

Research Article**A climate sensitive watch list for alien species in South African kelp forests**Clara Steyn¹, Tamara B. Robinson² and Laura K. Blamey³¹Department of Botany and Zoology, Centre for Invasion Biology, Stellenbosch University, South Africa²Centre for Invasion Biology, Stellenbosch University, South Africa³Commonwealth Scientific and Industrial Research Organisation, Environment, Brisbane, Queensland, AustraliaCorresponding author: Tamara B. Robinson (trobins@sun.ac.za)

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OPEN ACCESS**Abstract**

Following establishment, the probability of successful eradication of marine alien species is limited. In the context of kelp forest systems, this is particularly concerning as alien species can lead to dramatic changes in ecosystem structure and even the total loss of kelp. In South Africa, little is known about the status of alien species in kelp forests and there is a need for regular monitoring to support the early detection of incursions and maximise the potential for effective management interventions. However, limited resources dictate that monitoring be done in a cost-efficient manner. Watch lists can support such monitoring. In this study a watch list of alien species with the potential to invade South African kelp forests was developed through a climate-sensitive horizon-scanning approach that accounted for current conditions and predicted climate change. Temperature-matching was used to determine the suitability of the Benguela and Agulhas ecoregions for the watch list species under present and future climatic conditions. The watch list included seven species (the bryozoan *Membranipora membranacea*, and the algae *Bonnemaisonia hamifera*, *Dasysiphonia japonica*, *Fucus serratus*, *Sargassum muticum*, *Sargassum horneri*, and *Undaria pinnatifida*), some of which have had profound impacts in kelp forest ecosystems in other parts of the world. Overall, kelp forests in the cool temperate Benguela ecoregion appear most vulnerable to invasion, as current and future conditions closely match those under which the watch list species are known to occur elsewhere. This, together with the presence of important ports in the region, highlights the vulnerability of South African west coast kelp forests to invasions and the potential impacts that could result.

Key words: climate change, Early Detection and Rapid Response (EDRR), invasive bryozoan, horizon scanning, kelp bed, monitoring, temperature matching

Introduction

As the rate of biological invasions continues to rise (Seebens et al. 2021), associated impacts on natural systems and high costs for society become more prevalent (Diagne et al. 2021). In marine systems, management success is minimal once taxa become established (Hopkins et al. 2011; Ojaveer et al. 2015) and interventions become very costly (e.g. Mabin et al. 2020). This is evidenced by few successful eradication attempts (but see Willan et al. 2000; Culver and Kuris 2000; Miller et al. 2004; Anderson 2005; Hopkins et al. 2011). Ultimately, these low success rates reflect a limited ability to reverse

the impacts of marine invasions post-establishment and highlight the need for preventative management (Ojaveer et al. 2015, 2018) and rapid management responses once incursions are detected (Bertolino et al. 2020; Wallace et al. 2020).

Early Detection and Rapid Response (EDRR) to new introductions is facilitated by long-term standardised surveillance using consistent methods to track species occurrence, distribution, and impact through time and across different geographical scales (Pyšek et al. 2020; Loureiro et al. 2021). Long-term surveillance is of particular importance within the context of global change, where many drivers of change (e.g. global warming and pollution) may interact with biological invasions (Pyšek et al. 2020; Robinson et al. 2020a). Watch lists, (i.e. lists of non-native species that have the potential to invade and impact the biodiversity of a region of interest (*sensu* Roy et al. 2014; Gallardo et al. 2016)) can be used as a tool to support cost-effective monitoring. Watch lists are developed using horizon scanning, a process of systematic examination of future potential threats and opportunities within a given context (Roy et al. 2014). In an invasion context, horizon scanning can be used to prioritise the potential threat posed by alien species that have not yet established within a region, making this an essential component of alien species management (Sutherland et al. 2015). Once watch lists have been developed for a region of interest, they can be used to direct monitoring efforts and enable rapid response to incursions, thus maximising the success of management interventions (Roy et al. 2019). Most importantly, targeted watch lists can make monitoring more cost-efficient (Minchin 2007), an important consideration in resource poor settings.

Globally, watch lists have been developed for terrestrial, freshwater, and marine systems. These lists are an essential tool that support preventative management of invasions (Reaser et al. 2020) and have been applied in many regions including Great Britain (Roy et al. 2014), western Europe (Gallardo et al. 2016), Iberia (Oficialdegui et al. 2023), the European Union (Roy et al. 2019; Bertolino et al. 2020; Tsiamis et al. 2020) and North America (Davidson et al. 2021). While most watch lists are developed through a structured approach that combines literature reviews and risk assessments, with dynamic consensus methods, this two-phase approach is time consuming, data intensive and expensive, making it unsuitable for use in resource poor nations (Faulkner et al. 2014). Consequently, studies in South Africa have favoured a more rapid approach to horizon scanning. Here, Faulkner et al. (2014) developed a method for creating watch lists using invasion history, environmental suitability, and propagule pressure as predictors of invasion success. In an aligned approach, Swart and Robinson (2019) utilised the Blackburn framework for biological invasions (Blackburn et al. 2011) in horizon scanning for predatory marine crabs. As invasion stages are separated by barriers (biotic and/or abiotic) that must be overcome for species to advance to the next stage, the barriers can be applied as filters

to remove species from a starting list of potential invaders, ultimately creating a watch list of species of interest. It is important to bear in mind that watch lists based on the ability of potential invasive species to survive under present climatic conditions will not be useful as the climate continues to change at an unprecedented rate (Pörtner et al. 2019). Thus, in order to remain relevant, watch lists should account for both present and future climatic conditions (Swart and Robinson 2019).

Species that have been reported as alien in kelp forests around the world fall predominantly into the phyla and subphyla Bryozoa, Tunicata, Chlorophyta, and Rhodophyta (Harris and Tyrrell 2001; Levin et al. 2002; Dijkstra et al. 2017). The invasive bryozoan *Membranipora membranacea* (Linnaeus, 1767) is one of the most impactful alien species on kelp forests. This epiphytic bryozoan is native to the North-east Atlantic, South-west, and South-east Pacific oceans. It was first detected in the Gulf of Maine in 1987, presumably introduced to the North-west Atlantic via ballast water (Lambert et al. 1992). By 1992 the bryozoan was reported further north in Nova Scotia (Scheibling et al. 1999). Throughout the North-west Atlantic, heavy encrustations of *M. membranacea* have resulted in the defoliation of canopy forming kelps, leading to a marked decline in canopy cover (Scheibling et al. 1999; Chapman et al. 2002). In all cases, the invasion of *M. membranacea* has led to invasional meltdown (*sensu* Simberloff and Von Holle (1999)), enabling the establishment of other alien species including the highly invasive green understory algae *Codium fragile* (Suringar, 1867) (Harris and Tyrrell 2001; Levin et al. 2002; Scheibling and Gagnon 2006). Interestingly, *C. fragile* prevents the re-establishment of kelp in the region following defoliation by *M. membranacea*, resulting in a shift from kelp to understory algae dominated systems (Connell and Russell 2010). The invasion of *M. membranacea* in the North-west Atlantic provides a stark example of the potentially devastating impacts alien species can have on kelp forest ecosystems.

The South African coast is bound by the cold Benguela current on the west coast and the warm Agulhas current on the east coast, with some mixing on the south coast. The temperature gradient from west to east results in diverse marine ecoregions, each with their own unique species assemblages (Sink et al. 2012). South Africa has six marine ecoregions, four inshore (Benguela, Agulhas, Natal, and Delagoa) and two offshore (South-east Atlantic and South-west Indian) (Sink et al. 2010). Coastal temperatures and how they are affected by climate change are well understood in South Africa (Rouault et al. 2010; Smit et al. 2013; Schlegel et al. 2017). In contrast to global expectations, the west coast of South Africa has undergone a decadal decline in temperature driven by an increase in the intensity and frequency of wind-driven upwelling (Rouault et al. 2010; Lamont et al. 2018). This regional cooling is a unique phenomenon, given the global trend of ocean warming.

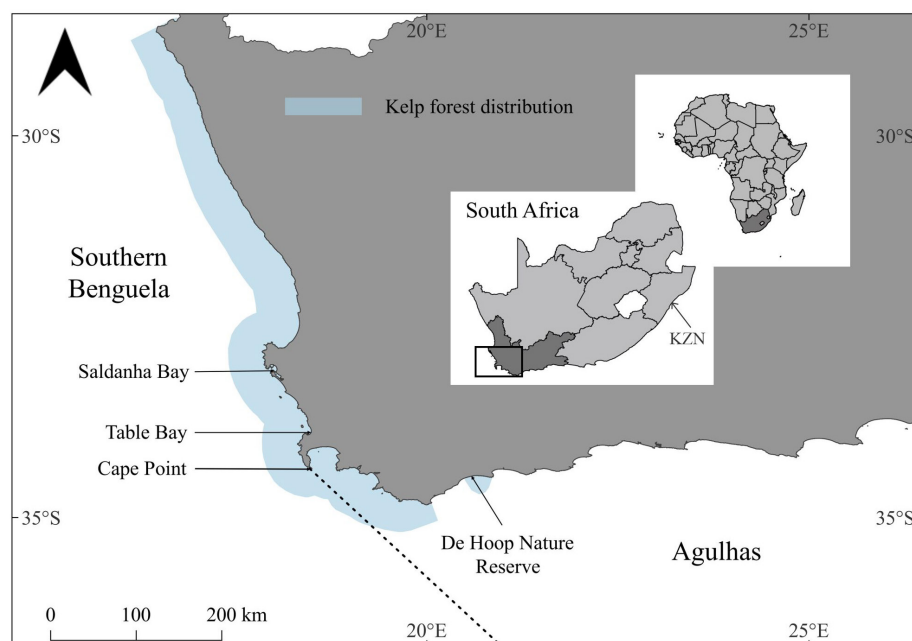


Figure 1. The distribution of canopy-forming kelp forests (blue shading) across the Benguela and Agulhas coastal ecoregions of South Africa (following Sink et al. 2012). The dashed lines separating the coastal ecoregions extend offshore linearly for illustrative purposes only. Kwa-Zulu Natal (KZN) is indicated on the insert map of South Africa along with other locations mentioned in the text.

Canopy-forming kelp forests in South Africa dominate the nearshore subtidal zone along the west and south-west coasts (Blamey and Bolton 2018), spanning the entire Benguela ecoregion with a small population on the western side of the Agulhas ecoregion (Figure 1). Four kelp species are currently recognised in South Africa: *Macrocystis pyrifera* (Linnaeus, 1771), *Ecklonia maxima* (Osbeck, 1757), *Ecklonia radiata* (C. Agardh, 1817), and *Laminaria pallida* Greville, 1848. In the Benguela, kelp forests on the west and south-west coasts are dominated by *E. maxima* in the shallows (~ 8 m depth) with *L. pallida* forming a subcanopy beneath, and eventually replacing *E. maxima* in deeper waters (~ 15–30 m) (Blamey and Bolton 2018). However, the benthic communities are markedly different between the two coasts, with the distinction occurring at Cape Point (Anderson et al. 1997). Coastal populations of *E. radiata* (the smaller congener of *E. maxima*) have been documented from De Hoop on the south coast all the way up the east coast to Kwa-Zulu Natal (Anderson et al. 2016). This species of kelp also has deeper populations in False Bay (~ 10–30 m), on the Agulhas Bank offshore from De Hoop (~35 m), and in northern Kwa-Zulu Natal (~ 60 m) (Anderson et al. 2016; Reddy 2024). Historically, *E. radiata* had been the only kelp species recorded on the south coast (Bolton and Stegenga 1990). However, since 2006 *E. maxima* has undergone an eastward shift along the south coast of South Africa, forming an established population in the De Hoop Nature Reserve (Bolton et al. 2012). In South Africa, kelp forest ecosystems provide a range of goods and services that are of immense ecological, social, and economic importance (Blamey and Bolton 2018). These

comprise a combination of commercial, recreational, and subsistence fishing, ecotourism, and other indirect services such as wave attenuation (Blamey and Bolton 2018). Overall, this ecosystem was valued at US\$ 434 million year⁻¹ contributing US\$ 290 million year⁻¹ to the South African gross domestic profit (GDP) (Blamey and Bolton 2018). Given their immense value, monitoring these ecosystems for alien species is vital considering the devastation they have caused in kelp forests elsewhere.

In South Africa there has been little consideration of biological invasions in kelp forest habitats. Currently, only one study has documented the presence of alien species in South African kelp forests (i.e. Lindberg et al. 2020). The authors found that the alien Mediterranean mussel *Mytilus galloprovincialis* Lamarck, 1819 had expanded its range subtidally, with mussels settling on the heads and stipes of the kelp *E. maxima*, ultimately causing the kelp to fall to the sea floor. Three alien species associated with the mussels were noted (i.e., the bryozoans *Virididentula dentata* (Lamouroux, 1816), *Watersipora subtorquata* (d'Orbigny, 1852), together with the hydrozoan *Pennaria disticha* Goldfuss, 1820). In recognition of the need for monitoring South African kelp forests for alien species, and the fact that this needs to be done in a cost-effective manner, this study aimed to develop a watch list of potential alien species that may arrive and establish in South African coastal kelp forests under both present day and future conditions. This study focused on inshore and canopy-forming kelp populations in South Africa, as such the ranges for offshore *E. radiata* kelp beds on the east coast in the Natal and Delagoa ecoregions were not included. The watch list developed will support the early detection of alien kelp forest species, minimising the probability of establishment and the impacts such an incursion may cause.

Materials and methods

Literature review

Following the approach developed by Swart and Robinson (2019), a global systematic literature review was carried out to identify reports of invasions in kelp forest ecosystems. The resulting list of alien species was established using information from peer reviewed papers and books. All information was sourced using Google Scholar, Scopus, and Web of Science. The search string used was: ((“alien species” OR “invasive species” OR “non-native species” OR “non-indigenous species” OR “introduced species” OR “invasion*”) AND (“kelp forest*” OR “kelp bed*”)) NOT (“aquaculture” OR “mariculture” OR “teacher”). Due to limited capabilities in Google Scholar, the above had to be separated into two strings: one using the term “kelp forest*” and another using “kelp bed*” when working in this search engine. Searches were conducted in April and May 2023. For each species identified in the literature review, information on their native range, alien distribution and pathway of introduction was sourced from the literature.

Horizon scanning using the Blackburn framework

Species that are native to South Africa or already recognised as established aliens in the country (following Robinson et al. 2020b), were excluded from the list of species resulting from the literature search. The remaining list was filtered using the Blackburn framework. Firstly, species without a pathway of introduction (*sensu* Faulkner et al. 2020) to South Africa were excluded from the list. Secondly, the congruence between the temperature in the realised range of each species (i.e., the native, alien, and cryptogenic ecoregions occupied), and the Benguela and Agulhas ecoregions was assessed. Although the Benguela ecoregion contains the majority of South African kelp forests, the Agulhas ecoregion has also been included given the recent establishment of *Ecklonia maxima* in this region (Bolton et al. 2012). To assess temperature congruency, the minimum and maximum sea surface temperatures (SSTs) of the realised range of each species, as well as that for the two South African ecoregions, were extracted from Bio-ORACLE, which provides marine data layers for ecological modelling (<https://www.bio-oracle.org/index.php>). Using these data, the present day (2000–2104) mean, and 95% CI of the minimum and maximum SSTs were calculated for each South African ecoregion and each alien species' realised range. Minimum and maximum SSTs were chosen, rather than mean SSTs, because it is more likely that species will be constrained by the extreme conditions in new regions, rather than their average environmental states (Swart and Robinson 2019). To account for near future (2040–2050) and long-term (2090–2100) changes in temperature, the predicted climate-induced changes in SSTs were extracted for two RCP (Representative Concentration Pathway) scenarios described by the Intergovernmental Panel on Climate Change (Pörtner et al. 2019) (i.e. RCP 2.6, a stringent emissions mitigating scenario that aims to keep global warming below 2 °C above pre-industrial temperatures, and RCP 8.5, a high emissions scenario where warming is likely to reach between 2.6–4.8 °C above pre-industrial temperatures by 2100).

Despite ocean temperatures increasing at the global scale, temperatures on the South African west coast and parts of the south coast have shown a cooling trend that is expected to continue into the future (Rouault et al. 2010; Dufois and Rouault 2012; Lamont et al. 2018; Duncan et al. 2019). Between 1982–2009, Rouault et al. (2010) measured a decline in temperature of 0.55 °C and 0.35 °C per decade on the west and south coasts respectively. In our study, this pattern was extrapolated to 2040–2050 and 2090–2100 as cooling scenarios for the southern Benguela (west coast) and Agulhas (south coast) ecoregions. Additionally, a more conservative cooling scenario (i.e. half the decadal decline measured by Rouault et al. 2010) was also considered.

The invasion potential of each species was considered for each ecoregion, to account for the thermal variability among these regions and the fact that they may support different suites of species with different environmental

Table 1. Criteria used to determine degree of congruency between the thermal ranges of the potentially invasive kelp forest species and the Benguela and Agulhas ecoregions (following Swart and Robinson (2019)).

Description of thermal range congruency	Classification of ecoregion
Species minimum (min.) and maximum (max.) above the ecoregion min. and max.	Too cold
Species min. 95% CI overlaps with the ecoregion max. CI.	Probably too cold
Species max. above the ecoregion max., and species min. mean falls between the ecoregion min. and max. (no overlap of species CI with ecoregion min.)	Possibly too cold
Species min. and max. fall below and above the ecoregion min. and max., respectively	Suitable
Species min. below the ecoregion min., and species max. mean falls between the ecoregion min. and max. (no overlap of species CI with the ecoregion max.)	Possibly too warm
Species max. CI overlaps with ecoregion min. CI.	Probably too warm
Species min. and max. below the ecoregion min. and max.	Too warm

tolerances. Any species for which temperature-matching indicated that they would be unable to survive under present-day or future climatic conditions were removed from the list. The degree of congruency between the thermal ranges of the alien species and the thermal characteristics of the two South African ecoregions was determined following Swart and Robinson (2019) (Table 1). This classified the ecoregions as: (i) too cold, (ii) probably too cold, (iii) possibly too cold, (iv) suitable, (v) possibly too warm, (vi) probably too warm, or (vii) too warm to support each alien species. When an ecoregion was too cold or too warm to support a species, that species was excluded from the watch list. Using a cautionary approach, when ecoregions are determined to be probably or possibly too cold or too warm, the species was retained.

Results

Literature search

The literature search yielded a total of 2099 records, of which 120 were detected by Scopus, 89 by Web of Science, 1530 by Google Scholar using the term “kelp forest*”, and 360 by Google Scholar using the term “kelp bed*”. Of these only 8.5% (179 papers) were relevant. A list of 15 potential alien species was extracted from this literature. Of these 15 potential alien species, eight were discarded as they are already present in South Africa as established alien species (Supplementary material Table S1), yielding a total of 7 potential species.

Watch list

The remaining seven species with invasion histories were found to have pathways to South Africa and are expected to survive under present and all future potential thermal conditions (Table 2, Figure 2). Of these, six were algal species from the phyla Rhodophyta and Ochrophyta, with the remaining

Table 2. Watch list depicting the potential survivability of likely alien species in the Benguela and Agulhas ecoregions under present and future predicted temperature conditions. ✓ indicates that a species could survive in an ecoregion. Colours correspond to those in Table 1 and denote the degree of congruency between each species' thermal range and that of the ecoregion. Species codes are used in Figures 3–7. Potential pathways (sensu Faulkner et al. (2020)) are provided: E = Escape, C = Contaminant, S = Stowaway.

Taxa	Species Codes	Potential pathways	Present	Moderate warming		Severe warming		Moderate cooling		Severe cooling	
				2040–2050	2090–2100	2040–2050	2090–2100	2040–2050	2090–2100	2040–2050	2090–2100
Benguela											
Bryozoa											
Membranipora membranacea	Mm	S	✓	✓	✓	✓	✓	✓	✓	✓	✓
Rhodophyta											
Bonnemaisonia hamifera	Bh	S, C	✓	✓	✓	✓	✓	✓	✓	✓	✓
Dasysiphonia japonica	Dj	S, C	✓	✓	✓	✓	✓	✓	✓	✓	✓
Ochrophyta											
Fucus serratus	Fs	S	✓	✓	✓	✓	✓	✓	✓	✓	✓
Sargassum horneri	Sh	S	✓	✓	✓	✓	✓	✓	✓	✓	✓
Sargassum muticum	Sm	S, C, E	✓	✓	✓	✓	✓	✓	✓	✓	✓
Undaria pinnatifida	Up	S, C, E,	✓	✓	✓	✓	✓	✓	✓	✓	✓
Agulhas											
Bryozoa											
Membranipora membranacea	Mm	S	✓	✓	✓	✓	✓	✓	✓	✓	✓
Rhodophyta											
Bonnemaisonia hamifera	Bh	S, C	✓	✓	✓	✓	✓	✓	✓	✓	✓
Dasysiphonia japonica	Dj	S, C	✓	✓	✓	✓	✓	✓	✓	✓	✓
Ochrophyta											
Fucus serratus	Fs	S	✓	✓	✓	✓	✓	✓	✓	✓	✓
Sargassum horneri	Sh	S	✓	✓	✓	✓	✓	✓	✓	✓	✓
Sargassum muticum	Sm	S, C, E	✓	✓	✓	✓	✓	✓	✓	✓	✓
Undaria pinnatifida	Up	S, C, E,	✓	✓	✓	✓	✓	✓	✓	✓	✓

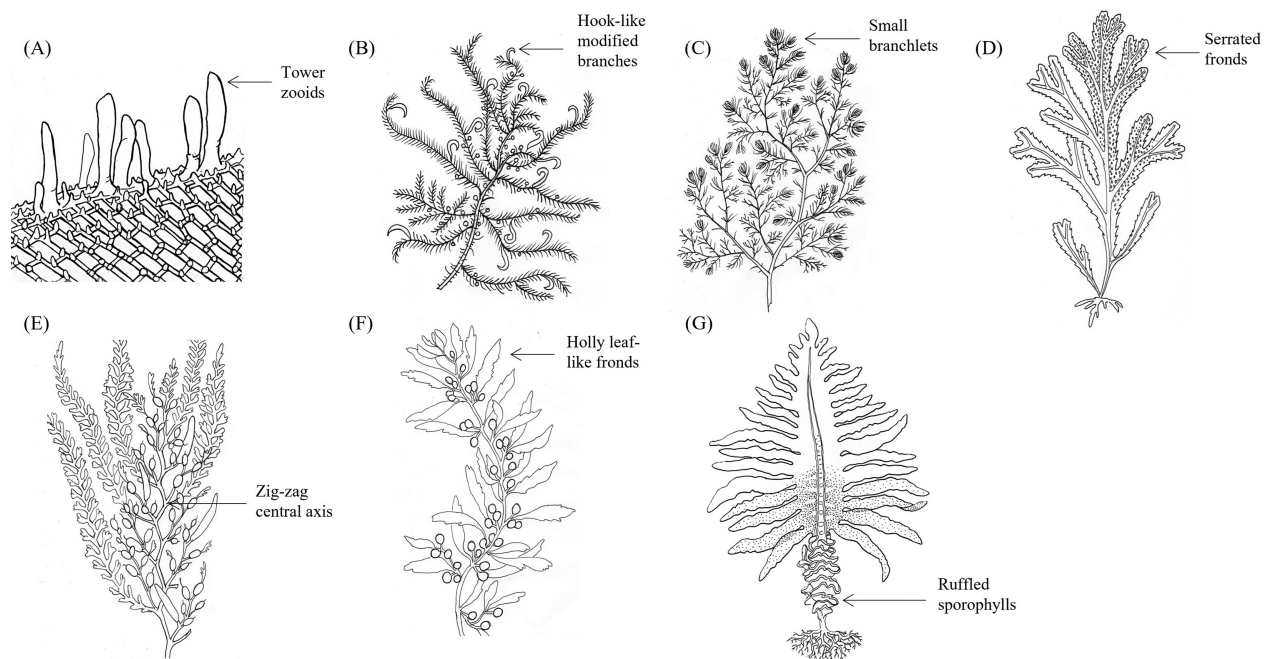


Figure 2. Descriptive drawings of the seven watch list species (a) *Membranipora membranacea*, (b) *Bonnemaisonia hamifera*, (c) *Dasysiphonia japonica*, (d) *Fucus serratus*, (e) *Sargassum horneri*, (f) *Sargassum muticum*, and (g) *Undaria pinnatifida*.

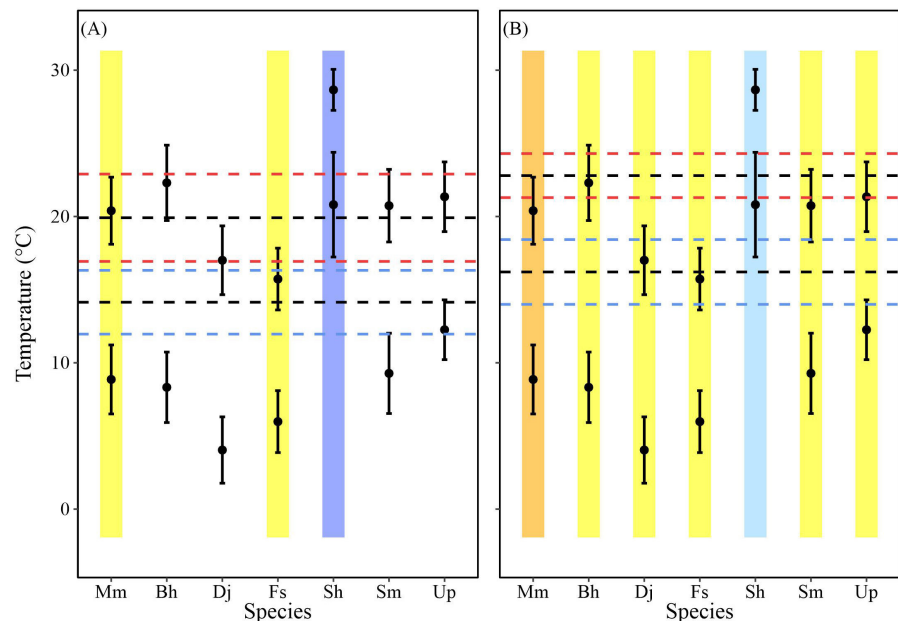


Figure 3. Mean minimum ($\pm 95\%$ CI) and maximum ($\pm 95\%$ CI) temperatures of the realised thermal range of the seven watch list species (*Membranipora membranacea* (Mm), *Bonnemaisonia hamifera* (Bh), *Dasysiphonia japonica* (Dj), *Fucus serratus* (Fs), *Sargassum horneri*, *Sargassum muticum* (Sm), *Undaria pinnatifida* (Up)). Overlaid are the present mean minimum SST $\pm 95\%$ CI (lower dashed black line with CI indicated in blue) and maximum SST $\pm 95\%$ CI (upper dashed black line with CI indicated in red for the (a) Benguela and (b) Agulhas ecoregions (Data provided in Supplementary material Table S3). The coloured vertical bars indicate the degree of congruency between the species thermal range and that of the ecoregion. No colour represents the most suitable temperature for survivability. Colours correspond to those in Table 2.

species being a bryozoan. Three potential pathway categories were identified: (1) escape (via aquaculture or research activities), (2) contaminant (as a food or animal contaminant), and (3) stowaway (via shipping, hull fouling, and ballast water). All species share stowaway as a common pathway, while four of the seven could be introduced by more than one pathway.

Under present conditions all species have the potential to survive in both the Benguela and Agulhas ecoregions (Figure 3; Table S2). In the Benguela ecoregion, the cooler thermal range is suitable for four algae species i.e. the red hookweed *Bonnemaisonia hamifera* Hariot, 1891 and siphoned feather weed *Dasysiphonia japonica* (Yendo, 1920), and the brown wireweed *Sargassum muticum* (Yendo, 1907) and *Undaria pinnatifida* (Harvey, 1860) commonly known as wakame. In contrast, temperatures in this region could possibly be too warm for the brown toothed wrack *Fucus serratus* Linnaeus, 1753 and the white, lacy encrusting bryozoan *Membranipora membranacea*, yet probably too cold for the brown devil weed *Sargassum horneri* (Turner, 1808). The warmer Agulhas region is probably too warm for *M. membranacea*, and possibly too warm for almost all algae, except for *S. horneri*.

Future warming

In the Benguela ecoregion under moderate warming conditions, the degree of congruency between each species' thermal range and that of the ecoregion

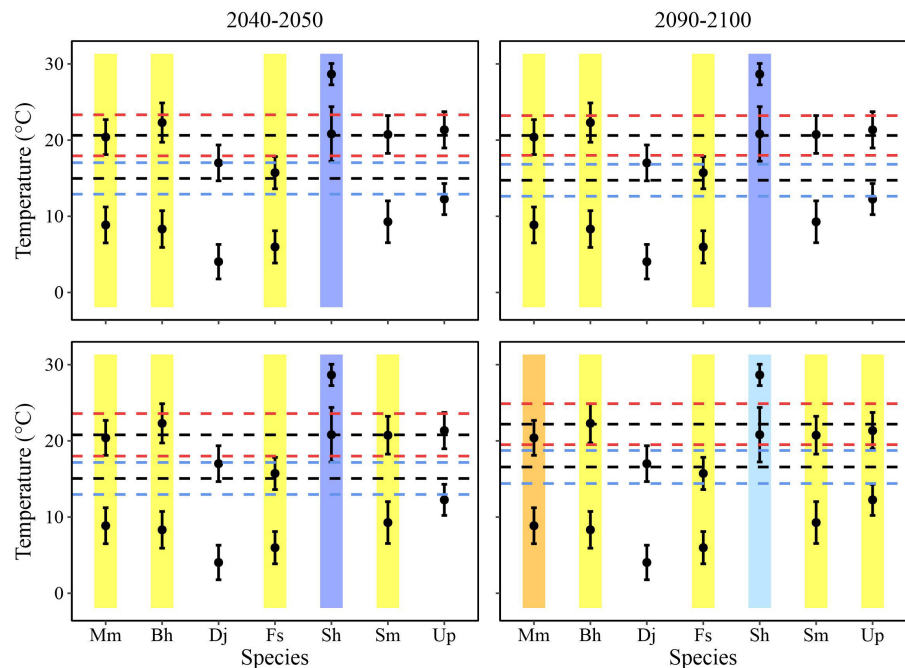


Figure 4. Mean minimum ($\pm 95\%$ CI) and maximum ($\pm 95\%$ CI) temperatures of the realised thermal range of the seven watch list species (*Membranipora membranacea* (Mm), *Bonnemaisonia hamifera* (Bh), *Dasysiphonia japonica* (Dj), *Fucus serratus* (Fs), *Sargassum horneri*, *Sargassum muticum* (Sm), *Undaria pinnatifida* (Up)) under future (2040–2050 and 2090–2100) moderate and severe warming conditions projected using the RCP 2.6 (moderate warming) and RCP 8.5 (severe warming) scenarios for the Benguela ecoregion. See Figure 3 for a full explanation of the graph features. The coloured vertical bars indicate the degree of congruency between the species thermal range and that of the ecoregion. No colour represents the most suitable temperature for survivability. Colours correspond to those in Table 2.

remain the same for both near future and long-term warming (Figure 4). Under these conditions, temperatures remain suitable for the red alga *D. japonica*, and the two brown algae *S. muticum* and *U. pinnatifida*. Under severe warming conditions, temperatures remain suitable for *D. japonica* and *U. pinnatifida* in the near future and *D. japonica* in the long-term future. However, conditions could become too warm for the remaining species, except *S. horneri* which typically occurs in warmer waters. Long-term warming in this region will increase the probability of conditions becoming too warm for *M. membranacea* and *U. pinnatifida*, but they could remain too cold for *S. horneri*.

In the Agulhas ecoregion, moderate and severe warming conditions are not expected to be well suited to any species regardless of the time frame considered (Figure 5). Under warming conditions, temperatures could possibly be too warm for five out of six algae species, while probably being too warm for *M. membranacea*, yet possibly too cold for *S. horneri*. Under severe warming conditions the degree of congruency between species and ecoregion thermal range remains the same over both timeframes. The only change from a moderate to severe warming scenario is that conditions would probably become too warm for *F. serratus*.

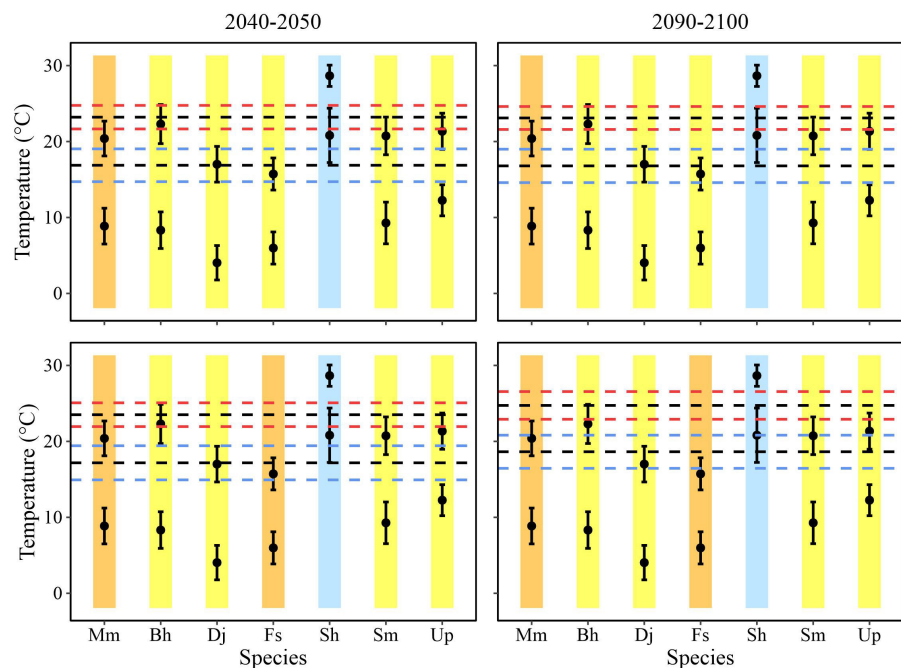


Figure 5. Mean minimum ($\pm$ 95% CI) and maximum ($\pm$ 95% CI) temperatures of the realised thermal range of the seven watch list species (*Membranipora membranacea* (Mm), *Bonnemaisonia hamifera* (Bh), *Dasyatisphonia japonica* (Dj), *Fucus serratus* (Fs), *Sargassum horneri*, *Sargassum muticum* (Sm), *Undaria pinnatifida* (Up)) under future (2040–2050 and 2090–2100) moderate and severe warming conditions projected using the RCP 2.6 (moderate) and RCP 8.5 (severe) scenarios for the Agulhas ecoregion. See Figure 3 for a full explanation of the graph features. The coloured vertical bars indicate the degree of congruency between the species thermal range and that of the ecoregion. No colour represents the most suitable temperature for survivability. Colours correspond to those in Table 2.

Future cooling

Under moderate cooling, the near future temperature of the Benguela ecoregion is expected to be suitable for the red algae *B. hamifera* and *D. japonica*, and brown algae *S. muticum* and *U. pinnatifida* (Figure 6). Temperatures will possibly be too warm for the brown alga *F. serratus* and the bryozoan *M. membranacea* and are likely to be too cold for *S. horneri*. In the long-term, there was little change in suitability of temperatures compared to the near-term. However, it could become too cold for the alga *U. pinnatifida*. Under severe cooling, long-term future temperatures are expected to be suitable for most species, but could pose a challenge for *S. horneri*, *S. muticum*, and *U. pinnatifida*.

In the near future under moderate cooling conditions, temperatures in the Agulhas ecoregion will likely only be suitable for the red alga *D. japonica* (Figure 7). Conditions are expected to possibly be too warm for almost all remaining species, except for the brown alga *S. horneri*, for which temperatures will possibly be too cold. In the long-term, further declines in temperature could result in the ecoregion becoming suitable for the brown alga *U. pinnatifida*. Long-term severe cooling conditions are expected to increase the thermal suitability of the region for *B. hamifera* and *S. muticum*, but temperatures will probably become too cold for *S. horneri*.

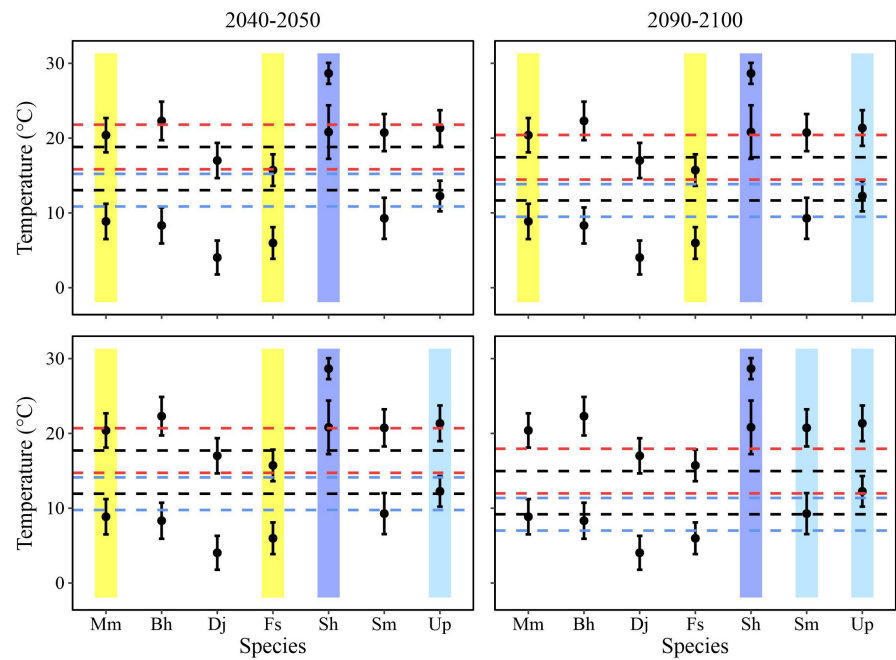


Figure 6. Mean minimum ($\pm 95\%$ CI) and maximum ($\pm 95\%$ CI) temperatures of the realised thermal range of the seven watch list species (*Membranipora membranacea* (Mm), *Bonnemaisonia hamifera* (Bh), *Dasysiphonia japonica* (Dj), *Fucus serratus* (Fs), *Sargassum horneri*, *Sargassum muticum* (Sm), *Undaria pinnatifida* (Up)) under future (2040–2050 and 2090–2100) moderate and severe cooling conditions projected using trends calculated from Rouault et al. (2010) for the Benguela ecoregion. See Figure 3 for a full explanation of the graph features. The coloured vertical bars indicate the degree of congruency between the species thermal range and that of the ecoregion. No colour represents the most suitable temperature for survivability. Colours correspond to those in Table 2.

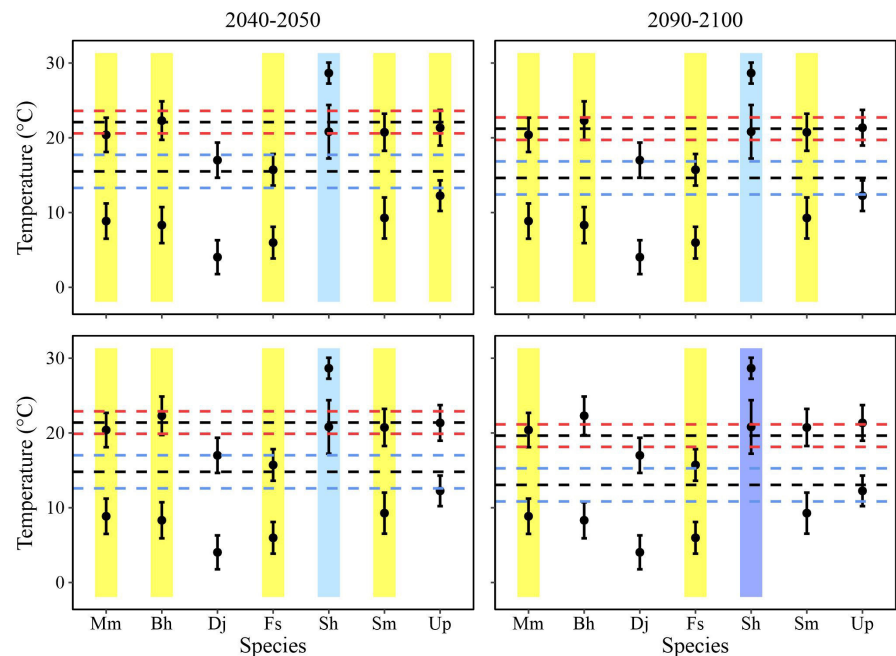


Figure 7. Mean minimum ($\pm 95\%$ CI) and maximum ($\pm 95\%$ CI) temperatures of the realised thermal range of the seven watch list species (*Membranipora membranacea* (Mm), *Bonnemaisonia hamifera* (Bh), *Dasysiphonia japonica* (Dj), *Fucus serratus* (Fs), *Sargassum horneri*, *Sargassum muticum* (Sm), *Undaria pinnatifida* (Up)) under future (2040–2050 and 2090–2100) moderate and severe cooling conditions projected using trends calculated from Rouault et al. (2010) for the Agulhas ecoregion. See Figure 3 for a full explanation of the graph features. The coloured vertical bars indicate the degree of congruency between the species thermal range and that of the ecoregion. No colour represents the most suitable temperature for survivability. Colours correspond to those in Table 2.

Discussion

In a changing climate, the risk of biological invasions is particularly concerning as previously unsuitable environments may become suitable to new alien species (Sorte et al. 2010; Finch et al. 2021). In kelp forest ecosystems, invasions of a single species can lead to invasional meltdown (Chapman et al. 2002) and ultimately an ecosystem regime shift (Levin et al. 2002). Alien species are understudied in South African kelp forests, with only a single study documenting three species (Lindberg et al. 2020). As such, the potential risks to these important ecosystems remain largely unknown. Consequently, understanding which species may have the ability to invade South African kelp forests is of utmost importance if they are to be prevented. This study identified 15 alien species with an invasion history in other kelp forests that could pose a threat to South African systems. Of the 15 species, eight are already present in South Africa. While these species have not been included in the watch list, it would be prudent for any future monitoring efforts to look out for them, as they have been recorded in South Africa, although not yet specifically in South African kelp forests to the best of our knowledge. This could be achieved by placing them on a Black list (*sensu* Gallardo et al. (2016)) that would support directed field surveys. The remaining seven species make up the watch list identified in our study. These species pose a potential threat to the South African coast as they have invaded kelp systems elsewhere, and this threat remains even under future climate conditions. Kelp forests in the Benguela ecoregion appear more vulnerable to invasion than the Agulhas under current and warming conditions, highlighted by this ecoregion being suitable for at least one species (*Dasysiphonia japonica*) under present and all potential future conditions. However, continued cooling could increase the suitability of the Agulhas ecoregion for some species.

Currently six algae species from the phyla Rhodophyta (*Antithamnionella spirographidis* (Schiffner, 1916), *Asparagopsis armata* Harvey, 1855, *Asparagopsis taxiformis* (Delile, 1813), *Schimmelmannia elegans* Baardseth, 1941) and Chlorophyta (*Cladophora prolifera* (Roth, 1797), *Codium fragile*) are recognised as alien in South Africa (Robinson et al. 2020b). These algae have been found in a variety of habitats including on artificial substrata like boats and harbours, rocky shores, saltmarshes, and estuaries (Robinson et al. 2016). Of the six species, five (*A. spirographidis*, *A. armata*, *A. taxiformis*, *C. prolifera*, *C. fragile*) are considered invasive (Robinson et al. 2016). In addition, *A. armata*, *A. taxiformis*, *S. elegans* are listed under South Africa's national legislation (i.e. National Environmental Management: Biodiversity Act of 2004 (NEM:BA)) that prohibits their import, movement, and sale within South Africa. Interestingly, the edible brown algae *Undaria pinnatifida*, which is not present in South Africa and has been placed on the watch list, has pre-emptively been listed as a species requiring control, should it be detected. Globally, invasions by non-indigenous algae are becoming increasingly problematic

(Filbee-Dexter and Wernberg 2018), and in some cases have led to a complete shift from kelp forest ecosystems to degraded turf algae dominated ecosystems (Wernberg et al. 2016; Filbee-Dexter and Wernberg 2018). Alien algae threaten biodiversity by outcompeting and inhibiting native taxa (Ambrose and Nelson 1982; Svensson et al. 2013), monopolising space, and altering both ecosystem structure and function (Dijkstra et al. 2017). Given that the watch list developed in this study is comprising mostly algae and the fact that alien algae are increasingly being reported elsewhere, careful attention should be paid to this group in the context of invasions in South African kelp forests. For the most part, the algae on the watch list are easily distinguishable from native species. However, *D. japonica* could be easily confused with the native red algae *Pseudoceramium planum* (Kützinger, 1849) in the field as both algae are small, delicate, and flattened with many branches. This is concerning given the level of compatibility *D. japonica* has with conditions in the Benguela ecoregion. Furthermore, *D. japonica* is known to be problematic elsewhere as it forms harmful blooms that can lead to mortality of fish and bivalves (Young et al. 2022). In light of this, future studies in South African kelp forests could use tools such as eDNA to identify the presence cryptogenic species like *D. japonica* (e.g. Ellis et al. 2022; Zeng et al. 2024). This method should be used in conjunction with the targeted collection of specimens that look like *P. planum* for taxonomic verification. This would provide a robust means to ensure that any incursions of *D. japonica* are detected early. The early detection of *D. japonica* in the Benguela ecoregion is critical given the suitability of the ecoregion for this species. Although detection on its own cannot address the issue of an alien species incursion, it does highlight the need to establish a management protocol where roles and responsibilities are predefined as demonstrated in Loureiro et al. (2021). Despite being the only animal on the watch list, the bryozoan *M. membranacea* is a species of great concern given its destructive invasion history elsewhere (Lambert et al. 1992; Scheibling et al. 1999; Chapman et al. 2002). In South Africa, samples found in False Bay were previously misidentified as *M. membranacea* (Florence et al. 2007). However, further examination of these specimens determined them to be the native species *Membranipora rustica* Florence, Hayward & Gibbons, 2007. The two species are only distinguishable under a microscope, highlighting the need for future monitoring efforts to include routine collection of specimens of white, lacy encrusting bryozoans for taxonomic verification.

Identifying pathways of invasion is an important step in alien species management (Hulme 2008; Lodge et al. 2016). In this study, stowaway, contaminant, and escape were all identified as potential pathways of introduction. The fact that multiple potential pathways exist for the introduction of alien species to South African kelp systems highlights the risk of potential invasion. All the watch list species shared stowaway as a common pathway to introduction. This is reflective of these taxa having

been transported by ships as hull fouling or in ballast water. Currently, South Africa is a signatory to the International Convention for the Control and Management of Ship's Ballast Water and Sediments (BWM Convention) but is yet to sign a bill into law to guide the implementation of this legal tool at a national level. As in most countries, hull fouling remains unregulated in South Africa, despite the important role this pathway plays in dispersing marine alien taxa (Peters and Robinson 2017; Peters et al. 2019). The fact that these important pathways remain unregulated in South Africa highlights South Africa's vulnerability to new introductions. Alien species introduced as contaminants are often done so through mariculture (Faulkner et al. 2020). In South Africa, the Pacific oyster *Magallana gigas* (Thunberg, 1793) is farmed in sheltered bays along the west and south coasts (Haupt et al. 2010a, b). The oysters are grown from spat imported primarily from Namibia, Chile, and France (Nel et al. 2014). Haupt et al. (2012) found that despite cleansing and treatment measures, some epifaunal taxa survived and could be successfully translocated. Several introductions of alien species into South Africa have been linked to the translocation of *M. gigas* (Haupt et al. 2010a). All four watch list species associated with the contaminant pathway (i.e. *B. hamifera*, *D. japonica*, *S. muticum*, and *U. pinnatifida*) have a history of invasion linked to the translocation of *M. gigas* and other shellfish (Sabour et al. 2013). This is worrying in the South African context as farming of shellfish (particularly *M. gigas*) has been a particular focus in efforts to develop the South African blue economy (Findlay 2018). It is thus clear that biosecurity agencies need to play a crucial role going forward, as economic development needs to be facilitated while concurrently protecting against introductions that could negatively affect ecosystem services. The final pathway of introduction identified in this study was escape. The intentional importation, growing, translocating, or release of the highly invasive species *U. pinnatifida* is prohibited by law in South Africa according to NEM:BA. Given that *U. pinnatifida* is not present in South Africa and possessing live specimens in the country is prohibited, the escape of this species into South Africa should not be possible. Conversely, the brown wireweed *S. muticum* is not regulated in the same way despite a similarly significant invasion history (Salvaterra et al. 2013; Engelen et al. 2015; Marks et al. 2015). This allows for permit applications to be made to import the species. *Sargassum muticum* is widely used in traditional oriental medicine for the treatment of a variety of ailments (Sharifuddin et al. 2015) and is being studied for its antioxidant, antimicrobial, anti-inflammatory, and photoprotective properties (Pinteus et al. 2017; Susano et al. 2022). As such, demand for this species to be grown or imported into South Africa for medicinal or nutritional use may grow. The possibility of increasing interest in *S. muticum* is worrying given that there are no regulations in place preventing the application to import this species. As a precautionary measure this species should be subject to a Risk Analysis for Alien Taxa (Kumschick et al. 2020). The results from this analysis can then be used to inform steps to more tightly regulate the species.

Temperature is an important factor influencing the distribution of marine species (Tittensor et al. 2010) and the invasion potential of species is expected to be greatest in areas that are thermally similar to their native range (Peterson 2003). Consequently, temperature-matching is a vital tool in predicting the invasion potential and the potential distribution of alien species (Matthews et al. 2017). On a practical level, information gained from temperature matching enables monitoring to be more targeted in terms of knowing which areas to prioritise. Ultimately, this minimises costs. In our study, temperature-matching revealed that the thermal characteristics for both the Benguela and Agulhas ecoregions would not automatically exclude any of the seven species on the watch list, although the likelihood of the various species being regulated by temperature varied. Overall, the temperature of the Benguela ecoregion is better matched to the thermal landscape that the watch list species experience in their realised ranges, with four out of seven species being well suited to the Benguela ecoregion under present conditions, compared to none in the Agulhas ecoregion. Consequently, the kelp forests in the Benguela ecoregion could be more vulnerable to incursions. As such, this ecoregion should be prioritised for monitoring, particularly given the high volume of ship traffic along this coastline. The suitability of the Benguela ecoregion is not surprising, as kelps themselves are considered temperate species (Steneck et al. 2002; Wernberg et al. 2019), and the Benguela ecoregion reflects the core of the range for South African kelp forests (Blamey and Bolton 2018), with only a small range in the western part of the Agulhas region. Kelp forests in the Agulhas ecoregion reflect a recent eastward spread in response to cooling of the warmer south coast (Bolton et al. 2012). Thus, the Agulhas kelp forests are likely on the thermal cusp for kelp and less suitable for alien taxa that would normally invade temperate regions. Of the future conditions that could manifest along the south and south-west coasts of South Africa, cooling improved the thermal suitability for more than half the species on the watch list, whilst conditions become increasingly less favourable for the brown algae *Sargassum horneri*, *Sargassum muticum*, and *Undaria pinnatifida*. Given that the south-west and south coasts of South Africa are expected to continue cooling rather than warming (Rouault et al. 2010; Lamont et al. 2018), with time South African kelp forests will likely become more vulnerable to invasion by the taxa on the watch list. These results highlight the importance of using localised patterns of change when considering the implications of global change. Despite the value of using thermal matching, areas suitable for invasion may not always be identified if the fundamental niche of the species is not fully captured (de Andrade et al. 2019). Furthermore, Laeseke et al. (2024) has shown that thermal limits, particularly the cold tolerance of seaweeds, have limited predictive power for seaweed distribution and may have large deviations. Consequently, species which appear to be on their lower thermal limit in the Benguela and Agulhas ecoregions may have a much greater thermal tolerance and a greater chance of successfully invading these ecoregions than identified in this study.

As applied in this study, horizon scanning offers an evidence-based approach to identifying species that might reach the region and helps to develop a watch list of species which may be used by management to monitor local kelp forest ecosystems. However, this method relies on a global review of species with an invasion history. Invasions that have not been detected or reported have thus inherently not been captured in this study, although such species may be able to reach South Africa and survive local conditions. As such the watch list developed in this study offers a foundation on which to begin long-term monitoring for alien species that could invade South African kelp forests.

To mitigate potential impacts and avoid costly eradication programs, the pro-active prevention of alien establishment is needed. While preventative measures are most effective when focused on preventing the arrival of new taxa (Ojaveer et al. 2015), prevention of establishment post-arrival can occur if management action is swift (e.g. Anderson 2005). Rapid response could be facilitated by the establishment of a standardised monitoring program that routinely surveys kelp forests to (1) detect new alien species; (2) track the spread of incursions and (3) measure impacts on native species. The watch list developed in this study can be used to facilitate targeted and cost-effective monitoring. While it would be desirable to monitor both ecoregions, the vulnerability of the Benguela ecoregion suggests that should resources not be available to monitor both, efforts should focus on the west coast. This initial monitoring program could be used as a test case to streamline administration and on the ground implementation, that can then inform an extended program into the Agulhas ecoregion. As harbours and aquaculture facilities are most likely the sources of introductions, kelp forests near these should be prioritised for monitoring. Key locations to survey would be those that support international ports like Table Bay and Saldanha Bay. Collaboration with scientists and taxonomists is essential to establish a monitoring protocol and train divers in field methodology and taxonomy (Douglas et al. 2009; Loureiro et al. 2021). The value of a monitoring program would be maximised if it were embedded into a broader biosecurity system where roles and responsibilities are well established (Loureiro et al. 2021). This would likely draw together various government departments including those focused on biosecurity, biodiversity, and aquaculture. To remain current, the watch list must be updated as new invasions are recorded in kelp forests elsewhere in the world.

Authors' contribution

CS: data collection, data analysis and interpretation, writing (original draft, review and editing). TBR: research conceptualisation, sample design and methodology, supervision, funding provision, writing (review and editing). LKB: sample design and methodology, supervision, writing (review and editing).

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References

- Ambrose RF, Nelson BV (1982) Inhibition of giant kelp recruitment by an introduced brown alga. *Botanica Marina* 25: 265–268, <https://doi.org/10.1515/botm.1982.25.6.265>
- Anderson L (2005) California's reaction to *Caulerpa taxifolia*: a model for invasive species rapid response. *Biological Invasions* 7: 1003–1016, <https://doi.org/10.1007/s10530-004-3123-z>
- Anderson RJ, Carrick P, Levitt GJ, Share A (1997) Holdfasts of adult kelp *Ecklonia maxima* provide refuges from grazing for recruitment of juvenile kelps. *Marine Ecology Progress Series* 159: 265–273, <https://doi.org/10.3354/meps159265>
- de Andrade AFA, Velazco SJE, De Marco P (2019) Niche mismatches can impair our ability to predict potential invasions. *Biological Invasions* 21: 3135–3150, <https://doi.org/10.1007/s10530-019-02037-2>
- Bertolino S, Ancillotto L, Bartolommei P, Benassi G, Capizzi D, Gasperini S, Lucchesi M, Mori E, Scillitani L, Sozio G (2020) A framework for prioritising present and potentially invasive mammal species for a national list. *NeoBiota* 62: 31–54, <https://doi.org/10.3897/neobiota.62.52934>
- Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JR, Richardson DM (2011) A proposed unified framework for biological invasions. *Trends in Ecology and Evolution* 26: 333–339, <https://doi.org/10.1016/j.tree.2011.03.023>
- Blamey LK, Bolton JJ (2018) The economic value of South African kelp forests and temperate reefs: past, present and future. *Journal of Marine Systems* 188: 172–181, <https://doi.org/10.1016/j.jmarsys.2017.06.003>
- Bolton JJ, Stegenga H (1990) The seaweeds of De Hoop Nature Reserve and their phytogeographical significance. *South African Journal of Botany* 56: 233–238
- Bolton JJ, Anderson RJ, Smit AJ, Rothman MD (2012) South African kelp moving eastwards: the discovery of *Ecklonia maxima* (Osbeck) Papenfuss at De Hoop Nature Reserve on the south coast of South Africa. *African Journal of Marine Science* 34: 147–151, <https://doi.org/10.2989/1814232X.2012.675125>
- Chapman AS, Scheibling RE, Chapman ARO (2002) Species introductions and changes in marine vegetation of Atlantic Canada. In: Claudi R, Nantel ME (eds), *Alien invaders in Canada's waters, wetlands and forests*. Natural Resources Canada, Canadian Forest Service Science Branch, Ottawa, pp 133–148
- Connell SD, Russell BD (2010) The direct effects of increasing CO₂ and temperature on non-calcifying organisms: increasing the potential for phase shifts in kelp forests. *Proceedings of the Royal Society B: Biological Sciences* 277: 1409–1415, <https://doi.org/10.1098/rspb.2009.2069>
- Culver C, Kuris A (2000) The apparent eradication of a locally established introduced marine pest. *Biological Invasions* 2: 245–253, <https://doi.org/10.1023/A:1010082407254>
- Diagne C, Leroy B, Vaissière A-C, Gozlan RE, Roiz D, Jarić I, Salles J-M, Bradshaw CJ, Courchamp F (2021) High and rising economic costs of biological invasions worldwide. *Nature* 592: 571–576, <https://doi.org/10.1038/s41586-022-05100-6>
- Davidson A, Tucker AJ, Chadderton WL, Weibert C (2021) Development of a surveillance species list to inform aquatic invasive species management in the Laurentian Great Lakes. *Management of Biological Invasions* 12: 272–293, <https://doi.org/10.3391/mbi.2021.12.2.05>
- Dijkstra JA, Harris LG, Mello K, Litterer A, Wells C, Ware C (2017) Invasive seaweeds transform habitat structure and increase biodiversity of associated species. *Journal of Ecology* 105: 1668–1678, <https://doi.org/10.1111/1365-2745.12775>
- Douglas H, Dang PT, Gill BD, Huber J, Mason PG, Parker DJ, Sinclair BJ (2009) The importance of taxonomy in responses to invasive alien species. *Biodiversity* 10: 92–99, <https://doi.org/10.1080/14888386.2009.9712850>
- Dufois F, Rouault M (2012) Sea surface temperature in False Bay (South Africa): Towards a better understanding of its seasonal and inter-annual variability. *Continental Shelf Research* 43: 24–35, <https://doi.org/10.1016/j.csr.2012.04.009>

- Duncan M, James N, Bates A, Goschen W, Potts W (2019) Localised intermittent upwelling intensity has increased along South Africa's south coast due to *El Niño* – Southern Oscillation phase state. *African Journal of Marine Science* 41: 325–330, <https://doi.org/10.2989/1814232X.2019.1656105>
- Ellis MR, Clark ZS, Trembl EA, Brown MS, Matthews TG, Pocklington JB, Stafford-Bell RE, Bott NJ, Nai YH, Miller AD, Sherman CD (2022) Detecting marine pests using environmental DNA and biophysical models. *Science of the Total Environment* 816: 151666, <https://doi.org/10.1016/j.scitotenv.2021.151666>
- Engelen AH, Serebryakova A, Ang P, Britton-Simmons K, Mineur F, Pedersen MF, Arenas F, Fernandez C, Steen H, Svenson R (2015) Circumglobal invasion by the brown seaweed *Sargassum muticum*. *Oceanography and Marine Biology* 53: 81–126
- Faulkner KT, Robertson MP, Rouget M, Wilson JR (2014) A simple, rapid methodology for developing invasive species watch lists. *Biological Conservation* 179: 25–32, <https://doi.org/10.1016/j.biocon.2014.08.014>
- Faulkner KT, Hulme PE, Pagad S, Wilson JR, Robertson MP (2020) Classifying the introduction pathways of alien species: are we moving in the right direction? *NeoBiota* 62: 143–159, <https://doi.org/10.3897/neobiota.62.53543>
- Filbee-Dexter K, Wernberg T (2018) Rise of turfs: a new battlefield for globally declining kelp forests. *Bioscience* 68: 64–76, <https://doi.org/10.1093/biosci/bix147>
- Finch DM, Butler JL, Runyon JB, Fettig CJ, Kilkenny FF, Jose S, Frankel SJ, Cushman SA, Cobb RC, Dukes JS, Hicke JA, Amelon SK (2021) Effects of Climate Change on Invasive Species. In: Poland TM, Patel-Weynand T, Finch DM, Miniati CF, Hayes DC, Lopez VM (eds), *Invasive Species in Forests and Rangelands of the United States: A Comprehensive Science Synthesis for the United States Forest Sector*. Springer International Publishing, Cham, pp 57–83, https://doi.org/10.1007/978-3-030-45367-1_4
- Findlay K (2018) Operation Phakisa and unlocking South Africa's ocean economy. *Journal of the Indian Ocean Region* 14: 248–254, <https://doi.org/10.1080/19480881.2018.1475857>
- Florence WK, Hayward PJ, Gibbons MJ (2007) Taxonomy of shallow-water Bryozoa from the west coast of South Africa. *African Natural History* 3(1): 1–58
- Gallardo B, Zieritz A, Adriaens T, Bellard C, Boets P, Britton JR, Newman JR, van Valkenburg JL, Aldridge DC (2016) Trans-national horizon scanning for invasive non-native species: a case study in western Europe. *Biological Invasions* 18: 17–30, <https://doi.org/10.1007/s10530-015-0986-0>
- Harris LG, Tyrrell MC (2001) Changing community states in the Gulf of Maine: synergism between invaders, overfishing and climate change. *Biological Invasions* 3: 9–21, <https://doi.org/10.1023/A:1011487219735>
- Haupt TM, Griffiths CL, Robinson TB, Tonin AFG (2010a) 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/10.1080/15627020.2010.11657254>
- Haupt TM, Griffiths CL, Robinson TB, Tonin AF, De Bruyn PA (2010b) The history and status of oyster exploitation and culture in South Africa. *Journal of Shellfish Research* 29: 151–159, <https://doi.org/10.2983/035.029.0109>
- Haupt T, Griffiths C, Robinson T (2012) Intra-regional translocations of epifaunal and infaunal species associated with cultured Pacific oysters *Crassostrea gigas*. *African Journal of Marine Science* 34: 187–194, <https://doi.org/10.2989/1814232X.2012.673293>
- Hopkins GA, Forrest BM, Jiang W, Gardner JP (2011) Successful eradication of a non-indigenous marine bivalve from a subtidal soft-sediment environment. *Journal of Applied Ecology* 48: 424–431, <https://doi.org/10.1111/j.1365-2664.2010.01941.x>
- Hulme PE (2008) Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology* 46: 10–18, <https://doi.org/10.1111/j.1365-2664.2008.01600.x>
- Kumschick S, Wilson JR, Foxcroft LC (2020) A framework to support alien species regulation: the Risk Analysis for Alien Taxa (RAAT). *NeoBiota* 62: 213–239, <https://doi.org/10.3897/neobiota.62.51031>
- Laeseke P, Martínez BD-C, Bischof K (2024) Large-scale deviations between realized and fundamental thermal niches in global seaweed distributions. *Diversity and Distributions* 30: e13868, <https://doi.org/10.1111/ddi.13868>
- Lambert WJ, Levin PS, Berman J (1992) Changes in the structure of a New England (USA) kelp bed: the effects of an introduced species? *Marine Ecology Progress Series* 88: 303–307, <https://doi.org/10.3354/meps088303>
- Lamont T, García-Reyes M, Bograd SJ, van der Lingen CD, Sydeman WJ (2018) Upwelling indices for comparative ecosystem studies: variability in the Benguela Upwelling System. *Journal of Marine Systems* 188: 3–16, <https://doi.org/10.1016/j.jmarsys.2017.05.007>
- Levin PS, Coyer JA, Petrik R, Good TP (2002) Community-wide effects of nonindigenous species on temperate rocky reefs. *Ecology* 83: 3182–3193, <https://doi.org/10.2307/3071852>
- Lindberg C, Griffiths C, Anderson R (2020) Colonisation of South African kelp-bed canopies by the alien mussel *Mytilus galloprovincialis*: extent and implications of a novel bioinvasion. *African Journal of Marine Science* 42: 167–176, <https://doi.org/10.2989/1814232X.2020.1754908>

- Lodge DM, Simonin PW, Burgiel SW, Keller RP, Bossenbroek JM, Jerde CL, Kramer AM, Rutherford ES, Barnes MA, Wittmann ME (2016) Risk analysis and bioeconomics of invasive species to inform policy and management. *Annual Review of Environment and Resources* 41: 453–88, <https://doi.org/10.1146/annurev-environ-110615-085532>
- Loureiro TG, Peters K, Robinson TB (2021) Dropping plates to pick up aliens: towards a standardised approach for monitoring alien fouling species. *African Journal of Marine Science* 43: 483–497, <https://doi.org/10.2989/1814232X.2021.1989488>
- Mabin CA, Wilson JR, Le Roux JJ, Majiedt P, Robinson TB (2020) The first management of a marine invader in Africa: the importance of trials prior to setting long-term management goals. *Journal of Environmental Management* 261: 110213, <https://doi.org/10.1016/j.jenvman.2020.110213>
- Marks LM, Salinas-Ruiz P, Reed DC, Holbrook SJ, Culver CS, Engle JM, Kushner DJ, Caselle JE, Freiwald J, Williams JP (2015) Range expansion of a non-native, invasive macroalga *Sargassum horneri* (Turner) C. Agardh, 1820 in the eastern Pacific. *BiolInvasions Records* 4: 243–248, <https://doi.org/10.3391/bir.2015.4.4.02>
- Matthews J, Beringen R, Creemers R, Hollander HD, Kessel N van, Kleef H van, Koppel S, Lemaire A, Odé B, Verbrugge LN (2017) A new approach to horizon-scanning: identifying potentially invasive alien species and their introduction pathways. *Management of Biological Invasions* 8: 37–52, <https://doi.org/10.3391/mbi.2017.8.1.04>
- Miller AW, Chang AL, Cosentino-Manning N, Ruiz GM (2004) New record and eradication of the northern Atlantic alga *Ascophyllum nodosum* (Phaeophyceae) from San Francisco Bay, California, USA. *Journal of Phycology* 40: 1028–1031, <https://doi.org/10.1111/j.1529-8817.2004.04081.x>
- Minchin D (2007) Rapid coastal survey for targeted alien species associated with floating pontoons in Ireland. *Aquatic Invasions* 2: 63–70, <https://doi.org/10.3391/ai.2007.2.1.8>
- Nel A, Pitcher G, Richoux N, Jackson S (2014) Culture environment and hatchery of origin influence growth, condition and feeding organ morphology in the Pacific oyster *Crassostrea gigas* in South Africa. *African Journal of Marine Science* 36: 481–491, <https://doi.org/10.2989/1814232X.2014.982187>
- Oficialdegui FJ, Zamora-Marín JM, Guareschi S, Anastácio PM, García-Murillo P, Ribeiro F, Miranda R, Cobo F, Gallardo B, García-Berthou E (2023) A horizon scan exercise for aquatic invasive alien species in Iberian inland waters. *Science of the Total Environment* 869: 161798, <https://doi.org/10.1016/j.scitotenv.2023.161798>
- Ojaveer H, Galil BS, Campbell ML, Carlton JT, Canning-Clode J, Cook EJ, Davidson AD, Hewitt CL, Jelmert A, Marchini A, McKenzie CH, Minchin D, Occhipinti-Ambrogi A, Olenin S, Ruiz G (2015) Classification of non-indigenous species based on their impacts: considerations for application in marine management. *PLoS Biology* 13: e1002130, <https://doi.org/10.1371/journal.pbio.1002130>
- Ojaveer H, Galil BS, Carlton JT, Alleway H, Gouletquer P, Lehtiniemi M, Marchini A, Miller W, Occhipinti-Ambrogi A, Peharda M, Ruiz GM, Williams SL, Zaiko A (2018) Historical baselines in marine bioinvasions: implications for policy and management. *PLoS ONE* 13: e0202383, <https://doi.org/10.1371/journal.pone.0202383>
- Pörtner H-O, Roberts DC, Masson-Delmotte V, Zhai P, Poloczanska E, Mintenbeck K, Tignor M, Alegría A, Nicolai M, Okem A, Petzold J, Rama B, Weyer NM (eds) (2019) IPCC: Technical Summary. In: IPCC Special Report on the Ocean and Cryosphere in a Changing Climate. Cambridge University Press, Cambridge, UK and New York, NY, USA, pp 39–69, <https://doi.org/10.1017/9781009157964.002>
- Peters K, Robinson TB (2017) First record of the marine alien amphipod *Caprella mutica* (Schurin, 1935) in South Africa. *BiolInvasions Records* 6: 61–66, <https://doi.org/10.3391/bir.2017.6.1.10>
- Peters K, Sink KJ, Robinson TB (2019) Sampling methods and approaches to inform standardized detection of marine alien fouling species on recreational vessels. *Journal of Environmental Management* 230: 159–167, <https://doi.org/10.1016/j.jenvman.2018.09.063>
- Peterson AT (2003) Predicting the geography of species' invasions via ecological niche modeling. *The Quarterly Review of Biology* 78: 419–433, <https://doi.org/10.1086/378926>
- Pinteus S, Lemos MFL, Silva J, Alves C, Neugebauer A, Freitas R, Duarte A, Pedrosa R (2017) An insight into *Sargassum muticum* cytoprotective mechanisms against oxidative stress on a human cell in vitro model. *Marine Drugs* 15: 353, <https://doi.org/10.3390/md15110353>
- Pyšek P, Hulme PE, Simberloff D, Bacher S, Blackburn TM, Carlton JT, Dawson W, Essl F, Foxcroft LC, Genovesi P, Jeschke JM, Kühn I, Liebhold AM, Mandrak NE, Meyerson LA, Pauchard A, Pergl J, Roy HE, Seebens H, Kleunen M, Vilà M, Wingfield MJ, Richardson DM (2020) Scientists' warning on invasive alien species. *Biological Reviews* 95: 1511–1534, <https://doi.org/10.1111/brv.12627>
- Reaser JK, Frey M, Meyers NM (2020) Invasive species watch lists: guidance for development, communication, and application. *Biological Invasions* 22: 47–51, <https://doi.org/10.1007/s10530-019-02176-6>
- Reddy MM (2024) Well-known mesophotic kelp populations in the iSimangaliso Wetland Park marine-protected area, east coast, South Africa. *Journal of the Marine Biological Association of the United Kingdom* 104: e29, <https://doi.org/10.1017/S0025315424000195>

- Robinson T, Alexander M, Simon C, Griffiths C, Peters K, Sibanda S, Miza S, Groenewald B, Majiedt P, Sink K (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, Martin N, Loureiro TG, Matikinca P, Robertson MP (2020a) Double trouble: the implications of climate change for biological invasions. *NeoBiota* 62: 463–487, <https://doi.org/10.3897/neobiota.62.55729>
- Robinson TB, Peters K, Brooker B (2020b) Coastal Invasions: The South African Context. In: van Wilgen B, Measey J, Richardson D, Wilson J, Zengeya T (eds), *Biological Invasions in South Africa. Invading Nature - Springer Series in Invasion Ecology*, 14. Springer, pp 229–247, https://doi.org/10.1007/978-3-030-32394-3_9
- Rouault M, Pohl B, Penven P (2010) Coastal oceanic climate change and variability from 1982 to 2009 around South Africa. *African Journal of Marine Science* 32: 237–246, <https://doi.org/10.2989/1814232X.2010.501563>
- Roy HE, Peyton JM, Aldridge DC, Bantock T, Blackburn TM, Britton JR, Clark P, Cook E, Shaw H, Stebbing PD (2014) Horizon scanning for invasive alien species with the potential to threaten biodiversity in Great Britain. *Global Change Biology* 20: 3859–3871, <https://doi.org/10.1111/gcb.12603>
- Roy HE, Bacher S, Essl F, Adriaens T, Aldridge DC, Bishop JDD, Blackburn TM, Branquart E, Brodie J, Carboneras C, Cottier-Cook EJ, Copp GH, Dean HJ, Eilenberg J, Gallardo B, Garcia M, García-Berthou E, Genovesi P, Hulme PE, Kenis M, Kerckhof F, Kettunen M, Minchin D, Nentwig W, Nieto A, Pergl J, Pescott OL, M. Peyton J, Preda C, Roques A, Rorke SL, Scalera R, Schindler S, Schönrogge K, Sewell J, Solarz W, Stewart AJA, Tricarico E, Vanderhoeven S, Van Der Velde G, Vilà M, Wood CA, Zenetos A, Rabitsch W (2019) Developing a list of invasive alien species likely to threaten biodiversity and ecosystems in the European Union. *Global Change Biology* 25: 1032–1048, <https://doi.org/10.1111/gcb.14527>
- Sabour B, Reani A, Magouri HE, Haroun R (2013) *Sargassum muticum* (Yendo) Fensholt (Fucales, Phaeophyta) in Morocco, an invasive marine species new to the Atlantic coast of Africa. *Aquatic Invasions* 8: 97–102, <https://doi.org/10.3391/ai.2013.8.1.11>
- Salvaterra T, Green DS, Crowe TP, O’Gorman EJ (2013) Impacts of the invasive alga *Sargassum muticum* on ecosystem functioning and food web structure. *Biological Invasions* 15: 2563–2576, <https://doi.org/10.1007/s10530-013-0473-4>
- Scheibling RE, Gagnon P (2006) Competitive interactions between the invasive green alga *Codium fragile* ssp. *tomentosoides* and native canopy-forming seaweeds in Nova Scotia (Canada). *Marine Ecology Progress Series* 325: 1–14, <https://doi.org/10.3354/meps325001>
- Scheibling RE, Hennigar AW, Balch T (1999) Destructive grazing, epiphytism, and disease: the dynamics of sea urchin–kelp interactions in Nova Scotia. *Canadian Journal of Fisheries and Aquatic Sciences* 56: 2300–2314, <https://doi.org/10.1139/f99-163>
- Schlegel RW, Oliver ECJ, Wernberg T, Smit AJ (2017) Nearshore and offshore co-occurrence of marine heatwaves and cold-spells. *Progress in Oceanography* 151: 189–205, <https://doi.org/10.1016/j.pocan.2017.01.004>
- Seebens H, Blackburn TM, Hulme PE, van Kleunen M, Liebhold AM, Orlova-Bienkowskaja M, Pyšek P, Schindler S, Essl F (2021) Around the world in 500 years: Inter-regional spread of alien species over recent centuries. *Global Ecology and Biogeography* 30: 1621–1632, <https://doi.org/10.1111/gcb.13325>
- Sharifuddin Y, Chin Y-X, Lim P-E, Phang S-M (2015) Potential bioactive compounds from seaweed for diabetes management. *Marine Drugs* 13: 5447–5491, <https://doi.org/10.3390/md13085447>
- Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions* 1: 21–32, <https://doi.org/10.1023/A:1010086329619>
- Sink KJ, Atkinson LJ, Kerwath S, Samaai T (2010) Assessment of offshore benthic biodiversity on the Agulhas Bank and the potential role of petroleum infrastructure in offshore spatial management. Report prepared for WWF South Africa and PetroSA through a SANBI initiative, 77 pp
- Sink K, Holness S, Harris L, Majiedt P, Atkinson L, Robinson T, Hutchings L, Leslie R, Lamberth S, Kerwath S, Lombard A, Attwood C, Branch G, Fairweather T, Taljaard S, Cowley P, Awad A, Halpern B, Grantham H, Wolf T (2012) National Biodiversity Assessment 2011: technical report. Volume 4: marine and coastal component. South African National Biodiversity Institute, Pretoria, 325 pp
- Smit AJ, Roberts M, Anderson RJ, Dufois F, Dudley SFJ, Bornman TG, Olbers J, Bolton JJ (2013) A coastal seawater temperature dataset for biogeographical studies: large biases between in situ and remotely-sensed data sets around the coast of South Africa. *PLoS ONE* 8: e81944, <https://doi.org/10.1371/journal.pone.0081944>
- Sorte CJ, Williams SL, Zerebecki RA (2010) Ocean warming increases threat of invasive species in a marine fouling community. *Ecology* 91: 2198–2204, <https://doi.org/10.1890/10-0238.1>
- Steneck R, Graham MH, Bourque BJ, Corbett D, Erlandson JM (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental Conservation* 29: 436–459, <https://doi.org/10.1017/S0376892902000322>

- Susano P, Silva J, Alves C, Martins A, Pinteus S, Gaspar H, Goettert MI, Pedrosa R (2022) Mitigating the negative impacts of marine invasive species – *Sargassum muticum* – a key seaweed for skincare products development. *Algal Research* 62: 102634, <https://doi.org/10.1016/j.algal.2022.102634>
- Sutherland WJ, Clout M, Depledge M, Dicks LV, Dinsdale J, Entwistle AC, Fleishman E, Gibbons DW, Keim B, Lickorish FA (2015) A horizon scan of global conservation issues for 2015. *Trends in Ecology & Evolution* 30: 17, <https://doi.org/10.1016/j.tree.2014.11.002>
- Svensson JR, Nylund GM, Cervin G, Toth GB, Pavia H (2013) Novel chemical weapon of an exotic macroalga inhibits recruitment of native competitors in the invaded range. *Journal of Ecology* 101: 140–148, <https://doi.org/10.1111/1365-2745.12028>
- Swart C, Robinson T (2019) Horizon scanning for alien predatory crabs: insights from South Africa. *African Journal of Marine Science* 41: 125–135, <https://doi.org/10.2989/1814232X.2019.1588782>
- Tittensor DP, Mora C, Jetz W, Lotze HK, Ricard D, Berghe EV, Worm B (2010) Global patterns and predictors of marine biodiversity across taxa. *Nature* 466: 1098–1101, <https://doi.org/10.1038/nature09329>
- Tsiamis K, Azzurro E, Bariche M, Çinar ME, Crocetta F, De Clerck O, Galil B, Gómez F, Hoffman R, Jensen KR (2020) Prioritizing marine invasive alien species in the European Union through horizon scanning. *Aquatic Conservation: Marine & Freshwater Ecosystems* 30: 794–845, <https://doi.org/10.1002/aqc.3267>
- Wallace RD, Barger CT, Reaser JK (2020) Enabling decisions that make a difference: guidance for improving access to and analysis of invasive species information. *Biological Invasions* 22: 37–45, <https://doi.org/10.1007/s10530-019-02142-2>
- Wernberg T, Bennett S, Babcock RC, De Bettignies T, Cure K, Depczynski M, Dufois F, Fromont J, Fulton CJ, Hovey RK (2016) Climate-driven regime shift of a temperate marine ecosystem. *Science* 353: 169–172, <https://doi.org/10.1126/science.aad8745>
- Wernberg T, Krumhansl K, Filbee-Dexter K, Pedersen M (2019) Status and trends for the world's kelp forests. In: Sheppard C (ed), *World seas: an environmental evaluation*. Academic Press, pp 57–78, <https://doi.org/10.1016/B978-0-12-805052-1.00003-6>
- Willan RC, Russell BC, Murfet NB, Moore KL, McEnnulty FR, Horner SK, Hewitt CL, Dally GM, Campbell ML, Bourke ST (2000) Outbreak of *Mytilopsis sallei* (Récluz, 1849) (Bivalvia: Dreissenidae) in Australia. *Molluscan Research* 20: 25–30, <https://doi.org/10.1080/13235818.2000.10673730>
- Young CS, Lee C-S, Sylvers LH, Venkatesan AK, Gobler CJ (2022) The invasive red seaweed, *Dasysiphonia japonica*, forms harmful algal blooms: Mortality in early life stage fish and bivalves and identification of putative toxins. *Harmful Algae* 118: 102294, <https://doi.org/10.1016/j.hal.2022.102294>
- Zeng Y, Wang X, Liu J, Cao J, Sun Y, Zhao S, Chen Z, Kim JK, Zhang J, He P (2024) Harnessing the power of eDNA technology for macroalgal ecological studies: Recent advances, challenges, and future perspectives. *Algal Research* 77: 103340, <https://doi.org/10.1016/j.algal.2023.103340>

Web sites, online databases and software

- Anderson RJ, Stegenga H, Bolton JJ (2016) Seaweeds of the South African south coast. University of Cape Town, Cape Town, South Africa. <http://southafrseaweeds.uct.ac.za> (accessed 1 December 2024)

Supplementary material

The following supplementary material is available for this article:

Table S1. The 15 potential alien species identified from the literature. The eight species already present in South African (SA) kelp forests were discarded and the remaining seven species form the watch list.

Table S2. Mean ($\bar{Y}$) ($\pm$ 95% CI) minimum and maximum SSTs ($^{\circ}$ C) for each species across its native and alien range.

Table S3. Mean ($\pm$ 95% CI) minimum and maximum SSTs ($^{\circ}$ C) for the Benguela and Agulhas ecoregions. Present conditions and predicted future scenarios (both warming and cooling) are also presented.

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