Chapter 5

The Ecology and Food Web Dynamics of South African Intermittently Open Estuaries

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Additional information is available at the end of the chapter

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Abstract

This chapter provides an overview of the ecology and food web dynamics of southern African intermittently open/closed estuaries (IOCEs). Intermittently open/closed estuaries experience periodic isolation from the ocean due to a sandbar at the mouth and account for some 71% of all estuaries along the southern African coastline. Field studies indicate that the ecosystem functioning of IOCEs is strongly linked mouth phase (open vs. closed) of these systems. During the closed phase, these systems are generally characterised by low biological diversity and elevated biomass of both invertebrates and vertebrates, which are thought to be sustained by elevated biomass of microphytoplankton and zooplankton within these systems. The low diversity can be related to the virtual absence of marine species within these systems due to the presence of a sandbar at the mouth which limits recruitment. The overflow of marine waters into the estuary during winter storms or spring high tides contributes to the recruit of marine breeding species into these systems. Heavy rainfall in the catchment areas of these systems culminates in the water levels of these systems rising until such time the estuary breaches. The breaching event coincides with the outflow of biologically rich estuarine waters into the marine environment and provides an opportunity for marine breeding species to recruit into these systems. Global warming is likely to contribute to changes in the hydrodynamics of these systems with a concurrent impact on the food webs of these systems.

Keywords: southern Africa, estuaries, intermittently open/closed, ecology, global change

1. Introduction

The South African coastline stretching some 3100 km can broadly be divided into three biogeographic zones: the warm subtropical zone along the east coast, the warm temperate

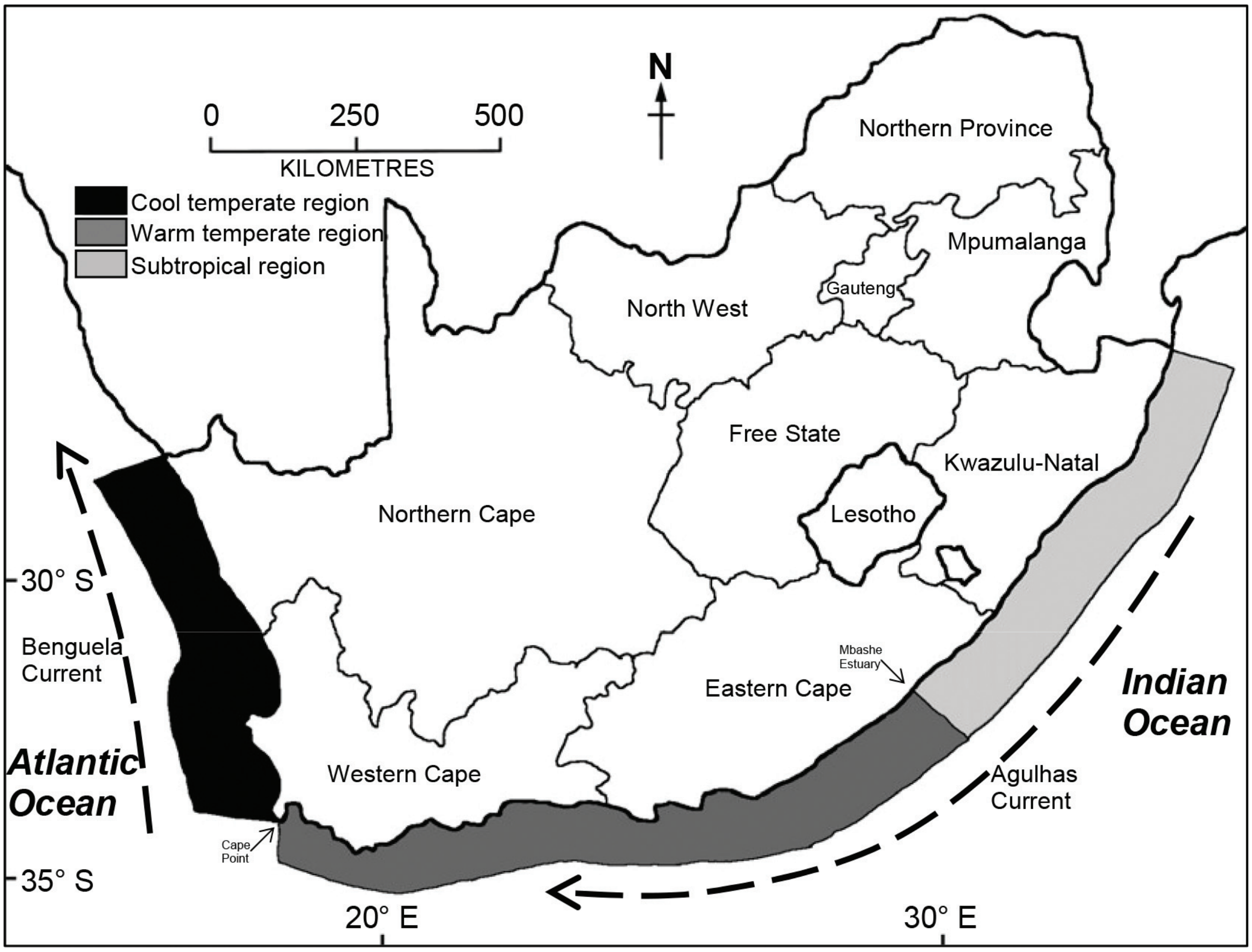

Figure 1. The geographic extent of the three biogeographical zones along the South African coastline (after Whitfield 1992b).

zone along the south coast and the cool temperature zone along the west coast (**Figure 1**). Within these three zones, there are 258 functional estuaries of which 71% can be categorised as intermittently open/closed (IOCEs) or temporary open/closed estuaries [1, 2]. Intermittently open/closed systems experience periodic isolation from the ocean, usually during periods of drought or no river inflow, during which a sand berm develops across the mouth of the estuary [2, 3]. Following periods of high rainfall (>100 mm in a month) and freshwater run-off, the volume of water in the estuary rises until it exceeds the height of the sandbar [1–3]. It is at this stage that breaching usually occurs, with a consequent drastic drop in water level exposing large areas of substratum [2, 4]. During the subsequent period, the estuary will be tidally dominated until such time that long-shore drift contributes to the reformation of the sandbar at the mouth of the system.

A link to the marine environment can also be established through the overtopping of marine waters across the sand bank at the mouth of the estuary during winter storms or during spring high tides [2, 3]. In addition to altering the physico-chemical properties (temperature, salinity and dissolved oxygen) in the lower reaches of these systems, these events represent important recruitment opportunities for marine breeding invertebrates and vertebrates, mainly ichthyo-fauna into these systems [5, 6].

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There are two main types of ICOEs found along the southern African coastline, non-perched estuaries, which predominate in the subtropical zone and perched estuaries which are found along the east and west coast of the country [2, 7] (**Figure 2**). Perched estuaries have an average surface water level exceeding that of the marine environment [2, 7]. Non-perched systems are the more common system with the average surface water level similar to that of the marine environment [7]. Generally, lower salinities are observed in perched systems due to the

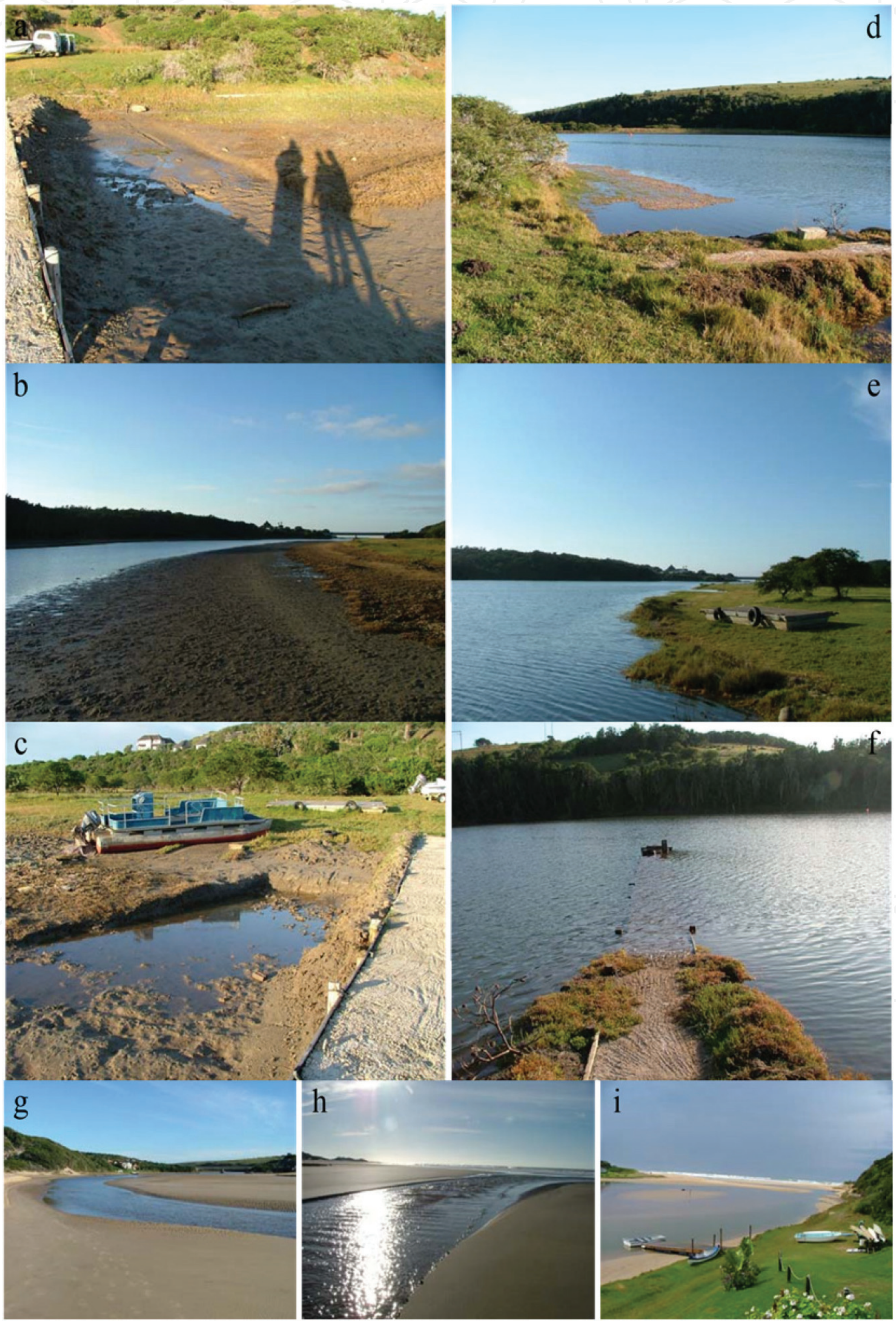

Figure 2. Images of an intermittently open/closed estuary under open conditions (a–c), closed conditions (d–f) and the mouth of the estuary under open conditions (g–i). Photographs courtesy of G Tweddle.

reduced frequency of occurrence over washing events with the dominant source of water being freshwater run-off [7]. Moreover, when a perched system breaches, it drains rapidly and will not experience tidal ebbing due to its height above the marine high water mark [7, 8]. Non-perched systems are tidally dominated following a breach event until mouth closure (**Figure 3**). The intrusion of marine waters into the estuary depends on numerous factors, including tide range, freshwater inflow rates, and the morphology of the channel [7–9].

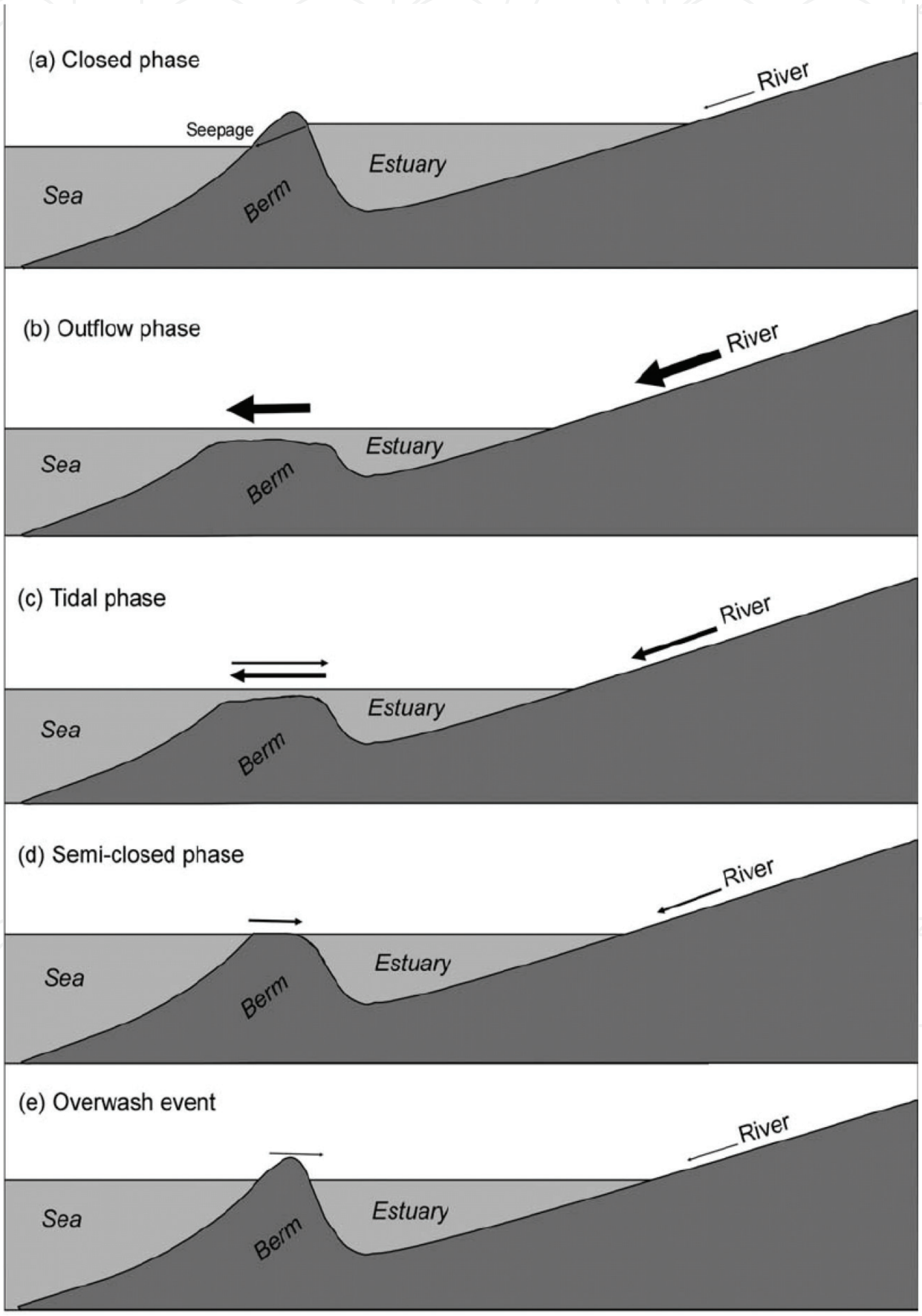

Figure 3. Hydrodynamics of perched and non-perched intermittently open/closed estuary along the southern African coastline.

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The mouth dynamics of IOCEs play a key role in the overall ecosystem functioning of these systems. Intermittent breaching of the sand barriers of these systems leads to rapid changes in the physico-chemical environment, which in turn triggers major biological responses, including the out- and in-recruitment of estuarine and marine breeding invertebrates and vertebrates [2, 3]. The breaching process can also cause significant geomorphological changes because the strong breach outflows can scour large quantities of accumulated sediments from an estuary [2, 3, 9].

2. Physico-chemical environment

During closed conditions, the water temperatures in IOCEs are predominantly determined by regional climate and season and range between 18 and 30°C [7, 10–12]. Under closed conditions, salinities in IOCEs exhibit greater stability than in larger permanently open counterparts due to the lack of tidal influence [2, 12, 13]. Following rainfall, changes in salinity may be much as 30 over the course of a few days or weeks depending on freshwater input and over-washing events [12]. Mesohaline conditions (5–18) generally predominate during the closed phase, although limnetic conditions (0.1–0.5) may be recorded during periods of high rainfall [2, 3, 12, 14], while hypersaline (>40) conditions may occur during drought periods or high evaporation [1]. During the closed phase of these systems, the water column demonstrates little horizontal or vertical stratification due the reduced freshwater inflow as a result of their generally small catchment areas (<50km^2), shallow depth (generally <2 m), and strong coastal winds which facilitate the mixing of the water column [12, 14].

3. Biology

The total chlorophyll-*a* (chl-*a*) concentrations in IOCEs (0.1 and 15.4 mg chl-*a*.m^{-3}) are lower than those reported for permanently open systems (POEs) (20–100 mg chl-*a*.m^{-3}) within the same geographic region [4, 12, 15] (**Table 1**) due to reduced macronutrient availability as a result of limited freshwater inflow [12, 14, 16]. The inflow of freshwater into these systems is characterised by increased phytoplankton biomass likely sustained by the increase in macronutrient availability [12, 16]. Additionally, changes in the total chl-*a* concentration within these systems have been linked to seasonality and mouth phase [11, 14, 17]. The total phytoplankton biomass during the breaching events decreases as a result of the outflow of biologically rich estuarine waters into the marine environment [3, 14]. In contrast to the water column, microphytobenthic algae concentrations in IOCEs are two to three orders of magnitude higher than the water column phytoplankton biomass and substantially higher than those recorded in permanently open systems within the same region [4, 14, 25–28]. A combination of low turbidity, high concentrations of macronutrients in the sediments, and reduced current flow contributes to the elevated microphytobenthic algae biomass in IOCEs [4].

The total zooplankton abundance and biomass values recorded in IOCEs during the closed phase generally exceeds those levels recorded in the larger permanently open estuaries within

Estuary	Biogeographic region	Pelagic chl-a conc. (μg L^{-1})	Microphytbenthic conc. (mg chl-a m^{-2})	Zooplankton abundances (ind m^{-3})
Intermittently open/closed estuaries				
Mpenjati [15]	Subtropical	0.14–15.40	19.9–616.0	8.3×10^3–8.0×10^4
Mdloti [16]	Subtropical	0.89–111.10	ND	ND
Mngazi [17]	Subtropical	ND	30–568	ND
Nyara [18]	Warm temperate	0.01–4.10	170–200	1.8×10^3–2.03×10^4
East Kleinemonde [19]	Warm temperate	0.12–6.19	ND	ND
Kasouga [12]	Warm temperate	0.29–8.01	3.87–209.9	1.06×10^3–6.1×10^4
Permanently open estuaries				
Great Fish [20]	Warm temperate	0.40–21.80	ND	ND
Kariega [21]	Warm temperate	0.64–1.13	13.6–43.8	0.9–1.6×10^3
Sundays [22]	Warm temperate	8.6–22.4	ND	1.0×10^3–5.5×10^4
Swartkops [23]	Warm temperate	4.1–8.6	ND	ND
Kromme [24]	Warm temperate	ND	ND	1.7×10^3–1.2×10^4

ND = no data

Table 1. Estimates of total water column and microphytoplankton concentrations and zooplankton abundances at selected permanently open and IOCEs within the subtropical and warm temperate biogeographic provinces along the South African coastline.

the same biogeographic region (**Table 1**) [3, 12, 29, 30]. The elevated zooplankton biomass values during closed periods are thought to be sustained by the substantial microphytobenthic stocks in these systems. Due to the limited number of marine species recorded and the virtual absence of typical estuarine zooplankton in these systems [2, 3, 31], the zooplankton communities are dominated by a few but, highly abundant hardy species, mainly copepods of the genera *Pseudodiaptomus, Acartiella*, and *Oithona* [19, 20, 32]. Changes in the zooplankton community structure within IOCEs have been linked to amongst others, mouth phase, freshwater inflow, seasonality and over-wash events [14, 32]. More recent studies indicate that predation by early life history fish may also play an important role in structuring the zooplankton communities within these systems during the close phase [33, 34]. Breaching events are typically associated with a reduction in the abundance and biomass of the zooplankton as estuarine rich waters are exported to the marine environment [14, 20]. The inflow of seawater into the estuary following the breaching event is, however, associated with an increase in the average size and zooplankton diversity as marine spawning species recruit into the system. Similarly, the over-washing of marine waters across the sandbar during spring high tides and winter storms may also contribute to an increase in the zooplankton diversity within these systems [30, 35].

Macrofaunal community composition within southern African IOCEs also demonstrates reduced diversity and is almost exclusively dominated by estuarine species [36, 37]. The low diversity can in part be attributed to the poor representation of marine breeding species to the total macrofaunal community and reduced habitat availability (submerged macrophytes and different sediment types) [36, 37]. In the virtual absence of any distinct horizontal gradients in salinity within these systems, sediment type, habitat availability, predation, and the activity of ecosystem engineers have been identified as important in determining the distribution of macrofauna within these systems [36, 37].

Due to the virtual absence of sheltered bays and increased food availability, southern African IOCEs represent important nursery areas for a large variety of marine breeding fish species [38–40]. The ichthyofaunal community structure, like the other components of the food web within these systems, is strongly determined by mouth status [38, 41–43]. Ichthyofaunal diversity and species richness during the closed phase of IOCEs are lower than those recorded in POEs within the same geographic region, due to the limited recruitment opportunities of marine breeding species associated with mouth closure and reduced habitat availability [38–40, 44]. The abundances of selected ichthofauna within IOCEs often exceed those recorded in permanently open estuaries within the same ecozone [39, 40]. The observed pattern appears largely to reflect increased food availability (mainly zooplankton and microphytoplankton stocks) within these systems. In the absence of any link to the marine environment, the ichthyofaunal community within these systems is numerically and gravimetrically dominated by estuarine species [5, 39, 44–46]. A link to the marine environment either through breaching or over-wash events has been shown to coincide with an increased contribution of marine spawning species to the total ichthyofaunal community [39, 44–46]. This has the net effect of increasing the ichthyofaunal diversity within these systems [39, 44, 45]. The magnitude of recruitment during the over-wash events is, however, substantially lower than that recorded during the open phase [3, 6, 35, 46]. The timing of the breaching events has been demonstrated to be critical in determining the magnitude of fish recruitment into these systems with maximum recruitment typically taking place in spring and summer reflecting increased availability of recruiters in the near-shore marine environment as a result of seasonal reproductive cycles [45]. The ichthyofaunal assemblages in open IOCEs are broadly similar to those recorded in the larger POEs within the same geographic region [44].

4. Anthropogenic impacts

The marine environment off the coast of South Africa is dominated by the western boundary Agulhas Current on the south-eastern seaboard and the cooler eastern boundary Benguela Current on the west coast (**Figure 1**). Like many other regions of the world, the characteristics of these currents are beginning to demonstrate the effects of global warming [47–49, 38, 39]. Sea surface temperatures (SSTs) within the Agulhas Current have increased by 1.5°C over the past four decades due to the intensification of the current caused by an increase in trade and westerly winds in the southern Indian Ocean, which have been associated with increased wind stress and curl [47]. By contrast, SSTs along the west coast have decreased resulting from the increased frequency and intensity of coastal upwelling due to upwelling favourable southerly winds [47, 49]. The warming of the Agulhas Current waters has through thermal expansion contributed to a rise in sea levels, estimated at approximately 2.74 mm y^{-1} [50], while increased wind stress has resulted in an increase in wave height (5 cm per decade), since the mid 1950s [51].

Global climate models predict that the observed changes in SST is likely to contribute to wetter conditions along the south coast of South Africa, while dryer conditions are expected along the eastern and western seaboards [52]. Moreover, global warming will be associated with an overall shortening of the wet season along the south-eastern seaboard and an increased frequency of occurrence of extreme weather events (rainfall, floods and maximum temperatures) within the region [49, 52, 53]. Regional investigations have demonstrated that the warming of marine waters along the south-eastern seaboard of southern Africa has coincided with a range expansion of warmer subtropical zone fish species into estuaries in warm temperate ecozone along the coastline [39, 49]. At the same time, there has been a concurrent decrease (10–13%) in the contribution of warm temperate species to the total fish catches within the transition zone between the two ecozones contributing to an overall decline in fish diversity within the region [39, 49]. Global climate change has probably resulted in geographic shift in the ecozone along the southern African coastline which is likely to influence connectivity and gene flow within the major phylogeographic zones between the warm temperate and subtropical ecozones [54]. It is unclear whether the observed change will be associated with a reduction in total biomass of fish within these systems, although such changes likely have knock-on effects on the importance of these systems as feeding grounds for flying birds and a source of renewable resources [55].

The impact of global climate change on the ecosystem functioning of IOCE is difficult to predict, reflecting the complex interaction between the marine and terrestrial environments. There is, however, anecdotal evidence to suggest that the impact of global climate change on the ecosystem functioning of IOCE along the South African coastline will demonstrate strong regional variability. Recent work on Intermittently Closed and Open Lakes and Lagoons (ICOLLs) along the coast of New South Wales, Australia [56] suggests that in sand deposition environments, a rise in sea level associated with climate change will increase height of the sand berm that separates the estuary from the marine environment. Such conditions are common to the warm temperate ecozone of South Africa [49]. The increase in berm height coupled with the reduction in rain season is likely to result in IOCE's being separated from the marine environment for extended periods of time. Prolonged mouth close in IOCEs is associated with a dramatic decline in species diversity and zooplankton biomass, reflecting reduced recruitment opportunities of marine breeding species into these systems (**Figure 4**) [57]. The prolonged mouth closure contributed to hypersaline conditions (salinity >40) prevailing throughout the system which was associated with decrease in the areal extent of the submerged macrophytes within the system [57]. Physiological constraints resulting from the increase temperatures and salinities and the loss of habitat (mainly submerged macrophytes) likely further contributed to the decline is species diversity observed within the systems [57, 58]. Under prolonged mouth closure, particularly during drought conditions, high evaporation rates may further increase the salinity within these systems. Under such conditions, IOCE food webs suffer a catastrophic collapse reflecting the physiological constraints of the flora and fauna within the system. Although recent models suggest that global climate change has been associated with increase in wave height, suggesting that over-wash events are likely to be more frequent; these events contribute little to the recruitment of marine breeding species into these systems [6, 35].

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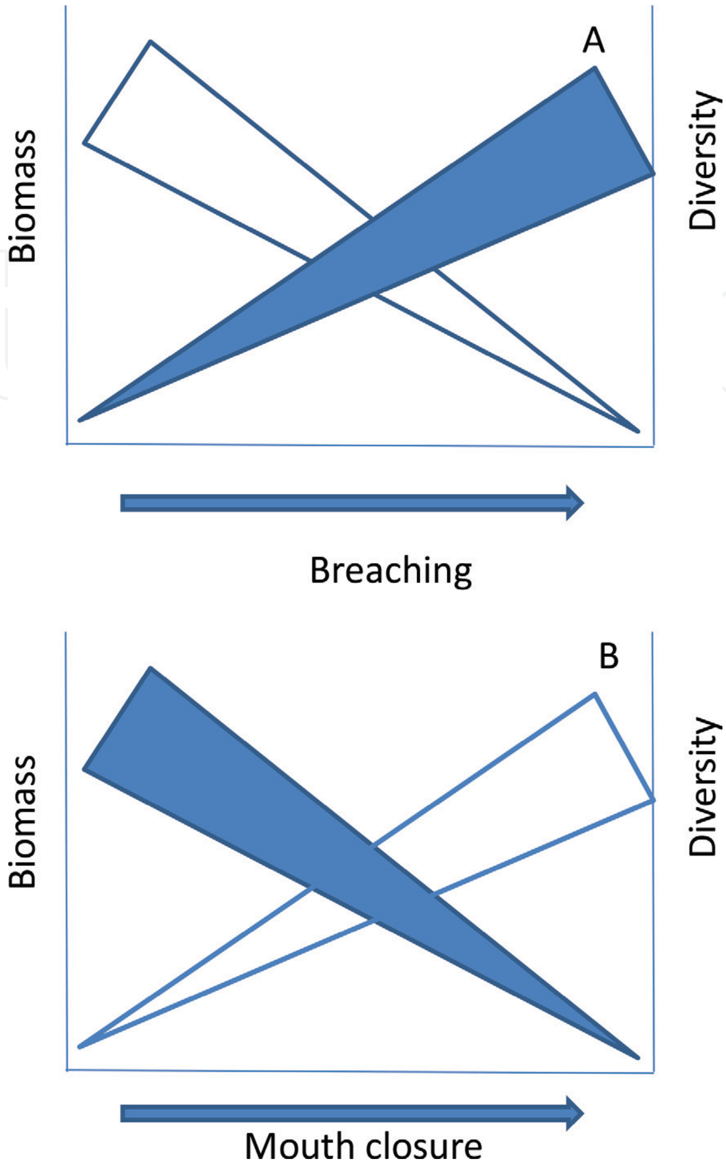

Figure 4. Predicted changes in the abundance and diversity within southern African temporarily open/closed estuaries in response to breaching (A) and prolonged mouth close (B) as a result of to global warming. Blue triangle = diversity; open triangle = biomass.

The reduced recruitment of fish into IOCE resulting from extended mouth closure may have unexpected consequences on the food web structure of these systems. Recent studies have demonstrated that the predation impact of juvenile fish, through trophic cascades, contributed to plankton food web stability within IOCE [33]. In the absence of the predators, total water column chlorophyll-a concentrations were reduced reflecting increased grazing activity by smaller heterotrophs [33, 44]. The reduced recruitment of fish into IOCEs is likely to have implications on community structure and the energy flow within these systems. Further studies are, however, required to fully appreciate the impact of changes in recruitment of the food web structure of these systems.

With regard to the IOCEs along the southern coastline of South Africa, it is likely that the projected increase in rainfall for the region coincides with the increased frequency of occurrence of breaching events, which would contribute to higher species diversity within these systems as a result of extended recruitment opportunities for marine breeding species into these systems [3]. On the other hand, frequent breaching will prevent the build-up of biomass, thus likely resulting in reduced abundances of selected components of the food web (**Figure 4**). Furthermore, the anticipated extreme flood events will likely contribute to deep mouth breaching resulting in these systems having a connection to the sea for extended periods of time.

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