetry (14.47%) were the most important predictors of *C. pedunculatus* occurrence in the ensemble. Whereas the mean primary productivity accounted for less than 1% of model variation. This order of variable importance was consistent across all models except MaxEnt, which ranked bathymetry and maximum salinity above maximum temperature (Suppl. material 2: fig. S6). According to the ensemble model, the most suitable conditions for *C. pedunculatus* are estimated to be between 15–25 °C maximum temperature and 35–40 ppt maximum salinity (Suppl. material 2: fig. S7).

The ensemble projection revealed suitable conditions for *C. pedunculatus* along the South African coast from the Namibian border to East London (Fig. 4). Within this range, 31 sites were found to be highly suitable for *C. pedunculatus*. These included four sites within South African marine protected areas (MPAs): Namaqua National Park MPA, Betty's Bay MPA, Stilbaai MPA, and Goukamma MPA. Most of these sites represent small pockets of sheltered area within the pixel identified by the species distribution model (Table 1). The South African coast east of East London was found to be environmentally unsuitable (≤ 0.25 suitability score).

The ensemble projection highlights several other highly suitable regions for *C. pedunculatus* across the globe, where the anemone has not yet been reported. These regions include northwest Africa, northern Scandinavia, Alaska, southern Australia, New Zealand, and portions of the Argentinean coast (Fig. 5).

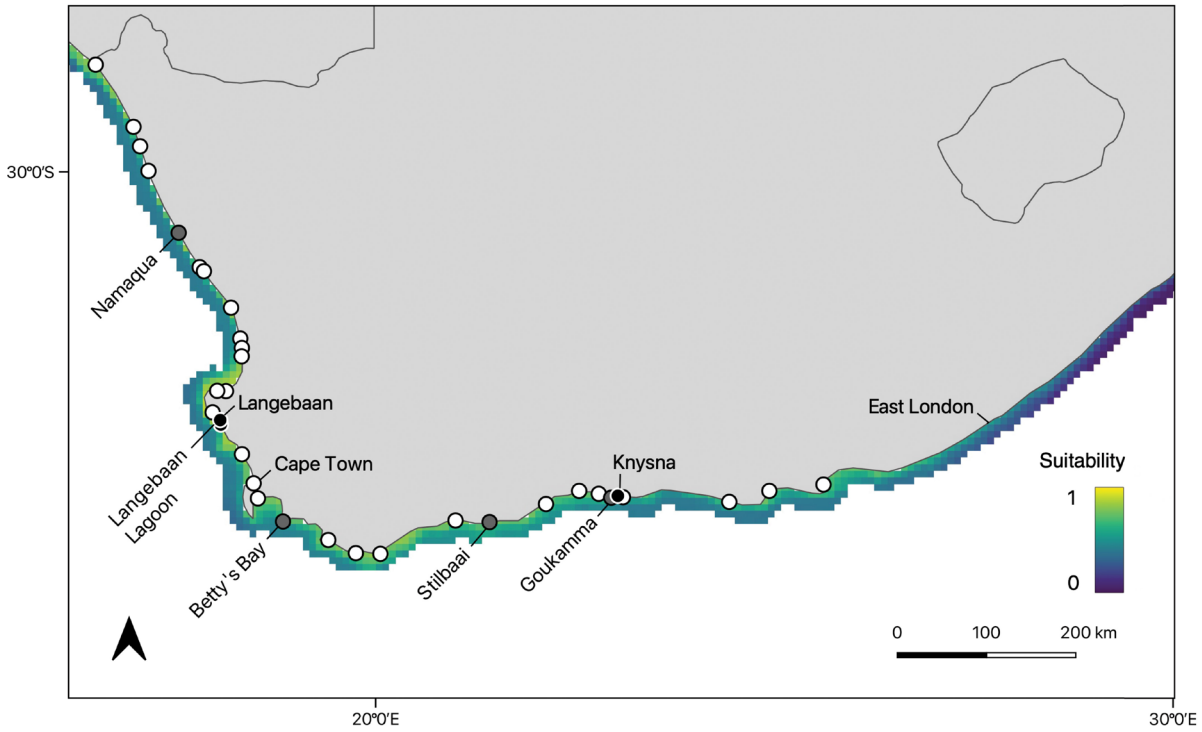

Figure 4. The suitable region for *Cereus pedunculatus* along the South African coast. White dots indicate sites with high suitability (≥ 0.75 suitability score and ecologically relevant habitat type). Grey dots show sites with high suitability that are in marine protected areas (MPAs). Thinned occurrence records are indicated with black dots. Reference cities are labelled on land, with MPAs labelled over ocean.

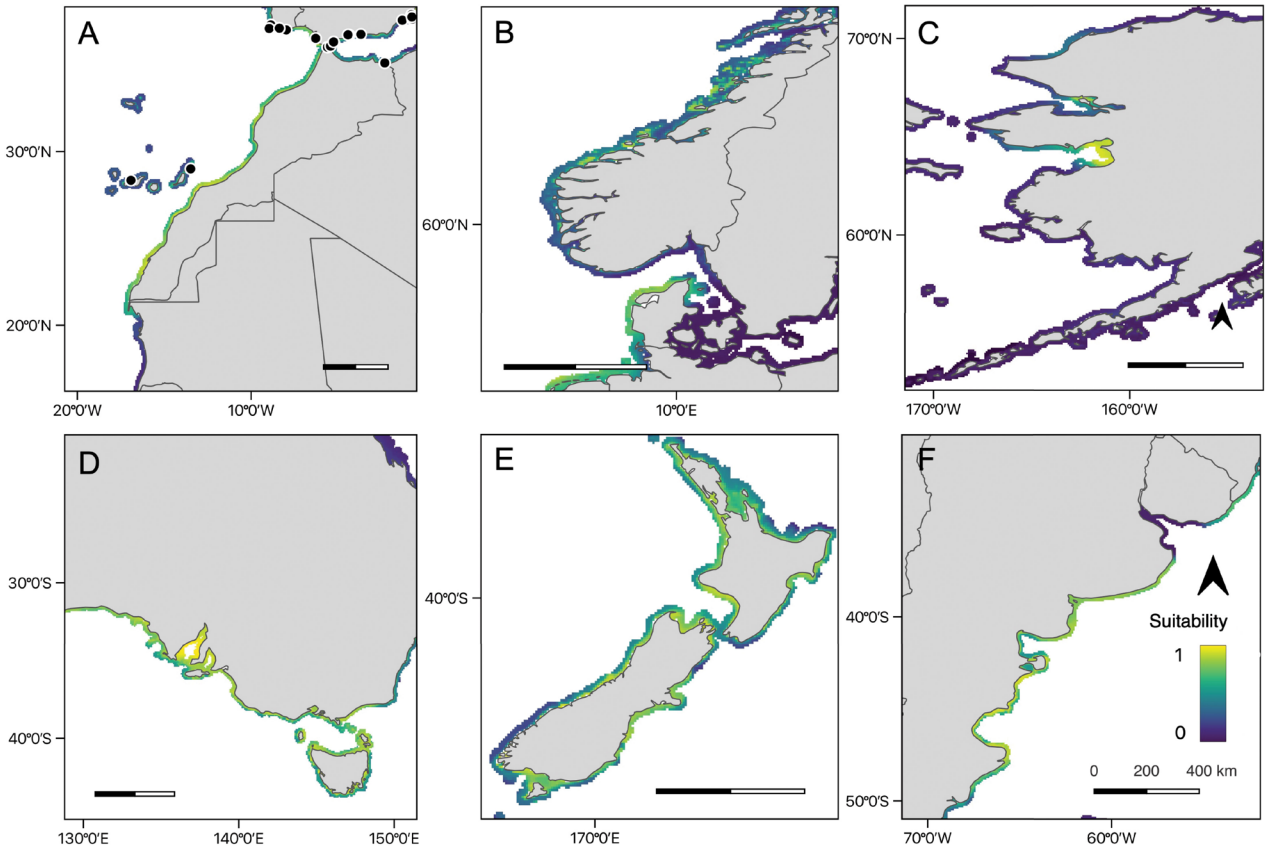

Figure 5. Highly suitable regions from which *Cereus pedunculatus* is currently unknown. These include **A.** Northwest Africa (thinned occurrence records from the native range are indicated with black dots); **B.** Northern Scandinavia; **C.** Alaska; **D.** Southern Australia; **E.** New Zealand, and **F.** The Argentinean coast. Note that all scale bars represent 400 km.

Table 1. Sites identified as highly suitable for *Cereus pedunculatus* along the South African coast (listed from west to east). A description is provided for each. Marine protected area is abbreviated as MPA.

Site	Latitude, Longitude	Description
South of Orange River Estuary	-28.6557, 16.4887	Mixed shore beside estuarine shore ~3 km south of the estuary mouth
South of Port Nolloth	-29.4351, 16.9627	Pocket of sheltered rocky coast ~15 km south of Port Nolloth
Kleinsee	-29.6789, 17.0454	Mixed shore beside estuarine shore
Swartkop	-29.9877, 17.1511	Small pocket of sheltered rocky coast
Namaqua MPA	-30.7629, 17.5295	Small pocket of sheltered rocky coast between Namaqua estuaries
Karoetjieskop North	-31.1943, 17.7925	Pocket of sheltered rocky coast
Karoetjieskop South	-31.2446, 17.8460	Mixed shore beside estuarine shore ~7 km south of Karoetjieskop North
Olifantsrivier Estuary	-31.7020, 18.1856	Mixed shore beside estuarine shore near Papendorp
Meeuland	-32.0862, 18.3111	Pocket of mixed shore beside estuarine shore in Lambert's Bay
Lanvleirivier Estuary	-32.2066, 18.3214	Pocket of mixed shore beside estuarine shore
North of Baboon Point	-32.3125, 18.3185	Sheltered rocky shore and mixed shore beside the river mouth in Elands Bay
Berg River Estuary	-32.7735, 18.1385	Mixed shore beside estuary shore; seagrass is present; freshwater flooding occurs annually
St Helena Bay Harbour	-32.7450, 18.0124	Pocket of sheltered rocky shore just south of St. Helena harbour
Hoedjiesbaai	-33.0214, 17.9979	Sheltered habitat within Saldanha Bay
South of Grotto Bay	-33.5393, 18.3223	Small pocket of sheltered rocky coast ~4 km south of Grotto Bay
South of Milnerton Lagoon	-33.8970, 18.4764	Mixed shore beside estuarine shore between Milnerton and Salt River in Table Bay
Sonwabe Beach	-34.0985, 18.5041	Small pocket of mixed shore beside estuarine shore in False Bay
Betty's Bay MPA	-34.3832, 18.8374	Mixed shore beside estuarine shore and a pocket of sheltered rocky shore near Hangklip
Franskraal	-34.6148, 19.4053	Mixed shore beside estuarine shore
Ratelrivier Estuary	-34.7795, 19.7505	Mixed shore beside estuarine shore
Struisbaai	-34.7883, 20.0598	Pocket of sheltered rocky coast
Duiwenhoks River Estuary	-34.3702, 21.0019	Mixed shore beside estuarine shore
Stilbaai MPA	-34.3821, 21.4243	Mixed shore beside estuarine shore
Santos Bay	-34.1643, 22.1364	Sheltered rocky coast in Mossel Bay
Kaaimans River Estuary	-33.9970, 22.5560	Pocket of mixed shore beside estuarine shore
Sedgefield Lagoon	-34.0357, 22.7979	Small pocket of mixed shore beside estuarine shore at lagoon mouth
Goukamma MPA	-34.0849, 22.9543	Mixed shore beside estuarine shore ~1.5 km west of Buffels Bay
Knysna Breakwaters	-34.0785, 23.1019	Mixed shore beside estuarine shore ~4 km east of Knysna Estuary mouth
Tsitsikammarivier Estuary	-34.1373, 24.4344	Pocket of mixed shore beside estuarine shore
Kabeljousriviermond	-33.9995, 24.9386	Estuarine shore north of the river mouth
Kings Beach	-33.9788, 25.6588	Sheltered rocky shore near Summerstrand in Algoa Bay

Discussion

Monitoring the abundance and distribution of alien species is an important prerequisite for evidence-based management (Giakoumi et al. 2019) and for fulfilling national and international regulatory obligations (Lehtiniemi et al. 2015). Yet many marine alien species go unmonitored after they are first reported (e.g. alien anemones (Gimenez and Brante 2021; Gimenez et al. 2022)). The present study provides an updated assessment of the abundance and distribution of the alien anemone *Cereus pedunculatus* in Langebaan Lagoon marine protected area (MPA), contributing to a long-term dataset for the species and supporting compliance with reporting requirements (NEMBA Act No. 10 of 2004). Surveys suggest that *C. pedunculatus*

populations are persistent and widespread across the lagoon, as the anemone was detected in six previously uninvaded areas and has extended into the high- and low-shore zones for the first time. Particularly concerning are the high anemone abundances recorded in *Zostera capensis* beds, given the regionally endangered status of this seagrass (Adams 2016). Of the 31 highly suitable sites detected by the species distribution model between the Namibian border and East London, four are located within MPAs. The knowledge that these sites, and several other regions identified across the globe, are vulnerable to *C. pedunculatus* can support focused surveillance efforts and trigger proactive management measures at these locations.

Introductions of *C. pedunculatus* to South Africa and other highly suitable regions, such as Denmark and Norway, Alaska, Australia, New Zealand, and Argentina, may be facilitated by two key pathways. The first is commercial shipping, particularly via sea-chests (i.e. cavities within the hulls of ships through which seawater is taken up for use). Although *C. pedunculatus* has occasionally been recorded on artificial hard substrata in its native range (Lenzi et al. 2009), its absence from such habitats in South Africa suggests that hull fouling is not a likely mechanism. In contrast, sea-chests have been known to provide refuge for fouling organisms in transit, including several alien anemones (Coutts and Dodgshun 2007; Frey et al. 2014). The reproductive strategies of *C. pedunculatus*, which include planktonic planula larvae in its native range (Rossi 1975) and the asexual release of live young (Bocharova and Kozevich 2011; Andersen et al. in press), are conducive to the uptake and release of viable offspring by sea-chests. Additionally, the recognised tolerance of this anemone to anoxic conditions (Riedel et al. 2008) supports the plausibility of survival over long-distance translocation in sea-chests. Given the proximity of the Port of Saldanha Bay to Langebaan Lagoon, it is possible that *C. pedunculatus* was introduced via shipping activity in the bay (e.g. iron ore export (Henrico and Bezuidenhout 2020)) and subsequently transported into the lagoon by tidal currents, as has been reported for other alien taxa (e.g. Ackland et al. 2025a).

The second possible pathway of introduction for *C. pedunculatus* is via oyster mariculture. South Africa has a long history of importing oyster spat from Chile and Europe for cultivation (Keightley et al. 2015). This practice has been linked to several species introductions across South Africa, including in Saldanha Bay and Knysna Estuary (Haupt et al. 2010a). In Europe, range expansions of *C. pedunculatus* have been linked to shellfish imports (e.g. in the Oosterschelde estuary, Netherlands (den Hartog and Ates 2011)). Given that South Africa has received oyster spat from the native range of the anemone (i.e. France (Haupt et al. 2010a)), this pathway provides a clear link to its presence in South Africa. Saldanha Bay is the focus of South African mariculture (Probyn et al. 2015, 2023), with oyster cultivation dating back to 1985 (Haupt et al. 2010b). An experimental oyster farm was run in Langebaan Lagoon for a short time before the MPA was established (Haupt et al. 2010b). Oyster cultivation in Knysna Estuary dates back to 1973 (Haupt et al. 2010b) but ceased in the early 2010s (Keightley et al. 2015). Given that there are no published records of *C. pedunculatus* in Knysna Estuary before early 2025 (van Blerk unpublished data), despite numerous benthic surveys (e.g. Allanson et al. 2000; Barnes 2021), it is unlikely that *C. pedunculatus* was introduced to Knysna before Langebaan Lagoon. However, it is unclear as to whether the presence of the anemone in Knysna is the result of a secondary introduction or spread from Langebaan Lagoon (over 650 km away). Surveys of highly suitable areas with past mariculture operations (i.e. Kleinsee (Haupt et al. 2010a) and Swartkops Estuary in Algoa Bay (Haupt et al. 2010b)) may help elucidate the current distribution and invasion history of the anemone within the country. Given the known prevalence

of the species in brackish and polluted lagoons in its native range (e.g. Cognetti and Maltagliati 2000), surveys should not be limited to pristine sites.

Considering that the anemone is not tolerant to turbulent conditions (Schmidt et al. 1972), like those observed along South Africa's wave-exposed coastline, natural dispersal from Langebaan and Knysna is unlikely. However, both domestic oyster spat transport (Haupt et al. 2010a) and recreational activities may facilitate more localized spread of *C. pedunculatus* between suitable sites. Yachts are documented mechanisms for the dispersal of marine alien species in South Africa (Peters et al. 2017). Although *C. pedunculatus* is unlikely to foul vessel hulls, juveniles may be transported in bilge water, which is periodically discharged at new locations, including harbours and estuaries (Fletcher et al. 2020). Another plausible mechanism is the translocation of live bait species, a recognized pathway for the unintentional dispersal of associated marine organisms (Sá et al. 2017; Smith et al. 2020). In both Langebaan Lagoon and Knysna Estuary, recreational fishers frequently collect sand and mud prawns (Nel and Branch 2014; Simon et al. 2019). As a sediment-dwelling species, *C. pedunculatus* may be transported alongside prawns and unintentionally released into new habitats. Inspecting bilge water, fishing gear, and bait aboard recreational vessels in Langebaan Lagoon and Knysna Estuary may provide insights into the intra-regional spread of this anemone.

Given that the species distribution model found much of the South African west and south coasts suitable for *C. pedunculatus*, it may already be present at several of the sheltered sites identified near Langebaan and Knysna that have not yet been surveyed. As such, highly suitable sites like the Berg River Estuary, St Helena Bay Harbour, Hoedjiesbaai, and Grotto Bay (near Langebaan), as well as Goukamma MPA and the site east of the Knysna Estuary mouth, should be prioritised for surveys of *C. pedunculatus.* Likewise, management agencies for the four MPAs should consider surveying for this species and developing contingency plans (*sensu* Booy et al. 2017) to support effective responses to future incursions at these ecologically important sites. Uninvaded but suitable sites near oyster mariculture operations (e.g. Kleinsee and Kings Beach), commercial ports (e.g. Santos Bay and Kings Beach), or recreational vessels traffic (e.g. North of Baboon Point and Kabeljousriviermond) should be closely monitored for future introductions of *C. pedunculatus* so that management action can be applied upon first detection of the species. As for sites that are already invaded, understanding the extent of the invasion is an essential first step for management (Giakoumi et al. 2019). Given that this information is unknown for Knysna Estuary, distribution and abundance surveys are necessary to determine whether the species has become established and if management interventions are still feasible. Considering that much of this estuary contains suitable habitat for the anemone (i.e. mudflats, seagrass beds, and cordgrass (Claassens et al. 2020)), it is likely that *C. pedunculatus* will spread within the estuary if it has not already done so.

Looking beyond South Africa, this study identified several highly suitable regions across the globe from where *C. pedunculatus* is not yet known. Monitoring programs in these regions should include *C. pedunculatus* on their watchlists. To avoid possible impacts associated with an invasion, priority should be placed on critical habitats, such as seagrass beds, within ecologically, culturally, or economically significant areas (i.e. MPAs and World Heritage Sites). Interestingly, northwestern Africa is also highly suitable for the species and lacks occurrence records despite its vicinity to more well-studied regions where the anemone is known (i.e. The Canary Islands and Morocco). Given the relatively low survey effort in northwestern Africa (Ackland et al. 2025b), it is possible that the anemone is present there but has not yet been detected. If *C. pedunculatus* is present, this region may either represent part of its native range or a range expansion.

Conclusion

While this study provides a crucial update to the long-term dataset for *C. pedunculatus* in Langebaan Lagoon MPA and highlights its potential for establishment in other parts of South Africa and various regions globally, the source of the invasion and the relationship between the Langebaan Lagoon and Knysna Estuary populations remain unknown. A population genomics approach could offer insights into connectivity between these locations and the native range helping to inform effective management going forward. Collectively this knowledge supports prioritisation of suitable sites for targeted monitoring and proactive management, providing an opportunity to institute preventative measures to manage pathways to these sites (Padayachee et al. 2019). Such a two-pronged approach will minimise the probability of spread and the potential for establishment of new populations, ultimately mitigating impacts that may be associated with this alien anemone.

Authors contribution

MNA: conceptualization, methodology, investigation, data curation, formal analysis, writing - original draft, review and editing; GS: methodology; writing - review and editing; TBR: conceptualization, methodology, writing - review and editing, supervision.

Competing interests

The authors have declared that no competing interests exist.

Ethics statement

No ethical approval was required for this study. Fieldwork was conducted under research permits CRC/2024-2025/011--2024/V1 and RES2025/67.

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Data availability

All datasets and associated code have been uploaded to Zenodo and are available at https://doi.org/10.5281/zenodo.17097997.

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Supplementary material 1

Supplementary tables

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Data type: xlsx

Explanation note: **table S1.** geo-referenced records of *Cereus pedunculatus*. **table S2.** candidate environmental and topographical predictors. **table S3.** selected algorithms and parameters for the ensemble model. **table S4.** densities of *Cereus pedunculatus* in 2025 survey areas.

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Link: https://doi.org/10.3391/ai.2025.21.3.200590.suppl1

Supplementary material 2

Supplementary images

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Data type: docx

Explanation note: **figure S1.** current distribution of *Cereus pedunculatus*. **figure S2.** comparison of environmental predictor time periods. **figure S3.** predictor correlation plot. **figure S4.** model performance plot. **figure S5.** model accuracy plot. **figure S6.** predictor importance plot. **figure S7.** predictor response curves. **figure S8.** habitat suitability in the Azores Islands, Sea of Marmara, and Lebanon.

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