SCIENCE BRIEF

DECEMBER 2022 - SCIENCE BRIEF

The WRC operates in terms of the Water Research Act (Act 34 of 1971) and its mandate is to support water research and development as well as the building of a sustainable water research capacity in South Africa.

Response of South African coastal wetlands to climate change¹

Janine Barbara Adams^{1*}, Johan Wasserman¹, Jacqueline Leoni Raw¹ and Lara Van Niekerk^{1,2}

 $^1\mathrm{DSI/NRF}$ Research Chair in Shallow Water Ecosystems, Nelson Mandela University $^2\mathrm{CSIR}$

The South African coastline has 290 estuaries that span over four biogeographic zones and support seagrasses, salt marshes and mangroves. These coastal wetland habitats provide a multitude of ecosystem services, but these services are threatened by the impacts of climate change. Predicted effects include sea level rise, increased sea storms and wave height, increased flood intensity, droughts, closure of estuary mouths salinisation, and increased atmospheric CO, and temperature. These impacts alter key abiotic stressors such as inundation patterns, salinity gradients and sediment biogeochemistry. Sea level rise raises concerns of habitat loss due to coastal squeeze and macrophyte dieback due to mouth closure and the associated changes in salinity and inundation regimes. Droughts may also increase mouth closure and salinity leading to changes in coastal wetlands. More intense sea storms and flooding can lead to increased deposition of sediments resulting in the smothering of mangroves and salt marsh. Increased temperatures are expected to facilitate the encroachment of mangroves into salt marsh habitats. The biogeographical patterns observed along the South African coastline present an important opportunity for climate change research as the transition between subtropical and warm temperate regions and between cool temperate and warm temperate regions are expected to be significantly influenced. Conservation and management plans need to include future changes in climate to ensure the protection of estuarine ecosystems at the southern tip of Africa.

¹This science brief has been extracted from B. Petja (Ed), Climate change impacts on water resources: Implications and practical responses in selected South African systems (WRC report no. SP. 155/22), Water Research Commission: Pretoria.

Introduction

The estuaries of South Africa host important coastal wetland habitats (seagrasses, salt marshes and mangroves) that provide a multitude of valuable ecosystem services. Estuaries are dynamic environments at the interface of the land and the sea, thus are subjected to multiple natural stressors. Coastal areas have also been historically heavily populated; thus estuaries are susceptible to anthropogenic activities associated with transformation and development. In South Africa, estuaries are under high anthropogenic pressure and most of the estuarine area has already been impacted to some extent [1]. The natural stressors acting on estuaries will be altered with climate change and acting synergistically with anthropogenic pressures, threaten estuarine habitats over a range of spatial extents and temporal periods [2,3]. An understanding of how climate change will affect coastal wetlands is necessary for producing realistic and achievable management and conservation strategies and plans.

The South African coastline, spanning roughly 3,000 km, covers four biogeographical regions. In the country's northeastern corner lies the tropical region, which transitions into a subtropical region on the east coast, the warm temperate region on the southern coast, and the cool temperate region along the west coast. Furthermore, the variation in climatic, oceanographic and geological characteristics along the South African coast results in a diversity of estuarine ecosystems. The country's 290 estuaries have been classified into nine ecosystem types based on key ecological features and biogeographic settings [4,5]. The variation in estuary type and climate result in local and regional differences in abiotic stressors, which influences the distribution of macrophytes throughout South African estuaries [6]. The diverse climate and estuarine types of South Africa presents a unique opportunity to investigate the response of coastal wetland habitats to climate change.

Six distinct macrophyte habitat types occur in South African estuaries: submerged macrophytes, salt marsh, reeds and sedges, mangroves, swamp forests and macroalgae (Table 1, Figure 1) [6,7]. Submerged macrophytes such as the endangered seagrass Zostera capensis occur mainly in the country's permanently open estuaries [8]. The fresher and calmer conditions of temporarily closed estuaries (TCEs) and estuarine lakes often allow for the establishment of other submerged macrophyte species like *Ruppia cirrhosa* and *Stuckenia pectinata* [6]. Salt marshes occur in sheltered estuaries throughout South Africa with the greatest area occurring in the cool temperate and warm temperate regions, respectively [9]. Salt marsh plants occur in zones along a distinct tidal inundation gradient (Figure 2). Reeds and sedges (e.g. Phragmites australis, Schoenoplectus scirpoides and Bolboschoenus maritimus) are the most widespread and dominant (in terms of area cover) habitat type nationally and are typically found in fresh and brackish areas of estuaries across all biogeographical regions [6].

Mangroves grow in 32 sheltered estuaries along a 1800 km stretch of the east coast spanning from the warm temperate to the tropical bioregion [10]. Swamp forests are limited to the subtropical to tropical east coast [6]. Attached and free-floating macroalgae are common in estuaries throughout South Africa (Table 1), and filamentous macroalgal mats often form in nutrient-enriched systems in closed estuaries with calm and sheltered conditions [7]. Information on the extent and distribution of these various habitats have been collated and catalogued in a national Estuary Botanical Database [6,11].

Coastal wetland habitats will be influenced in multiple ways by anthropogenic climate change. Not only will the increased CO₂ levels directly influence the physiology of macrophytes, but the already dynamic abiotic environment of coastal wetlands will be changed by the multitude of consequent impacts. These impacts are not straightforward to predict, as they depend on the context of environmental conditions and anthropogenic activity, which can differ greatly among regions [12]. While many studies have speculated the response of estuaries to climate change in different parts of the world [2,13,14], local studies are needed that cover different region-specific contexts. This study aims to provide predictions on how climate change will impact seagrass, salt marsh and mangrove habitats in South African estuaries.

Study approach

This review synthesises available knowledge from peerreviewed literature on the ecological responses of coastal wetland habitats to the predicted impacts of climate change. Focus was placed on increased atmospheric CO₂ concentrations, increased temperatures, changes in hydrological processes, floods, droughts, sea-level rise and increased sea storms and wave height. While the emphasis was on South African literature, studies from elsewhere in the world were also consulted.

Results and discussion

The key estuarine abiotic processes expected to be altered by climate change and the resultant biotic responses and expected habitat trends toward the year 2050 are summarised in Table 2. Salt marsh and mangrove area are expected to decrease overall. To date mangrove area has remained fairly stable due to increases and decreases in certain estuaries. Submerged macrophyte habitats are highly dynamic, but little overall change in habitat area is predicted, however, some increased fluctuations in biomass are expected in response to increased occurrence of extreme events such as floods and droughts.

Macrophyte habitat types	Biogeographical Region					
	Cool temperate	Warm Temperate	Subtropical	Tropical		
Submerged Macrophytes	•	•	٠	•		
Salt Marsh	•	•	•	•		
Reeds and Sedges	•	•	•	•		
Mangroves		•				
Swamp Forests						
Macroalgae	•	•	•	•		

Table 1. Summary of the biogeographical distribution of six macrophyte habitat types

Figure 1. Mangrove, salt marsh and seagrass habitats in the Nahoon Estuary.



Figure 2. Salt marsh zonation along a tidal inundation gradient at Knysna Estuary.



	Ecological responses					
Abiotic change	Submerged macrophytes	Salt marsh	Mangroves			
↑ CO ₂	Increase in plant growth and	Increase in plant growth and productivity	Increase in plant growth and			
Higher C availability	t 4%	14%	productivity ↑4%			
↑Temperature	Competition with more abundant macroalgae	Increase in plant growth and productivity, however distributional range shifts and	Increase in plant growth and productivity			
Warming	Decreased growth due to higher	change in habitat diversity, mangroves	Distributional range shifts and			
Higher aridity	epiphyte cover	Increase in invasive species. Change in salt marsh phenology and extinctions	change in habitat diversity, mangroves replace salt marsh.			
	↓4%	↓ 3%	1 4%			
↑Floods	Submerged macrophyte loss due to	Macroalgal growth, smothering of salt	Manarove loss due to scouring.			
↑ Nutrient inputs &	scouring, sediment deposition and smothering	marsh	sediment deposition and smothering			
eutrophication	1 404	Loss of salt marsh cover, change in species	1 406			
i seaiment input	v⊤/0	composition	v⊤/0			
Scouring of estuary, decrease in salinity		↓ 4%				
↑Droughts	Higher water level will allow an increase	Change in species and community	Decrease in productivity and			
↑ Salinity and aridity	Seagrass cover increases in response to	Decrease in productivity	cover			
	higher salinity cover	Loss of salt marsh cover.	Flooding and die-back of mangroves			
↑Closed mouth condition	1 4%	Increase in water level, flooding and dieback of salt marsh. Loss of intertidal	↓5.5%			
↑Water level & inundation, loss of intertidal habitat		habitat and marine connectivity. ↓5.5%				
↓↑ Stream flow	Shift in water level will cause changes in submerged macrophyte cover	Shifts in water level, flooding will cause an increase/decrease in intertidal habitat and	Changes in mangroves			
$\table f$ Closed mouth condition	Higher/lower salinity will increase/	marine connectivity.	Inland / landward migration of			
↓1 Salinity penetration	decrease seagrass cover	changes in species composition	mangroves			
		NO OVERALL CHANGE	Decrease/increase in productivity and cover			
			productivity and cover			
^Sea level rise	Increase in intertidal area for seagrass	Possible salt marsh subsidence or	Expansion of mangroves in			
+1.5 – 2.7 mm.yr ⁻¹	colonisation	landward migration Die-back and loss	intertidal areas			
Inundation & waterlogging,	Seagrasses can become established	Changes in species composition	Inland / landward migration of			
		Expansion of salt marsh on exposed sand/	indigioves			
10pen mouth condition	1 4%	mudflats	1 4%			
<i>↑Saline conditions</i>		NO OVERALL CHANGE				
↑Sea storms & wave height Erosion	Removal of seagrass and submerged macrophytes	Smothering and loss of salt marsh	Smothering e.g. of pneumatophores by marine			
↑Sediment deposition,	↓4%	Increase in water level, flooding and dieback of salt marsh	sediment Loss of mangroves			
constricted mouth		44%	- 44%			
		▼ 170	▼ 1/0			
Ocean acidification	Possible increase in seagrass production	Not likely to cause significant impacts				
	and scagrass carbon storage					

Table 2. Climate change stressors and predicted habitat trends by 2050 for submerged macrophytes, salt marsh and mangroves in South African estuaries (*italics* indicate abiotic changes and responses in temporarily closed estuaries)

3.1. Increased atmospheric CO₂

Enhanced productivity due to higher CO₂ levels will occur for both mangroves and salt marshes as a result of increased photosynthetic efficiency and water use efficiency [17 and references therein]. Mangrove productivity will especially be favoured as these trees utilise the C3 photosynthetic pathway. Climate-related warming and an increase in CO₂ are positive conditions for mangroves to expand their distribution to higher latitudes but this will depend on propagule dispersal between estuaries and the availability of suitable habitats [25]. Many of the small estuaries are temporarily closed to the sea for different periods of time thus limiting recruitment [10]. Increased CO₂ concentrations are also expected to change the species composition of salt marshes. Higher CO₂ availability will favour the growth of C3 salt marsh species (e.g. *Salicornia spp* and *Juncus spp*) over C4 species such as *Spartina* maritima. [74]. Elevated CO. concentrations will likely also increase the productivity of seagrasses and macroalgae, as they mostly appear to use the C3 photosynthetic pathway as well [37].

3.2. Increased temperature

Over the last 50 years, land-based air temperatures in southern Africa have been rising at twice the global average and are projected to continue increasing at 1.5 times that of the global rate. In general, South Africa will experience a warmer and drier climate in the future. Increased temperatures will directly affect the growth and reproduction of estuarine macrophytes. In salt marshes and mangroves, productivity will increase until an upper temperature threshold is reached [9,16]. However, increased temperatures can inhibit the germination of certain salt marsh species and this could counteract potential increases in productivity [17]. Seagrasses are also sensitive to increased temperatures and may die-back in response to warming [18]. Warmer temperatures will also alter plant phenological patterns and species composition in coastal wetlands [9,19].

Increased temperatures, in conjunction with elevated CO₂ levels, will also change the distribution of estuarine habitats. Rising temperatures are associated with the expansion of mangroves towards higher latitudes, often into salt marsh habitats, in a phenomenon known as 'tropicalisation'. Such range shifts have been described for different regions around the world [20-22], including for our subtropical east coast of South Africa [23,24]. Temperature is not a limiting factor in the poleward expansion of mangroves on South Africa's east coast; instead successful colonisation of new sites by mangroves will depend on the effectiveness of propagule dispersal between estuaries, the local geomorphology (including the estuary mouth being open), and the availability of suitable riparian habitats [10,25]. Mangrove encroachment into salt marshes will result in a decrease in salt marsh cover [26].

Rising temperatures and the associated evaporation can

have dire impacts on the health of coastal wetlands. In extreme cases, estuaries can become highly desiccated and hypersaline leading to great declines or die-offs of flora and fauna [27]. The effects of warming will be most apparent in shallow estuaries, particularly those experiencing a prolonged phase of mouth closure [28]. South Africa's estuarine lakes will likely also be susceptible to increased evaporation. For example, St Lucia, the country's largest estuarine lake, persisted in a highly desiccated hypersaline state following an extended drought during a closed mouth phase, resulting in significant declines in biota [29]. Habitats such as submerged macrophytes and reeds and sedges are particularly susceptible to hypersalinity and desiccation [30-32]. Some salt marsh habitats can persist in extreme hypersaline environments, but increased evaporation would likely contribute to the threat of salt marsh desertification [9,33].

The effects of extended ocean heat waves have not been documented in South Africa but can have severe consequences. Above average temperatures for four months (2 - 4°C above average) caused 90% die-back of seagrass beds in Shark Bay, Western Australia [34]. In northern Australia the 2016 extreme El Niño event led to extensive dieback of mangroves in the Gulf of Carpentaria [35]. Ocean heat waves have increased notably in frequency and duration over the last century and are projected to become more common in the future [36]. These warming events will have profound impacts on species distributions and community structure [37,38]. In January to March 2021 South Africa's south and east coast experienced such a temperature anomaly due to meanders of the Agulhas current. Most of the impacts were only observed in the nearshore coastal environments, but should serve as a warning that could this become a more frequent occurrence in our estuaries.

3.3. Changes to hydrological process (streamflow)

The ecological functioning and health of estuaries depends strongly on freshwater inflows, which will change with climate change-driven alterations in rainfall patterns. The most widespread impact resulting from the predicted hydrological changes will be changes in the mouth dynamics of estuaries. Approximately 75% of South Africa's estuaries close to the sea for varying periods of time due to the formation of sand berms at the mouth resulting from high-wave energy, high sediment availability, and low tidal flows and fluvial inflows [4,27]. These temporarily closed estuaries will be susceptible to change in hydrological regimes, but in extreme cases even predominantly open estuaries can close to the sea as occurred at the Gamtoos Estuary, which closed for the first time in 49 years due to drought and freshwater abstraction [39]. Drier conditions and higher inter-annual variability in rainfall patterns are expected on the western coast of South Africa (Table 3) [41,42]. The frequency and duration of mouth closure are expected to increase in this region [42]. Along the rest of the coastline, extreme rainfall events are projected to increase in spring and summer but decrease in autumn and winter [40,41,43]. It is predicted that mouth dynamics will remain largely similar along the southern coast and that open mouth conditions will generally become more common further up the eastern coast due to increased freshwater flows and flooding [42].

Changes in mouth condition are likely to cause substantial changes in the extent and distribution of coastal wetland habitats and have been shown to cause shifts between macrophyte habitat types [44-46]. During periods of mouth closure, estuaries are unsuitable for the establishment of mangroves and intertidal salt marsh. Furthermore, extended periods of mouth closure can result in high water levels which cause inundation and die-back of intertidal salt marsh and mangroves [44,45,47]. Large mangrove die-back events have been recorded at the Kosi, Kobongaba and St Lucia estuaries [48-50]. Elevated salinity levels during periods of mouth closure also lead to the loss of submerged macrophytes and the proliferation of opportunistic macroalgae [45,46]. Macroalgal blooms will be particularly concerning in closed estuaries susceptible to eutrophication as they can shade and smother submerged macrophytes and salt marsh habitats [51-53]. However, more frequent mouth closure may increase the resilience of salt marshes to sea level rise as these intertidal habitats have greater elevation gains and sediment accretion rates than those that maintain a permanent connection to the sea [54]. Increased open mouth conditions, in contrast, will facilitate the establishment of salt marshes and mangroves and create a favourable environment for the persistence of submerged macrophytes [8,10]. However, the periods of high productivity typical of closed mouth conditions will be decreased [55,56].

3.4 Droughts

In addition to altering mouth dynamics, changes in freshwater inflows (particularly extreme events like droughts and floods) will decrease the resilience of coastal wetlands to the impacts of climate change. Decreased freshwater inflows and drought will result in the salinisation and desiccation of macrophyte habitats. High salinity and low moisture content in sediments decrease salt marsh species composition, cover, and productivity [9]. Salinisation and desiccation will particularly place pressure on the country's arid west coast estuaries such as the Groot Berg, Olifants and Orange (Table 3) where the desertification of large areas of salt marsh has been recorded [9]. On the east coast, drought stress will affect the physiological processes in mangrove trees related to water uptake and water use efficiency, and will inhibit growth and expansion [57,58]. Recent large-scale mangrove die-back events have occurred in northern and western Australia under drought conditions in combination with low sea levels and low humidity as a consequence of an El Niño-Southern Oscillation (ENSO) event [35,59,60]. Prolonged droughts can lead to soil shrinkage, which would

inhibit the ability of salt marshes and mangroves to maintain their elevation relative to rising sea levels [61,62]. Soil volumes, however, can recover after droughts have ended [62]. Droughts can also cause shifts in habitat type; for example, large scale drought-induced dieback of salt marsh at the Mississippi River Delta, USA resulted in mangrove encroachment until it became the dominant habitat type [63].

Lower freshwater inflows will also result in increased seawater penetration into estuaries, reducing the extent of the river-estuary interface and changing the distribution of habitats. Under these circumstances, a reverse estuary gradient is often formed. Increased salinity in the upper reaches of estuaries will facilitate an increase in seagrass biomass and distribution under clear-water conditions [64,65]. Prolonged periods of hypersalinity (salinity \geq 75), however, will lead to the die-back of submerged macrophytes [30]. Reeds and sedges may die-back or persist only in brackish areas (salinity < 20) such as sites of freshwater seepage [32].

3.5 Floods

Flooding and increased freshwater inflows can also be detrimental to coastal wetlands in several ways. Floods will scour estuary banks, removing macrophytes in intertidal habitats. Such habitats may be able to re-establish, but this can take place slowly. For example, mangroves that were removed by flooding in the Mnyameni and Mzimvubu estuaries only re-established after 11 years [10]. Floods can also deposit sediments causing smothering and die-back of submerged macrophytes and mangroves. However, such deposition events can expand intertidal areas available for colonization by macrophytes. Submerged macrophytes respond particularly strongly to flooding floods can completely remove them from estuaries as has occurred with Z. capensis habitats in Swartkops Estuary [66]. Recovery of submerged macrophytes after floods can have a lag period of up to three years [67]. Furthermore, increased siltation, turbidity and salinity changes associated with floods will influence the growth and distribution of submerged macrophytes [8]. Increased high intensity rainfall events and flooding will likely remove submerged macrophyte beds from estuaries, particularly along the east coast where floods are expected to increase (Table 3) [42]. The endangered *Z. capensis* is already absent from freshwater dominated estuaries in southern KwaZulu-Natal where flooding and highly turbid conditions are common [8].

Increased rainfall and runoff will contribute to the nutrient enrichment and eutrophication of estuaries, which is already a significant pressure on South African estuaries that will likely be exacerbated by climate change, especially in disturbed catchments [28,68]. Eutrophication can shift estuaries to an alternate state where algal blooms can outcompete, outshade and possibly exclude submerged

macrophytes and smother salt marshes [51,52]. Nutrient enrichment leads to dense epiphytic growth on the leaves of submerged macrophytes reducing light availability and limiting growth, and epiphytic fouling will increase as temperatures rise [69]. Increased nutrient loading due to runoff, along with increased temperatures, will also result in the proliferation of invasive alien aquatic plants (IAAPs) which are already widespread in South African estuaries, especially along the KwaZulu-Natal coast [68]. Predictive models suggest that climate change over coming decades will facilitate the range expansion of several IAAP species along the South African coast [70]. The proliferation of IAAPs leads to the loss of native species and biodiversity with impacts across trophic levels, and alters aquatic environments by decreasing light penetration, flow and connectivity between rivers and estuaries [68,71]. IAAPs can also displace important nursery habitats, for example, the spread of water hyacinth along with turbid conditions displaced Z. capensis beds in the Swartkops Estuary [66]. Although increased freshwater inflow and floods will generally contribute to eutrophication, they will also be important in opening estuary mouths, flushing systems, reoxygenating the water column, re-establishing salinity gradients following periods of mouth closure, inundating floodplains and decreasing soil salinity, maintaining sediment structure and building habitat (accretion) [73].

3.6. Sea level rise

Current SLR rates differ along the South African coast, with an increase of 1.9 mm.yr⁻¹ on the west coast, 1.5 mm.yr⁻¹ on the south coast and 2.7 mm.yr⁻¹ on the east coast [80,81]. Sea-level rise will increase inundation and waterlogging altering sediment biogeochemistry, moisture and salinity. This is the predicted scenario; however, if salt marshes and mangroves build elevation at a sufficient rate then inundation and waterlogging may not increase [82]. Local topography and coastal development constrain the availability of areas for landward migration, but the rate of sedimentation determines the capacity of mangrove and salt marsh ecosystems to resist SLR through surface elevation gain [83,84]. Predictive models that incorporate landward migration and surface elevation processes have been used to estimate changes in blue carbon stocks under different SLR scenarios at the Knysna and Swartkops estuaries [85,86].

Higher sea levels would cause salt marshes to migrate landwards [87,88]. Plant ecophysiology studies have shown lower intertidal salt marsh species will be able to survive in upper intertidal zones, but upper intertidal species will not be able to persist in waterlogged conditions [47]. The tolerance of salt marsh species to inundation will determine their survival, and the availability of areas with suitable elevation will allow for the landward migration of salt marsh habitats [9,89]. However, many South African estuaries are impacted by development and urban encroachment, which leads to 'coastal squeeze' which limits the amount of suitable area for salt marsh migration [90]. Recent research

has found that there is a deficit in elevation gain and local relative sea-level rise in South African intertidal salt marshes, and it will be necessary for accretion rates to increase for these salt marshes to persist in the long-term [91]. This is especially the case for the sediment starved estuaries fed by catchments dominated by Table Mountain Sandstone. Sea level rise modelling studies at the Swartkops Estuary have predicted that lower intertidal habitats characterised by the cordgrass Spartina maritima do not gain elevation at a rate sufficient to keep up with current and future sea-level rise, but these habitats would migrate landwards and replace habitats located higher in the tidal frame [85,92]. At the Knysna Estuary, the capacity of *S. maritima* habitats to build elevation is variable along the length of the estuary [86]. Most sites in the lower and middle reaches are subsiding and therefore will not persist under projected sea level rise without the potential for landward migration. This can only be facilitated by the removal of hard structures [86].

Sea-level rise may lead to an increase in open mouth conditions in temporarily closed estuaries creating favourable habitat for mangrove, salt marsh and seagrass colonisation in intertidal areas [10]. However, these positive effects may be counteracted by drought and a reduction in freshwater inflow that results in mouth closure, high water level flooding and die-back of mangrove and salt marsh. Nationally it is difficult to predict the future trajectory of change for the endangered seagrass *Zostera capensis*. Sealevel rise will increase salinity in estuaries and seagrass can expand upstream. However, an increase in high intensity rainfall events will likely remove submerged macrophyte beds [8].

3.7. Increased sea storms and wave height

South Africa's wave-dominated coast is sensitive to sea storminess that can result in erosion or sediment deposition and accretion [80]. More frequent and intense sea storms and wave action may further inhibit the ability of the mouth of estuaries to remain open [75]. The resultant increase in water levels within estuaries will cause prolonged inundation and waterlogging of intertidal areas, leading to the loss of macrophyte habitats. Sea storms can also deposit marine sediments onto habitats, smothering them and causing dieback. For example, a major storm at the Mbashe Estuary led to the die-back of mangroves, of which many died within three years and the area was subsequently colonised by salt marsh species [93]. However, increased wave action due to sea storms can erode the mouth area of estuaries increasing periods of open mouth conditions [76]. Salt marshes can be particularly sensitive to erosion, which has caused the loss of large areas of salt marsh in various parts of the world [94-96]. Salt marsh has already been lost to erosion in some South African estuaries and further losses are expected [97] (Figure 3). While some increase in the frequency and intensity of sea storms has been recorded along parts of the South African coast in recent decades, these have not yet been definitively linked to anthropogenically-driven climate change [98].

However, a global increase in sea storms has been projected [99], which will result in increased coastal erosion and the loss of estuarine habitats.

3.8. Ocean acidification

Ocean acidification is a concerning consequence of increased CO₂. Acidification will likely impact South Africa's permanently open estuaries, particularly those on the west coast where upwelling is prevalent (Table 3) [75]. Acidification impacts nutrient and carbon availability in aquatic environments, but the impacts of acidification on macrophytes are complex and requires species- and situation-specific investigations [76]. Acidification will impact calcifying fauna, possibly leading to indirect effects through species interactions – such changes in biotic controls – but these are also difficult to predict. Eutrophication and algal blooms, a widespread problem in South African estuaries, will exacerbate climate change-driven acidification [68]. This will particularly be an issue in eutrophic estuaries that are closed to the sea, especially since mouth closure is expected to increase with climate change in many of these systems in South Africa. During open mouth conditions, pH is regulated by tidal mixing but during closed mouth conditions, pH dynamics are dominated by *in situ* biological processes [78]. Closed estuaries that are susceptible to eutrophication will experience greater diurnal pH variability due to increased primary production by algal blooms [77]. When the algal blooms decay, remineralisation and aerobic respiration by bacteria decreases pH, particularly under the long water residence times experienced during a closed mouth phase [77,79]. These *in situ* processes are likely to be enhanced by increase temperatures.

Table 3. Summary of key processes that will be impacted by climate change stressors and the broad direction of change per biogeographical region (Solid \bullet = increase; Hollow O = decrease; Large \bullet = High degree of change, small \bullet small to moderate degree of change)

Key processes	Climate change stressors	Biogeographical Region			
		Cool temperate	Warm Temperate	Subtropical	Tropical
Atmospheric	CO ₂				
	Temperature			•	•
Hydrological	Floods	•			
	Droughts		•	•	•
	Streamflow	0	•		
Oceanic	Sea level rise				
	Sea storms & wave height				
	Ocean Acidification	0	0	0	0

Conclusions

Predicting the effect of multiple climate change stressors is difficult because of the natural variability of our coastal wetlands. Long-term monitoring is needed to support research findings. Monitoring of permanent plots and transects are necessary to identify changes such as salinisation and drying out of salt marshes. Synergistic interactions between climate change and human impacts need teasing out at a local scale so that we can understand the processes influencing the vulnerability and resilience of coastal wetlands. Long-term datasets are also needed to understand the change in the frequency and intensity of climatic cycles such as El Niño. Nationally we need policies and planning mechanisms to set aside buffers for landward migration of coastal wetlands in response to sea level rise. Estuary conservation and management plans need to include future changes in climate to ensure the protection of coastal wetlands. However successful management and restoration of coastal wetlands requires a socio-ecological systems approach to address the lack of alignment between ecosystem requirements, legislation, governance, implementation and social commitment.

Past research has identified patterns of change that allow for the prediction of potential future change. South Africa is an

important outdoor laboratory as changes are occurring across different biogeographic zones i.e. subtropical to warm temperate and warm temperate to cool temperate. Our research makes an important contribution globally as little is known about the response of African coastal wetlands to climate change. Data sets inform range expansions of species at a southern continental limit and responses characteristic of a wave-dominated high-energy coastline.

Funding: The DSI/NRF Research Chair in Shallow Water Ecosystems (UID 84375) supported JBA. LvN was funded through the Coastal Systems, Council for Scientific and Industrial Research DSI Parliamentary Grant (PG). The Water Research Commission funded Project K5/2769/1/19 titled 'Climate change and South Africa's blue carbon ecosystems'.

References

- Van Niekerk, L., Taljaard, S., Adams, J.B., Clark, B., Lamberth, S.J., MacKay, C.F., Weerts, S.P. Chapter 7: Condition of South Africa's estuarine ecosystems. In South African National Biodiversity Assessment 2018: Technical Report. Volume 3: Estuarine Realm. South African National Biodiversity Institute, Pretoria, 2019; Report Number: SANBI/NAT/NBA2018/2019/Vol3/A.
- Hallett, C.S., Hobday, A.J., Tweedley, J.R., Thompson, P.A., McMahon, K., Valesini, F.J. Observed and predicted impacts of climate change on the estuaries of southwestern Australia, a Mediterranean climate region. *Reg. Environ. Change* 2018, *18*, pp.1357-1373.
- Lovelock, C.E., Reef, R. Variable impacts of climate change on blue carbon. *One Earth* 2020, *3*, pp.195-211.
- Whitfield, A.K. A characterization of southern African estuarine systems. *S. Afr.J. Aquat. Sci.* 1992, *18*, pp.89-103.
- Van Niekerk, L., Adams, J.B., James, N.C., Lamberth, S.J., MacKay, C.F., Turpie, J.K., Rajkaran, A., Weerts, S.P., Whitfield, A.K. An Estuary Ecosystem Classification that encompasses biogeography and a high diversity of types in support of protection and management. *Afr.J. Aquat. Sci.* 2020, *45*, pp.199-216.
- Adams, J.B., Veldkornet, D., Tabot, P. Distribution of macrophyte species and habitats in South African estuaries. S. Afr. J. Bot. 2016, 107, pp.5-11.
- Adams, J.B., Bate, G.C., O'Callaghan, M. Primary producers. *Estuaries of South Africa*. Allanson, B., Baird, D., Eds.; *Cambridge University Press, Cambridge*, **1999**, pp.91-117.
- Adams, J.B.. Distribution and status of *Zostera capensis* in South African estuaries—A review. *S. Afr. J. Bot.* 2016, *107*, pp.63-73.
- Adams, J.B. Salt marsh at the tip of Africa: patterns, processes and changes in response to climate change. *Estuar., Coast. Shelf Sci.* 2020, 237, p.106650.
- Adams, J.B., Rajkaran, A. Changes in mangroves at their southernmost African distribution limit. *Estuar., Coast. Shelf Sci.* 2021, 248, p.107158.

- Adams, J., Fernandes, M., Riddin, T. Chapter 5: Estuarine Habitat extent and trend. In *South African National Biodiversity Assessment 2018: Technical Report. Volume 3: Estuarine Realm.* South African National Biodiversity Institute, Pretoria, **2019**; Report Number: SANBI/NAT/ NBA2018/2019/Vol3/A.
- Day, J.W., Christian, R.R., Boesch, D.M., Yáñez-Arancibia, A., Morris, J., Twilley, R.R., Naylor, L., Schaffner, L. Consequences of climate change on the ecogeomorphology of coastal wetlands. *Estuaries Coast* 2008, *31*, pp.477-491.
- Scavia, D., Field, J.C., Boesch, D.F., Buddemeier, R.W., Burkett, V., Cayan, D.R., Fogarty, M., Harwell, M.A., Howarth, R.W., Mason, C., Reed, D.J. Climate change impacts on US coastal and marine ecosystems. *Estuaries* 2002, 25, pp.149-164.
- Robins, P.E., Skov, M.W., Lewis, M.J., Giménez, L., Davies, A.G., Malham, S.K., Neill, S.P., McDonald, J.E., Whitton, T.A., Jackson, S.E., Jago, C.F. Impact of climate change on UK estuaries: A review of past trends and potential projections. *Estuar, Coast. Shelf Sci.* 2016, 169, pp.119-135.
- Engelbrecht, C.J., Landman, W.A., Engelbrecht, F.A., Malherbe, J. A synoptic decomposition of rainfall over the Cape south coast of South Africa. *Clim. Dyn.* 2015, 44, pp.2589-2607.
- Ellison, J.C. How South Pacific mangroves may respond to predicted climate change and sea-level rise. In *Climate change in the South Pacific: Impacts and responses in Australia, New Zealand, and small island states;* Gillespie, A., Burns, W.C.G., Eds. Springer, Dordrecht, **2000**; pp. 289-300
- McKee, K., Rogers, K., Saintilan, N. Response of salt marsh and mangrove wetlands to changes in atmospheric CO₂, climate, and sea level. In *Global change and the function and distribution of wetlands*; Middleton, B.A., Ed. Springer, Dordrecht, **2012**; pp. 63-96
- Marbà, N., Duarte, C.M. Mediterranean warming triggers seagrass (*Posidonia oceanica*) shoot mortality. *Glob. Change Biol.* 2010, 16, pp.2366-2375.
- Ward, R.D., Friess, D.A., Day, R.H., MacKenzie, R.A. Impacts of climate change on mangrove ecosystems: a region by region overview. *Ecosyst. Health Sustain.* 2016, 2, p.e01211.
- Saintilan, N., Wilson, N.C., Rogers, K., Rajkaran, A., Krauss, K.W. Mangrove expansion and salt marsh decline at mangrove poleward limits. *Glob. Change Biol.* 2014, 20, pp.147-157.
- Osland, M.J., Day, R.H., Hall, C.T., Brumfield, M.D., Dugas, J.L., Jones, W.R. Mangrove expansion and contraction at a poleward range limit: climate extremes and land-ocean temperature gradients. *Ecology* 2017, *98*, pp.125-137.
- Cavanaugh, K.C., Osland, M.J., Bardou, R., Hinojosa-Arango, G., López-Vivas, J.M., Parker, J.D., Rovai, A.S.. Sensitivity of mangrove range limits to climate variability. *Glob. Ecol. Biog.* 2018, *27*, pp.925-935.
- Whitfield, A.K., James, N.C., Lamberth, S.J., Adams, J.B., Perissinotto, R., Rajkaran, A., Bornman, T.G. The role of

pioneers as indicators of biogeographic range expansion caused by global change in southern African coastal waters. *Estuar., Coast. Shelf Sci.* **2016**, *172*, pp.138-153.

- Peer, N., Rajkaran, A., Miranda, N.A.F., Taylor, R.H., Newman, B., Porri, F., Raw, J.L., Mbense, S.P., Adams, J.B., Perissinotto, R. Latitudinal gradients and poleward expansion of mangrove ecosystems in South Africa: 50 years after Macnae's first assessment. *Afr. J. Mar. Sci.* 2018, 40, pp.101-120.
- Raw, J.L., Godbold, J.A., Van Niekerk, L., Adams, J.B. Drivers of mangrove distribution at the high-energy, wavedominated, southern African range limit. *Estuar., Coast. Shelf Sci.* 2019, 226, p.106296.
- Whitt, A.A., Coleman, R., Lovelock, C.E., Gillies, C., lerodiaconou, D., Liyanapathirana, M. and Macreadie, P.I. March of the mangroves: Drivers of encroachment into southern temperate saltmarsh. *Estuar., Coast. Shelf Sci.* 2020, 240, p. 106776.
- Cooper, J.A.G. Geomorphological variability among microtidal estuaries from the wave-dominated South African coast. *Geomorphology* 2001, 40, pp.99-122.
- James, N.C., Van Niekerk, L., Whitfield, A.K., Potts, W.M., Götz, A., Paterson, A.W. Effects of climate change on South African estuaries and associated fish species. *Clim. Res.* 2013, *57*, pp.233-248.
- Cyrus, D., Jerling, H., MacKay, F., Vivier, L. Lake St Lucia, Africa's largest estuarine lake in crisis: combined effects of mouth closure, low levels and hypersalinity. *Afr. J. Sci.* 2011, *107*, pp.01-13.
- Adams, J.B., Bate, G.C. The ecological implications of tolerance to salinity by *Ruppia cirrhosa* (Petagna) Grande and *Zostera capensis* Setchell. *Bot. Mar.* **1994**, *37*, pp.449-456.
- Adams, J.B., Bate, G.C. The tolerance to desiccation of the submerged macrophytes *Ruppia cirrhosa* (Petagna) Grande and *Zostera capensis* Setchell.
 J. Exp. Mar. Biol. Ecol. **1994**, *183*, pp.53-62.
- Adams, J.B., Bate, G.C. Growth and photosynthetic performance of *Phragmites australis* in estuarine waters: a field and experimental evaluation. *Aquat. Bot.* **1994**, *64*, pp.359-367.
- Wooldridge, T.H., Adams, J.B., Fernandes, M. Biotic responses to extreme hypersalinity in an arid zone estuary, South Africa. *S. Afr. J. Bot* 2016, *107*, pp.160-169.
- Nowicki, R.J., Thomson, J.A., Burkholder, D.A., Fourqurean, J.W., Heithaus, M.R. Predicting seagrass recovery times and their implications following an extreme climate event. *Mar. Ecol. Prog. Ser.* 2017, *567*, pp.79-93.
- Duke, N.C., Kovacs, J.M., Griffiths, A.D., Preece, L., Hill, D.J., Van Oosterzee, P., Mackenzie, J., Morning, H.S., Burrows, D. Large-scale dieback of mangroves in Australia's Gulf of Carpentaria: a severe ecosystem response, coincidental with an unusually extreme weather event. *Mar. Freshw. Res.* 2017, 68, pp.1816-1829.
- Oliver, E.C., Donat, M.G., Burrows, M.T., Moore, P.J., Smale, D.A., Alexander, L.V., Benthuysen, J.A., Feng, M., Gupta, A.S., Hobday, A.J., Holbrook, N.J. Longer and more frequent marine heatwaves over the past century. *Nat.*

Commun. 2018, 9, pp.1-12.

- Koch, M., Bowes, G., Ross, C., Zhang, X.H. Climate change and ocean acidification effects on seagrasses and marine macroalgae. *Global Change Biol.* 2013, *19*, pp.103-132.
- Smale, D.A., Wernberg, T. Extreme climatic event drives range contraction of a habitat-forming species. *Proc. Royal Soc. B: Biol. Sci.* 2013, 280, p.20122829.
- Lemley, D.A., Adams, J.B. Physico-chemical and microalgal gradients change rapidly in response to mouth closure in a predominantly open estuary. *Afr.J. Aquat. Sci.* 2020, 45, pp.11-21.
- Engelbrecht, F.A., McGregor, J.L., Engelbrecht, C.J. Dynamics of the Conformal-Cubic Atmospheric Model projected climate-change signal over southern Africa. *Int. J. Climatol.* 2009, 29, pp.1013-1033.
- Engelbrecht, C.J., Engelbrecht, F.A., Dyson, L.L.
 High-resolution model-projected changes in midtropospheric closed-lows and extreme rainfall events over southern Africa. *Int. J. Climatol.* 2013, *33*, pp.173-187.
- Van Niekerk, L, Lamberth SJ, James, N, Taljaard, S, Adams, JB, Theron, A, Krug, M. In prep. The vulnerability of South African estuaries to Climate Change: a review and synthesis. (in prep.).
- Christensen, J.H., Hewitson, B., Busuioc, A., Chen, A., Gao, X., Held, I., Jones, R., Kolli, R.K., Kwon, W.-T. Laprise, R., Magaña Rueda, V., Mearns, L., Menéndez, C.G., Räisänen, J., Rinke, A., Sarr, A., Whetton, P. Regional Climate Projections. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*; Solomon, S., Ed. Cambridge University Press, Cambridge, **2007**, pp. 848-940.
- Riddin, T., Adams, J.B. Influence of mouth status and water level on the macrophytes in a small temporarily open/closed estuary *Estuar., Coast. Shelf Sci.* 2008, 79, pp.86-92.
- Riddin, T., Adams, J.B. The effect of a storm surge event on the macrophytes of a temporarily open/ closed estuary, South Africa. *Estuar., Coast. Shelf Sci.* 2010, 89(1), pp.119-123.
- Riddin, T., Adams, J.B. Predicting macrophyte states in a small temporarily open/closed estuary. *Mar. Freshw. Res.* 2012, 63, pp.616-623.
- Tabot, P.T., Adams, J.B. Ecophysiology of salt marsh plants and predicted responses to climate change in South Africa. *Ocean Coast Manag.* 2013, *80*, pp.89-99.
- Breen, C.M., Hill, B.J. A mass mortality of mangroves in the Kosi Estuary. *Transactions of the royal society of South Africa* 1969, 38, pp.285-303.
- Adams, J.B., Human, L.R.D. Investigation into the mortality of mangroves at St. Lucia Estuary. *S. Afr. J. Bot* 2016, *107*, pp.121-128.
- Mbense, S., Rajkaran, A., Bolosha, U., Adams, J. Rapid colonization of degraded mangrove habitat by succulent salt marsh. *S. Afr. J. Bot* 2016, *107*, pp.129-136.
- Burkholder, J.M., Tomasko, D.A., Touchette,
 B.W. Seagrasses and eutrophication.

J. Exp. Mar. Biol. Ecol. 2007, 350, pp.46-72.

- Nunes, M., Adams, J.B. Responses of primary producers to mouth closure in the temporarily open/closed Great Brak Estuary in the warm-temperate region of South Africa. *Afr.J. Aquat. Sci.* 2014, *39*, pp.387-394.
- Human, L.R.D., Adams, J.B., Allanson, B.R. Insights into the cause of an *Ulva lactuca* Linnaeus bloom in the Knysna Estuary. S. Afr. J. Bot. 2016, 107, pp.55-62.
- Thorne, K.M., Buffington, K.J., Jones, S.F., Largier, J.L. Wetlands in intermittently closed estuaries can build elevations to keep pace with sea-level rise. *Estuar., Coast. Shelf Sci.* 2021, *257*, p.107386.
- Nozais, C., Perissinotto, R., Tita, G. Seasonal dynamics of meiofauna in a South African temporarily open/closed estuary (Mdloti Estuary, Indian Ocean). *Estuar., Coast. Shelf Sci.* 2005, *62*, pp.325-338.
- Thomas, C.M., Perissinotto, R., Kibirige, I. Phytoplankton biomass and size structure in two South African eutrophic, temporarily open/closed estuaries. *Estuar., Coast. Shelf Sci.* 2005, *65*, pp.223-238.
- Buckney, R.T. Three decades of habitat change: Kooragang Island, New South Wales. In *Nature conservation, the role of remnants of native vegetation in Melbourne*, Saunders, D.A., Arnold, G.W., Burrbidge, G., Hopkins, A.G.M., Eds.; Surrey, Beatty and Sons, Sydney.
 1987; pp. 227–232.
- Eslami-Andargoli, L., Dale, P.E.R., Sipe, N., Chaseling, J. Mangrove expansion and rainfall patterns in Moreton Bay, southeast Queensland, Australia. *Estuar., Coast. Shelf Sci.* 2009, *85*, pp.292-298.
- Lovelock, C.E., Feller, I.C., Reef, R., Hickey, S., Ball, M.C. Mangrove dieback during fluctuating sea levels. *Sci. Rep.* 2017, 7, pp.1-8.
- Asbridge, E.F., Bartolo, R., Finlayson, C.M., Lucas, R.M., Rogers, K., Woodroffe, C.D. Assessing the distribution and drivers of mangrove dieback in Kakadu National Park, northern Australia. *Estuar., Coast. Shelf Sci.* 2019, 228, p.106353.
- Rogers, K., Saintilan, N. and Cahoon, D. Surface elevation dynamics in a regenerating mangrove forest at Homebush Bay, Australia. *Wet. Ecol. Manag.* 2005, 13, pp.587-598.
- Rogers, K., Saintilan, N. Relationships between surface elevation and groundwater in mangrove forests of southeast Australia. *J. Coast. Res.* 2008, 24, pp.63-69.
- McKee, K.L., Mendelssohn, I.A., Materne, M. Acute salt marsh dieback in the Mississippi River deltaic plain: a drought-induced phenomenon?. Glob. Ecol. and Biogeogr. 2004, 13, pp.65-73.
- Adams, J.B., Knoop, W.T., Bate, G.C. The distribution of estuarine macrophytes in relation to freshwater. *Bot. Mar.* 1992, 37, pp. 449-456.
- Adams, J.B., Talbot, M.M.B. The influence of river impoundment on the estuarine seagrass *Zostera capensis* Setchell. *Bot. Mar.* **1992**, *35*, pp.69-75.
- Emmerson, W.D., Watling, H.R., Watling, R.J. A community analysis in the Kromme and the Swartkops estuaries and in the Algoa Bay region. *University of Port Elizabeth*,

Zoology Dept. Rep. Series 1982, 16, pp.1-128.

- Talbot, M.M.B., Knoop, W.T., Bate, G.C. The dynamics of estuarine macrophytes in relation to flood/siltation cycles. *Bot. Mar.* **1990**, *33*, pp.159-164.
- Adams, J.B., Taljaard, S., Van Niekerk, L., Lemley, D.A. Nutrient enrichment as a threat to the ecological resilience and health of South African microtidal estuaries. *Afr.J. Aquat. Sci.* 2020, 45, pp.23-40.
- Mvungi, E.F., Pillay, D. Eutrophication overrides warming as a stressor for a temperate African seagrass (*Zostera capensis*). *PLOS ONE* 2019, *14*, p.e0215129.
- Hoveka, L.N., Bezeng, B.S., Yessoufou, K., Boatwright, J.S., Van der Bank, M. Effects of climate change on the future distributions of the top five freshwater invasive plants in South Africa. S. Afr. J. Bot 2016, 102, pp.33-38.
- Hill, M.P., Coetzee, J.A., Martin, G.D., Smith, R., Strange, E.F. Invasive alien aquatic plants in South African freshwater ecosystems. In *Biological Invasions in South Africa*; van Wilgen, B., Measey, J., Richardson, D.M., Wilson, J.R., Zengeya, T.A., Eds.; Springer, Cham, **2020**; pp. 97-114.
- Van Niekerk, L., Adams, A.B., Lamberth, S.J., Taljaard, S., MacKay, C.F., Bachoo, S. Parak, O., Murison, G., Weerts, S.P. Chapter 6: Pressures on the Estuarine Realm. *In South African National Biodiversity Assessment 2018: Technical Report. Volume 3: Estuarine Realm*. South African National Biodiversity Institute, Pretoria, 2019; Report Number: SANBI/NAT/NBA2018/2019/Vol3/A.
- Human, L.R.D., Snow, G.C., Adams, J.B. Responses in a temporarily open/closed estuary to natural and artificial mouth breaching. *S. Afr. J. Bot* 2016, *107*, pp.39-48.
- Arp, W.J., Drake, B.G., Pockman, W.T., Curtis, P.S., Whigham, D.F. Interactions between C 3 and C 4 salt marsh plant species during four years of exposure to elevated atmospheric CO₂. In *CO₂ and Biosphere*, Rozema, J., Lambers, H., Van de Geijn, S.C., Cambridge, S.L., Eds.; Springer, Dordrecht, **1993**; pp. 133-143.
- Van Niekerk, L. Approaches to Detecting and Assessing Patterns, Processes and Responses to Change in South African Estuaries. PhD thesis. Nelson Mandela University, Port Elizabeth, 2018.
- Farmer, A.M. The effects of lake acidification on aquatic macrophytes — a review. *Environ. Pollut.* 1990, 65, pp.219-240.
- Wallace, R.B., Baumann, H., Grear, J.S., Aller, R.C., Gobler, C.J. Coastal ocean acidification: The other eutrophication problem. *Estuar., Coast. Shelf Sci.* 2014, 148, pp.1-13.
- Omarjee, A., Taljaard, S., Weerts, S.P., Adams, J.B. The influence of mouth status on pH variability in small temporarily closed estuaries. *Estuar., Coast. Shelf Sci.* 2020, 246, p.107043.
- Snow, G.C., Taljaard, S. Water quality in South African temporarily open/closed estuaries: a conceptual model. *Afr.J. Aquat. Sci.* 2007, *32*, pp.99-111.
- Mather, A.A., Stretch, D.D. A perspective on sea level rise and coastal storm surge from Southern and Eastern Africa: A case study near Durban, South Africa. *Water* 2012, *4*, pp.237-259.

- Mather, A.A., Garland, G.G., Stretch, D.D. Southern African sea levels: corrections, influences and trends. *Afr. J. Mar. Sci.* 2009, *31*, pp.145-156.
- Rogers, K., Mogensen, L.A., Davies, P., Kelleway, J., Saintilan, N., Withycombe, G. Impacts and adaptation options for estuarine vegetation in a large city. *Landsc. Urban Plan.* 2019, *182*, pp.1-11.
- Lovelock, C.E., Cahoon, D.R., Friess, D.A., Guntenspergen, G.R., Krauss, K.W., Reef, R., Rogers, K., Saunders, M.L., Sidik, F., Swales, A., Saintilan, N. The vulnerability of Indo-Pacific mangrove forests to sea-level rise. *Nature* 2015, *526*, pp.559-563.
- Baustian, J.J., Mendelssohn, I.A. Sea level rise impacts to coastal marshes may be ameliorated by natural sedimentation events. *Wetlands* 2018, *38*, pp.689-701.
- Raw, J.L., Adams, J.B., Bornman, T.G., Riddin, T., Vanderklift, M.A. Vulnerability to sea-level rise and the potential for restoration to enhance blue carbon sequestration in salt marshes of an urban estuary. *Estuar., Coast. Shelf Sci.*, 260, p. 107495.
- Raw, J.L., Riddin, T., Wasserman, J., Lehman, T.W.K., Bornman, T.G., Adams, J.B. Salt marsh elevation and responses to future sea-level rise in the Knysna Estuary, South Africa. *Afr.J. Aquat. Sci.* 2020, *45*, pp.49-64.
- Enwright, N.M., Griffith, K.T., Osland, M.J. Barriers to and opportunities for landward migration of coastal wetlands with sea-level rise. *Front. Ecol. Environ.* 2016, 14, pp.307-316.
- Kirwan, M.L., Walters, D.C., Reay, W.G., Carr, J.A. Sea level driven marsh expansion in a coupled model of marsh erosion and migration. *Geophys. Res. Lett.* 2016, 43, pp.4366-4373.
- Veldkornet, D.A., Adams, J.B., Potts, A.J. Where do you draw the line? Determining the transition thresholds between estuarine salt marshes and terrestrial vegetation. *S. Afr. J. Bot* 2015, *101*, pp.153-159.
- Veldkornet, D.A., Adams, J.B., Van Niekerk, L. Characteristics and landcover of estuarine boundaries: implications for the delineation of the South African estuarine functional zone. *Afr. J. Mar. Sci.* 2015, *37*, pp.313-323.
- Saintilan, N., Kovalenko, K.E., Guntenspergen, G., Rogers, K., Lynch, J.C., Cahoon, D., Lovelock, C., Friess, D.A., Ashe, E., Krauss, K., Cormier, N., Spencer, T., Adams, J.B., Raw, J., Ibanez, C., Scarton, F.W., Temmerman, S., Meire, P., Maris, T., Thorne, K., Brazner, J., Chmura, G., Bowron, T., Vishmie, P.G. Global patterns and drivers of tidal marsh response to accelerating sea-level rise. *Science* (Accepted).
- Bornman, T.G., Schmidt, J., Adams, J.B., Mfikili, A.N., Farre, R.E., Smit, A.J. Relative sea-level rise and the potential for subsidence of the Swartkops Estuary intertidal salt marshes, South Africa. *S. Afr. J. Bot* 2016, *107*, pp.91-100.
- James, N.C., Adams, J.B., Connell, A.D., Lamberth,

S.J., MacKay, C.F., Snow, G.C., Van Niekerk, L., Whitfield, A.K. High flow variability and storm events shape the ecology of the Mbhashe Estuary, South Africa. *Afr.J. Aquat. Sci.* **2020**, *45*, pp.131-151.

- Cooper, N.J., Cooper, T., Burd, F. 25 years of salt marsh erosion in Essex: Implications for coastal defence and nature conservation. *J Coast. Conserv.* 2001, 7, pp.31-40.
- Ravens, T.M., Thomas, R.C., Roberts, K.A., Santschi, P.H. Causes of salt marsh erosion in Galveston Bay, Texas. *Journal of Coastal Research* 2009, 25, pp.265-272.
- Leonardi, N., Fagherazzi, S. How waves shape salt marshes. *Geology* 2014, 42, pp.887-890.
- Riddin T, Adams JB. Salt marsh erosion in a microtidal estuary. *S.A.J.Mar. Sci.* (43(2), pp. 265-273. DOI: 10.2989/1814232X.2021.
- Guastella L, Rossouw J. Coastal vulnerability: are coastal storms increasing in frequency and intensity along the South African coast? *Reef Journal* 2012, 2, pp.129-139.
- IPCC. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change; Stocker, T.F., D. Qin, G.K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, Midgley, P.M., Eds.; Cambridge University Press, Cambridge, **2013**; 1535 pp.