Science of the Total Environment 954 (2024) 176356

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Empirical evidence of alternative stable states in an estuary

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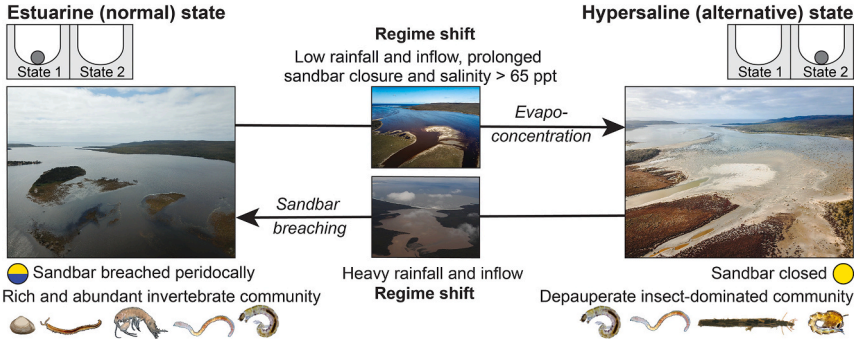
HIGHLIGHTS

- We provide evidence of estuaries existing in alternative stable states.
- Invertebrate communities were sampled for 3.5 years at system-wide scale.
- Severe hypersalinity caused a regime shift to a depauperate insect-dominated state.
- There was partial recovery of the speciose estuarine state with sandbar breaching.
- The hypersaline state could become more common with a drying climate.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Sergi Sabater

Keywords:
Benthic macroinvertebrates
Climate change
Low-inflow
Mediterranean climate
Temporarily open and closed estuaries

ABSTRACT

Due to human activity, ecosystems are exceeding their ecological thresholds and shifting into undesired alternative stable states with new ecological configurations. Despite their purported ubiquity, it is uncertain whether estuaries can exist in multiple stable states. We use data from a 3.5-year study of invertebrate communities in an Australian estuary that is usually closed to the ocean to test for their existence. Sampling spanned a 1.5-year period of hypersalinity (>40 ppt) during a prolonged estuary closure, where salinity reached 122 ppt, and for two years during and after the estuary opened to the ocean when salinities were mesohaline (5–19 ppt). Two distinct community states occurred before and after the sandbar breached, with an intermediary period of invertebrate community impoverishment due to sediment scouring. During the closure, the community was simple (average of one taxa 100 cm^{-2}) and dominated by larvae of terrestrial insects, most notably the halotolerant, non-biting midge *Tanytarsus barbitarsis*. After opening, the richness and abundance of invertebrates increased (average of four taxa and 84 individuals 100 cm^{-2}) as polychaetes, molluscs and crustaceans colonised the estuary, although recovery was incomplete according to previous species records. Duration of estuary closure and salinity were the strongest drivers of composition. This study, together with evidence from the literature, suggests a salinity threshold of 60–65 ppt between states. These empirical data meet key criteria of alternative states, i.e. a clear transition between two distinct self-sustaining communities, indicating a regime shift triggered by an exogenous event. Our findings suggest that temporarily open and closed estuaries can exist in alternative stable states, with prolonged closures, hypersalinity, and sandbar breaching being key determinants of the switch

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https://doi.org/10.1016/j.scitotenv.2024.176356
Received 21 June 2024; Received in revised form 27 August 2024; Accepted 16 September 2024
Available online 17 September 2024
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between states. This situation may apply to other low-inflow estuarine systems, particularly in arid, semi-arid, or seasonally arid climates, and may become more frequent with human-induced climate change.

1. Introduction

Alternative stable state theory posits that ecosystems and their biotic communities can exist in multiple equilibria or stable states (Holling, 1973; May, 1977; Scheffer et al., 2001). To illustrate this concept, May (1977) visualised each stable state as a marble seeking the bottom of a cup (i.e. the ball-in-cup model), where the position of the ball depicts the state of a community and the cup (i.e. the domain of attraction) is the environment in which the community resides. A community resilient to perturbation will maintain its structure and function, that is, stay within the same cup (Holling, 1973; Standish et al., 2014). If perturbations are excessive, however, ecosystems can reach a threshold and go through a regime shift to enter a new cup or an alternative stable state, with a different domain of attraction (Scheffer et al., 2001; Beisner et al., 2003). The theory is relevant to considering the impacts of changing environmental conditions on communities, i.e. the ecosystem perspective (Beisner et al., 2003). Alternative stable states are likely common in nature and particularly in response to global climate change (Scheffer et al., 2001), yet empirical evidence of their existence is rare (Mac Nally et al., 2014; Capon et al., 2015).

The paucity of empirical evidence for alternative stable states is, in part, due to the exacting experimental conditions required to demonstrate different states, including accommodating the large spatial and temporal scales in which communities exist (Connell and Sousa, 1983; Scheffer et al., 2001; Petraitis and Dudgeon, 2004). The theory originated from studies investigating the effects of eutrophication and fishing pressure on fish and invertebrate communities in self-contained freshwater lakes that experience relatively homogenous climate conditions (Holling, 1973). It has since been extended to other communities and ecosystems including shrimp and clam beds on sand flats, salt marshes experiencing grazing, and woodlands affected by secondary salinisation (Peterson, 1984; Handa et al., 2002; Standish et al., 2014). Until recently, empirical evidence for alternative stable states was limited to certain ecosystem types and overlooked those that are inherently 'unstable' due to the large degree of environmental variation they exhibit (Schröder et al., 2005; Mushet et al., 2020). Mushet et al. (2020) argued that communities in a highly dynamic prairie wetland can be viewed within the stable state framework, if an "ecologically relevant" time scale was considered. Distinguishing between persistent and temporary change – that is, separating alternative stable states from phase shifts – is critical to determining stable states unequivocally (Petraitis and Dudgeon, 2004; Dudgeon et al., 2010). Making this distinction is increasingly important for ecosystem managers attempting to manage impacted systems, as it can help to identify ecosystem states that are 'stuck' and require intervention (e.g. weedy old fields) or environmental conditions that lead to the development of undesired stable states, i.e. ecosystems with limited ecological structure (e.g. land-use legacies; Cramer et al., 2008). Thresholds between alternative stable states are invoked where there are irreversible or persistent changes to desired states (i.e. those with complex ecological structure) that require intervention (Standish et al., 2014).

Estuaries are highly dynamic, transitional ecosystems influenced by both terrestrial and marine environments. They have rarely been considered in terms of alternative stable state theory and it remains empirically uncertain if they experience regime shifts (Mac Nally et al., 2014). The fact that estuaries have not been considered 'stable' likely stems from their inherent environmental variability caused by differences in the magnitude of fresh (e.g. riverine inflow or runoff) and saline (e.g. tides or waves) water input that occurs over various temporal scales (Elliott and Whitfield, 2011). Despite their dynamic nature, estuaries exhibit predictable, temporal patterns in salinity based on, for example, tidal cycles and/or seasonal rainfall (Potter et al., 2010; Rich and Keller, 2013). Instead of considering each phase as a separate state, the culmination of this variability may be considered one entire stable state (Mushet et al., 2020). Estuaries can be divided into categories based on their geomorphology, tidal range, extent of connectivity to the ocean, hydrology and flow regime, with each estuary type harbouring a unique set of environmental conditions and biota (Roy et al., 2001; Van Niekerk et al., 2020; Largier, 2023). Low-inflow estuaries are those where freshwater input is low relative to tidal range, volume and evaporation, and fall into two broad categories based on their extent of connectivity to the ocean, (1) temporarily open and closed estuaries (TOCEs) and (2) hypersaline estuaries (Largier, 2023). TOCEs become disconnected from the ocean for periods (days to years) through the formation of a sandbar, and harbour unique environmental and biotic elements when they are opened or closed (Montagna et al., 2023). They account for 3 % of estuaries globally and are one of the dominant estuary types in countries such as Australia, South Africa and Mexico (McSweeney et al., 2017; Van Niekerk et al., 2020). TOCEs occur mostly along microtidal (<2 m tidal range) coastlines and in warm-temperate climates with low and/or seasonal rainfall (McSweeney et al., 2017). Due to their climate, flow regime and potential to become disconnected from the ocean, they are susceptible to environmental stressors such as hypersalinity (Hoeksema et al., 2018; Largier, 2023).

Hypersalinity (>40 ppt) is a global phenomenon in low-inflow estuaries where the salt content of a water body becomes concentrated due to net water loss (Potter et al., 2010; Largier, 2023). For many of these estuaries, the frequency and magnitude of hypersaline conditions are anticipated to increase due to anthropogenic activity (e.g. flow diversion and abstraction) and human-induced climate change (Hallett et al., 2018; Tweedley et al., 2019; Schutte et al., 2020). Salinities of up to 300 ppt (almost nine times the strength of seawater) have been recorded in Australian and South African estuaries (Wooldridge et al., 2016; Hoeksema et al., 2018). The situation can be further worsened by secondary salinisation, an effect of terrestrial human activities (e.g. land clearing, water extraction, salt mining) that increases the salinity of freshwater sources (Cunillera-Montcusí et al., 2022; Chessman, 2023). As salinity exceeds 60–65 ppt, estuaries begin to exhibit reduced eukaryotic diversity following a sequential loss of marine and estuarine taxa, ultimately resulting in the persistence of a few halotolerant species (Whitfield et al., 2006; Carrasco and Perissinotto, 2012; Dittmann et al., 2015; Tweedley et al., 2019; Schutte et al., 2020). The food web, in turn, becomes simplified, with a few dominant species comprising the trophic system, and fish movement restricted due to the increased energetic cost of osmoregulation under hypersaline conditions (Carrasco and Perissinotto, 2012; Breaux et al., 2019). While relatively fewer studies have documented community recovery from hypersalinity, they demonstrate that communities tend to increase in species richness, diversity and biomass after salinities return to normal, stable values (0–40 ppt; Montagna et al., 2002; Van Diggelen and Montagna, 2016).

Our study investigates the existence of alternative stable states in a TOCE in south-western Australia. The estuary suffered system-wide hypersalinity due to dry climate conditions and a prolonged estuary closure (2017–2021). The hypersalinity was severe, exceeding 100 ppt for six months, and caused mass mortality of fish (Krispyn et al., 2021). Following heavy, winter rainfall, the sandbar breached in June 2021, allowing tidal exchange to occur. Invertebrate sampling was conducted seasonally for 1.5 years during the prolonged closure, twice during the sandbar breach, and six months, one and two years after the breach. We hypothesized that (i) two taxonomically distinct invertebrate communities occurred before and after the sandbar breach that ended the period of hypersalinity, (ii) large differences in their univariate and

multivarite structure were present, and (iii) salinity was the primary environmental variable influencing the two communities. We conclude by examining the evidence for alternative stable states.

2. Material and methods

2.1. Site description

Beaufort Inlet (34°27′33.0″S, 118°53′14.8″E) is a low-inflow TOCE located ~130 km east of Albany on the south coast of Western Australia. As the estuary remains closed for several years at a time, it is classified locally as 'normally-closed' (Hodgkin and Hesp, 1998), and is similar in characteristics to estuaries in the 'arid predominantly closed' category used in South Africa (Van Niekerk et al., 2020). Beaufort Inlet covers an area of 6.5 km^2 and has a shallow basin (1–2 m deep) with some deeper areas (>7 m) in upstream reaches (WRC, 2003; Brearley, 2005). It has a 500 m long, ~150 m wide sandbar that is relatively high (~3 m above sea level) and breaches following heavy rainfall and high riverine inflow, allowing tidal exchange (Hodgkin and Hesp, 1998). Although the estuary is fringed by native vegetation, >80 % of its catchment is cleared (Brearley, 2005). The estuary is situated in a Mediterranean climate (hot, dry summers and warm, wet winters) where annual evaporation (average of ~1356 mm ±12 SE, 1990–2023) exceeds annual rainfall (average of ~385 mm ±15, 1990–2023; Table A.1). Flow into the estuary from the Pallinup River varies considerably among years (1990–2023 range of 2921–130,527 ML; average of 30,191 ± 6368 ML) and is typically polyhaline (average salinity of 25 ppt since 2008), although salinities can exceed 50 ppt in some months (Table A.1). While salinities >70 ppt were not recorded in the estuary during previous prolonged estuary closures (Lenanton, 1988; Brearley, 2005), the closure of 2017–2021 led to salinities >100 ppt for a ~6 month period (Krispyn et al., 2021). The sandbar breached in late June 2021 following winter rainfall (Table A.2). Mean annual flow into the estuary before the closure was 87,000 ML during the period of 2016–2017, which decreased to 4100 ML during the estuary closure in 2018–2020 and increased to 60,000 ML in 2021–2023 when several sandbar breaches occurred (Table A.1, A.2).

The estuary holds value for the Minang Noongar people, having provided camping grounds, drinking water holes, fish and a pathway between coastal and inland areas (WRC, 2003). It is a popular camping and fishing site as it contains species targeted by recreational and commercial fishers such as Black bream (*Acanthopagrus butcheri*). Reefs of the serpulid polychaete *Ficopomatus enigmaticus* are common throughout the basin and along the shoreline (Brearley, 2005). Mass fish mortality events occur, with their causes attributed to hypersalinity, high temperature, algal blooms, and hypoxia (Brearley, 2005; Krispyn et al., 2021). Like many Australian estuaries, Beaufort Inlet is in poor health due to human activity and climate change (Clark et al., 2021).

2.2. Sampling regime

Three estuary regions (upper, middle, lower) of Beaufort Inlet were sampled on 11 occasions between February 2020 and August 2023 (Fig. 1). Sampling was conducted seasonally for 1.5 years (i.e. February [summer], May [autumn], July [winter] and November [spring] of 2020, February and May of 2021) during the period of hypersalinity and opportunistically during (i.e. June and early August 2021, with the estuary later closing on 19 August 2021) and after (i.e. December 2021, September 2022, August 2023) the initial sandbar breach on 24 June 2021. Salinity (ppt), water temperature (°C), and dissolved oxygen concentration (mg L^{-1}) were recorded four times in each region on each sampling occasion using a YSI 556 multiparameter/ProSolo probe (Yellow Springs, Ohio, USA). As the instrument was only capable of reading a maximum salinity of 70 ppt, water samples were diluted up to two times to allow accurate measurement (Hoeksema et al., 2018).

Invertebrates were collected in shallow waters (<1.5 m depth) using a hand-held corer of 11 cm diameter and 15 cm height (sampled area of 96 cm^2). Four core samples were collected in each region, totalling 12 samples per occasion (total $n = 132$). Samples were sieved over a 500 μm mesh to remove excess sediment and preserved using a 4 % formalin solution buffered with estuary water. After >48 h had lapsed, samples were washed gently using freshwater over a 500 μm mesh to replace the formalin solution with a 70 % ethanol solution before further processing. Invertebrates were extracted from the sample residue, identified to the lowest practical taxonomic level, and counted. Note that insects were usually identified to a higher taxonomic level than other taxa due to differences in the resolution of identification keys for the various aquatic life stages (larva, pupa, adults).

2.3. Data analyses

Species tables were constructed to display, for each invertebrate

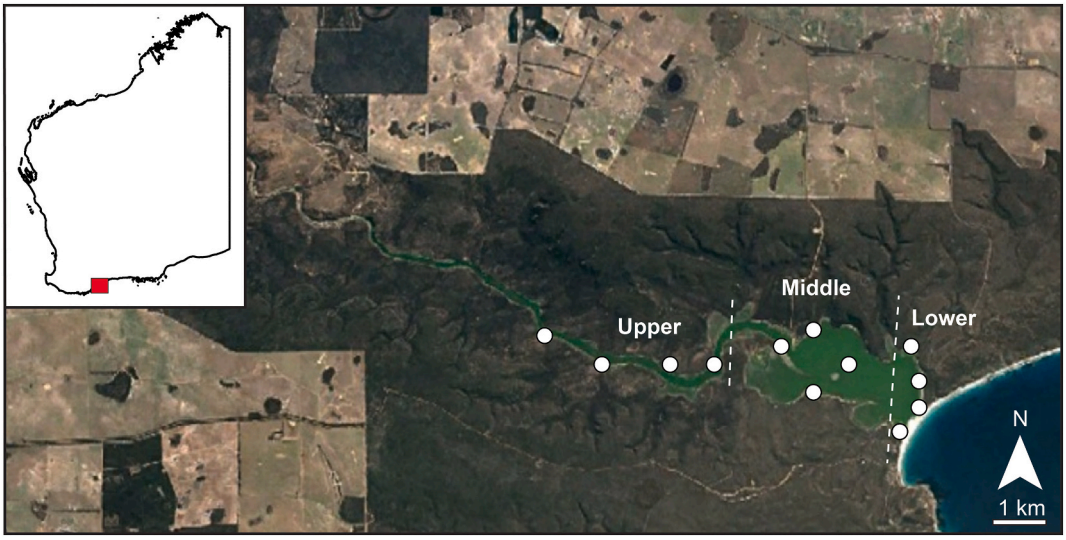

Fig. 1. Map of the three estuary regions sampled (4 samples per region) over the 3.5-year study in Beaufort Inlet, south-western Australia. The estuarine regions (upper, middle, and lower) are separated by dashed lines. Insert map shows location of the estuary in Western Australia. Image provided by Google Earth and CNES/Airbus.

taxon, the mean density per 100 cm^2, percentage contribution, and frequency of occurrence (i.e. the percentage of samples a taxon occurred in each sampling occasion or region). The following data analyses were performed using PRIMER v7 (Clarke and Gorley, 2015) with the PERMANOVA+ add-on (Anderson et al., 2008). Environmental variables (salinity, water temperature, and dissolved oxygen) were subjected to a two-way crossed univariate permutational analysis of variance (PERMANOVA; Anderson, 2001) test, using a Euclidean distance matrix, to determine if they differed significantly ($P < 0.05$) with Sampling occasion (11 levels) and/or Region (3 levels). A draftsman plot showed that none of the environmental variables were skewed and so did not require transformation. Post-hoc analyses using a pairwise PERMANOVA were conducted for Sampling occasion, and means plots were constructed to explore all significant PERMANOVA effects.

Taxonomic information was checked against the World Register of Marine Species database (https://www.marinespecies.org, accessed 10/01/2024) and, for insects, the Animal Diversity Web (https://animaldiversity.org, accessed 22/06/2023). Prior to analysis, three insect taxa, i.e. Ceratopogonidae sp. (adult), Chironomidae sp. (adult), and Empididae sp. (adult), were removed from the data as they are not aquatic and are thus bycatch. The number of taxa (*S*), number of invertebrates (*N*), and Simpson's index (*SI*, $1 - \lambda'$) were calculated for each sample. A draftsman plot and Pearson correlation showed no variables were highly correlated ($r > 0.9$) and, based on skewness, *N* was square-root transformed. Each variable was subjected to the univariate PERMANOVA regime as described above and the values were compared against a salinity threshold of 60–65 ppt, as determined by previous studies (Dittmann et al., 2015; Wooldridge et al., 2016).

Community composition data (i.e. the abundance of each taxon in each sample) were dispersion weighted to reduce the influence of highly abundant species that occurred inconsistently among samples (Clarke et al., 2006) and square-root transformed to balance the contribution of rare and abundant species. A zero-adjusted (dummy value of 0.01) Bray-Curtis resemblance matrix was calculated from the pre-treated abundances and subjected to a two-way (Sampling occasion × Region) multivariate PERMANOVA. Visual interpretation of the results was aided by a non-metric multidimensional scaling (nMDS) plot of group centroids, overlayed with a trajectory illustrating the passage of time. A CLUSTER-SIMPROF analysis, performed on an Index of Association matrix, was used to group taxa with statistically similar spatio-temporal abundance patterns and overlaid on a shade plot of the average, pre-treated abundance of each taxon in each region on each sampling occasion. Taxa were coded to identify their predominant aquatic environment, i.e. coastal, estuarine, or inland (e.g. salt lake, lake and/or river) waters.

Relationships between community composition and environmental variables (salinity, water temperature and dissolved oxygen) were examined using distance-based linear models (DISTLM; Legendre and Anderson, 1999; McArdle and Anderson, 2001). To concurrently investigate the influence of estuary closure on the community, the number of days the estuary had remained closed was also included as an explanatory variable. DISTLM assessed the amount of variation in the community that could be explained by each of the four variables separately (i.e. a marginal test) and in combination with each other (i.e. a sequential test). For sequential tests, a stepwise selection procedure was used with an R^2 selection criterion. Collinearity between explanatory variables was checked using Pearson correlations against a ±0.9 threshold for exclusion. A corresponding distance-based redundancy analysis (dbRDA) plot of the DISTLM was constructed. As DISTLM solely considers linear relationships with explanatory variables, biota-environmental (Bio-Env) matching using a Spearman rank correlation between the community matrix and Euclidean distance matrices of the explanatory variables was also conducted using the same collinearity check, followed by normalisation to place all values on common scale. For DISTLM and Bio-Env tests, a *P* of <0.05 was used.

3. Results

3.1. Environmental conditions

Salinity, temperature, and dissolved oxygen changed significantly with Sampling occasion, Region and their interaction, except for temperature across regions (Table A.3). Sampling occasion was the most influential factor for each variable, accounting for over 80 % of the total mean squares. Pairwise comparisons showed that salinity and temperature varied among most sampling occasions, while dissolved oxygen concentrations were mostly similar (i.e. not significantly different) from May 2021 onwards (Table A.4). Mean salinity exceeded 100 ppt (SE range: ±0.45–2.18) between February and July 2020, with a decrease to 62 ppt (±0.65) in November 2020, followed by an increase to 91 ppt (±0.53) in February 2021 (Fig. 2a). Salinity decreased in May 2021 to 58 ppt (±0.73) and continued to decline to mesohaline conditions (range 5–19 ppt) when the sandbar was open in late June and early August 2021. Mean salinity then remained at ~20 ppt (±0.07–0.61) until the end of the study in August 2023. Water temperature exhibited a cyclical seasonal pattern averaging above 21 °C (±0.14–0.21) in summer (December/February) and at ~15 °C (±0.16–0.89) in winter (May/July/August; Fig. 2b). Mean dissolved oxygen also exhibited seasonal cycling over the first five sampling occasions (5–6 mg L^{-1}, ±0.3–0.5), and then increased to >8 mg L^{-1} from May 2021 onwards (±0.28–0.72; Fig. 2c).

3.2. Community overview

A total of 5592 invertebrates comprising 37 taxa representing three phyla (Annelida, Arthropoda, Mollusca) and, for insects, including larva, pupa or adult, was recorded. Twenty-three of the 132 samples were azoic (i.e. no invertebrates recorded): six during the period of hypersalinity (8.3 % of samples); 16 during the sandbar breach (66.7 %), and one after the sandbar reformed from the initial breach (2.8 %). When the estuary was closed and hypersaline, 16 taxa, predominantly insects, were recorded (Table A.5). Two insects, larvae of the non-biting midge *Tanytarsus barbitarsis* (95 %) and a pupa form of Diptera sp. 2 (1.5 %), accounted for 97 % of the total number of invertebrates, with *T. barbitarsis* occurring in 87.5 % of samples. In contrast, oligochaetes, the polychaete *Capitella* sp., and two amphipods *Corophium minor* and *Grandidierella* sp. occurred once or in small numbers.

During the sandbar breach that ended the prolonged closure (June–August 2021), only five taxa were recorded (Table A.5). Among these, three were arthropods not captured during other periods: an isopod, an adult dagger fly (Empididae; bycatch), and a soldier fly larva (Stratiomyidae). *Capitella* sp. represented 67 % of the invertebrates recorded, with *T. barbitarsis* declining to 16.7 %.

Following the breach (post-August 2021), 25 taxa were present, 18 of which had not been recorded previously (Table A.5). *Capitella* sp. represented 54.3 % of all invertebrates and was recorded in 94 % of samples. The next most abundant species were the non-biting midge *Dicrotendipes* sp. (larva; 12.9 %), the serpulid *Ficopomatus enigmaticus* (11.9 %), the spionid *Pseudopolydora kempi* (8.3 %), and the amphipod *Barnardomelita matilda* (5 %). Notable occurrences after the estuary opened included the bivalves *Spisula trigonella* and *Arcuatula* sp., and nassariid (dog whelks, e.g. *Tritia burchardi*) and naticid (moon snails) gastropods. No molluscs were detected in previous sampling occasions.

Among the three regions, 23 taxa were recorded in the lower estuary, 18 in the middle estuary, and 24 in the upper estuary (Table A.6). Thirteen species, including all those representing ≥1 % of the individuals in a region, were recorded in all regions, among which *Capitella* sp., *T. barbitarsis*, *Dicrotendipes* sp., and *P. kempi* were particularly abundant.

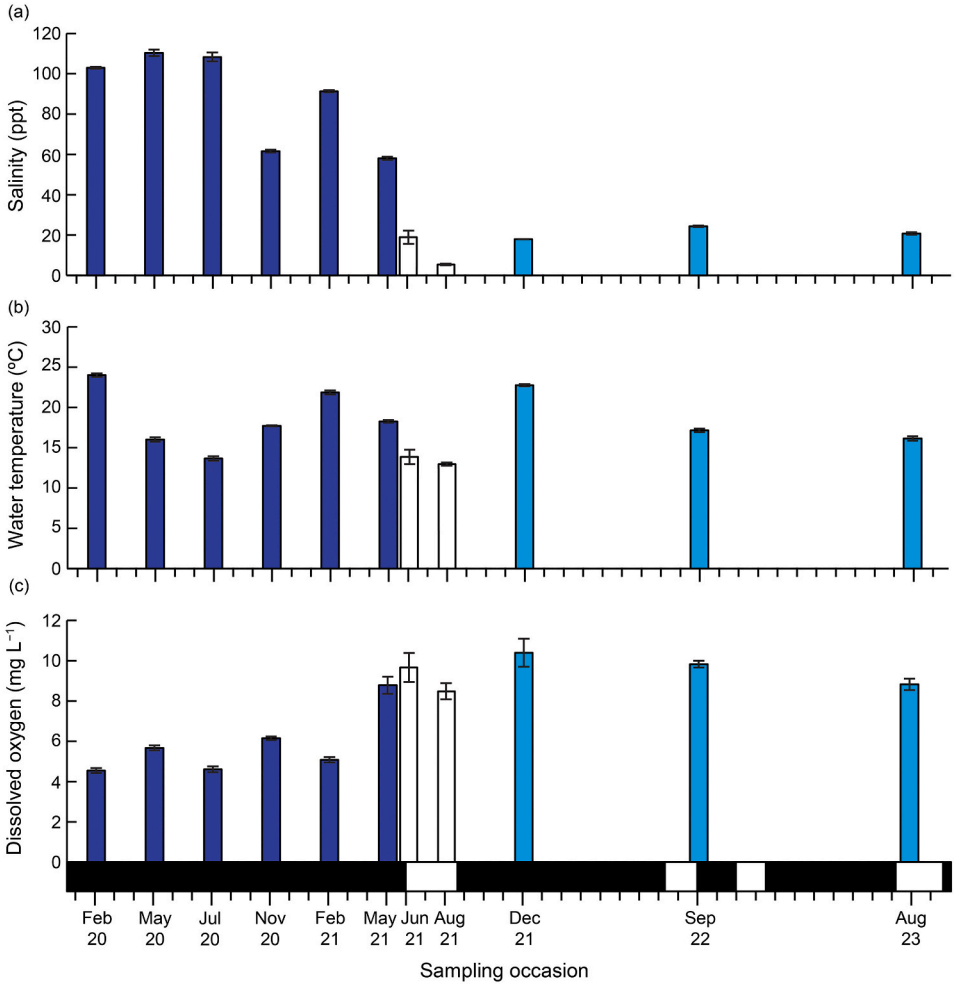

Fig. 2. Means (±1 standard error) of (a) salinity (ppt), (b) water temperature (°C), and (c) dissolved oxygen (DO; mg L^{-1}) of Beaufort Inlet, south-western Australia, over the study period. Black and white shading along the x-axis denotes the approximate times the estuary was closed and open, respectively. Colours denote sampling occasions that occurred before (dark blue), during (white), and after (light blue) the initial sandbar breach that ended the prolonged estuary closure. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.3. Evidence of different states

3.3.1. Univariate community structure

The number of taxa (*S*), number of invertebrates (*N*) and Simpson's index (*SI*) differed significantly among sampling occasions, and the Sampling occasion × Region interaction was also significant for the *S* and *SI* (Table 1). *N* also differed among regions ($P = 0.03$). Sampling occasion was always the most influential factor and accounted for the greatest proportion of the total mean squares (≥59 %). The largest pairwise differences usually occurred when comparing variable values between sampling occasions before and during the sandbar breach to those in December 2021 (Table A.7). During the hypersaline state, all univariate variables were low for the first year of sampling when salinities generally exceeded the estimated tolerance threshold of 60–65 ppt, with values somewhat increasing in the following two sampling occasions after mean salinities mostly fell within or below the tolerance threshold in November 2020 and May 2021 (Fig. 3). Less than two taxa and under 42 invertebrates 100 cm^{-2}, which corresponded to *SI* values of <0.1, were recorded between February and November 2020. In February 2021, the average of *S* increased to 2, *N* to >83 invertebrates 100 cm^{-2} and *SI* to 0.2. All univariate measures declined to their minimum values (<one taxon and invertebrate 100 cm^{-2}) during the sandbar breach of June 2021 (June and August 2021) when salinities were mesohaline. During this regime shift, mean values of *S* and *N* were significantly lower than those in all other periods, however, *SI* remained similar to measures during the hypersaline state when one species (i.e. *Tanytarsus barbitarsis*) usually dominated the community (*SI* < 0.01, Table A.7). All univariate measures increased to their maximum values six months (December 2021) after the regime shift and remained relatively high throughout the estuarine state (i.e. September 2022 and August 2023) when salinities were below the tolerance threshold (Fig. 3). During this time, there was an average of four taxa and 84 individuals 100 cm^{-2}, which corresponded to an average *SI* of 0.77 (Table A.5). The abundance of invertebrates was lower one year after the initial breach (September 2022) than five months (December 2021) or two years after (August 2023).

The significant Sampling occasion × Region interactions for *S* and *SI* were driven by spatial differences among regions occurring in sampling occasions in the estuarine state (Fig. A.1). *N* differed among regions due to abundances increasing from the lower to upper estuary (averages of 33 and 58 invertebrates 100 cm^{-2}, respectively; Table 1, Fig. A.1).

3.3.2. Multivariate community structure

Community composition differed significantly with Sampling occasion ($P = 0.01$), Region ($P = 0.003$) and their interaction ($P = 0.001$), with Sampling occasion being the most influential factor (65 % of the total mean squares, Table 1). Invertebrate community composition of the 11 sampling occasions formed three distinct clusters on the nMDS plot that align with two community states and a regime shift: samples from the period of hypersalinity lie on the lower left (i.e. a hypersaline

Table 1
Summary of two-way (Sampling occasion × Region) PERMANOVA tests of the (a) number of taxa (*S*), (b) number of invertebrates (*N*), (c) Simpson's index (*SI*), and (d) community composition of the invertebrate fauna of Beaufort Inlet, south-western Australia. The mean squares (MS), percentage of mean squares (% MS), Pseudo-*F* statistic and significance level (*P*) are shown. Significant results are emboldened.

Community measure	Factor	d. f.	MS	%MS	Pseudo-*F*	P
(a) S	Sampling occasion	10	26.67	84.09	23.842	**0.001**
	Region	2	1.19	3.75	1.063	0.326
	Occasion × region	20	2.74	8.64	2.449	**0.001**
	Residual	99	1.12			
(b) N	Sampling occasion	10	106.18	59.70	9.444	**0.001**
	Region	2	44.90	25.25	3.993	**0.027**
	Occasion × region	20	15.52	8.73	1.381	0.154
	Residual	99	11.24			
(c) SI	Sampling occasion	10	0.42	73.98	14.197	**0.001**
	Region	2	0.05	9.54	1.831	0.166
	Occasion × region	20	0.06	11.27	2.163	**0.007**
	Residual	99	0.03			
(d) Community composition	Sampling occasion	10	20,519	64.94	10.462	**0.001**
	Region	2	5829	18.45	2.972	**0.003**
	Occasion × region	20	3289	10.41	1.677	**0.001**
	Residual	99	1961			

state), those during bar opening in the top centre (i.e. a regime shift), and those following the initial opening on the lower right (i.e. a estuarine state; Fig. 4). Pairwise tests confirmed these communities were significantly distinct from each other (Table A.7). The largest pairwise differences occurred when comparing the community six months after the regime shift (i.e. December 2021) to the communities seen before (pseudo-t = 4.47–5.83) and during (pseudo-t = 4.32–5.33) the regime shift. During the hypersaline state, the community was relatively consistent as evidenced by six insignificant pairwise test results in this period. Community composition changed significantly among the three sampling occasions in the estuarine state.

Community composition shifted from an assemblage dominated by insects associated with inland waters in the hypersaline state, through a depauperate stage during the regime shift, to a normal, estuarine state containing estuarine and coastal polychaetes, molluscs, and arthropods (Fig. 5). In the hypersaline state, the invertebrate community was composed mainly of the early life stages of dipteran insects including *T. barbitarsis* (larva), and trichopteran insects such as larvae of *Triplectidina* sp. and two *Notoperata* species. Low numbers of the polychaete *Capitella* sp. were also present. During the regime shift, *Capitella* sp. was consistently recorded in low numbers, with a few insects and one isopod. Five months after the regime shift (December 2021), *Capitella* sp. increased in abundance and dominated the estuary. A consortium of new species characterized the estuarine state, including the polychaetes *P. kempi* and *F. enigmaticus* and the bivalves *S. trigonella* and *A. senhousia*. The amphipod *B. matilda* later occurred in the community in August 2023 (albeit infrequently), alongside the polychaete *Prionospio cirrifera*, an ostracod and *Procladius* sp. (larva). Species that occurred two years later included three gastropods (Naticidae sp., Nassariidae sp., *T. burchardi*) and a spionid polychaete. Only five of the 25 taxa recorded in the estuarine state were also recorded during the hypersaline state. These taxa were *Capitella* sp., *Notoperata* sp. 1 (larva), *T. barbitarsis* (larva), Diptera sp. 1 (pupa) and oligochaetes.

3.4. Environmental relationships

Preliminary correlations showed that the number of days the estuary remained closed for and salinity were positively correlated (r = 0.81). Salinity and dissolved oxygen were also negatively correlated (r = 0.80). All other correlations between variables were <0.7. In descending order of importance, Bio-Env selected dissolved oxygen and number of days closed as the best combination of variables explaining trends in community composition (ρ = 0.435, P = 0.001). Considered alone, the number of days the estuary remained closed was the most influential predictor (ρ = 0.390), followed by salinity (ρ = 0.348), dissolved oxygen (ρ = 0.312) and temperature (ρ = 0.119). The DISTLM analysis showed that each environmental variable fitted independently explained a significant proportion of multivariate community composition (all with P = 0.001; Table A.8). The number of days the estuary remained closed explained 21.2 % of the community variation present, salinity 17.1 %, dissolved oxygen 11.5 %, and temperature 7 %. In combination, DISTLM selected the following three variables to significantly explain 30 % of the community variation present: number of days closed, temperature, and dissolved oxygen concentration (R^2 = 0.298, P = 0.002). Salinity was also added as a final predictor, although its inclusion did not account for a significant proportion of the community variation present (Table A.8). The dbRDA plot of the DISTLM model shows clear groupings of the 11 sampling occasions due to the cumulative variation explained by the four variables included in the model (Fig. 6). The dbRDA axis 1 captured community changes due to duration of estuary closure (i.e. number of days closed) and salinity (21.7 % total variation explained, 70.6 % model of variation fitted), with sampling occasions broadly separated into two clusters: the hypersaline state and all others. Temperature and, to a lesser extent, dissolved oxygen, explain the spread of samples along dbRDA axis 2 (7.8 % total variation explained, 25.5 % of model variation fitted). This axis captures seasonal oscillations in temperature and invertebrate numbers, with higher abundances of invertebrates usually occuring in the warmer sampling periods (December/February) than the cooler sampling periods (July/August/September).

4. Discussion

The theory of alternative stable states was evaluated for a TOCE in south-western Australia by sampling invertebrate communities during a prolonged estuary closure when conditions were markedly hypersaline, when the estuary opened to the ocean, and for the following two years when salinities were mesohaline. Over the 3–5-year study, the invertebrate communities of Beaufort Inlet shifted dramatically. Two distinct communities were documented: (1) an insect-dominated community resembling that of a salt lake during the prolonged, hypersaline closure, and (2) an invertebrate community typical of an estuary which occurred after the initial sandbar breach. Both communities were separated by a period of benthic community impoverishment during the breach itself. Community structure and composition over time were mostly related to the duration of estuary closure and changes in salinity, followed by seasonal fluctuations in temperature and dissolved oxygen. The richness, abundance and diversity of invertebrates increased when estuarine and marine species colonised the estuary after the estuary opened. Together these findings are examined for the existence of alternative stable states in an estuary.

4.1. Evidence of alternative stable states

Alternative stable state theory posits that an ecosystem must harbour distinct biotic assemblages between at least two alternative states (Holling, 1973; Scheffer et al., 2001). This condition is evident in Beaufort Inlet as two overarching invertebrate communities occurred before and after the estuary opened to the ocean. During the prolonged closure and period of severe hypersalinity, the estuary harboured a community comprising insects and an annelid taxon (*Capitella* sp.), with

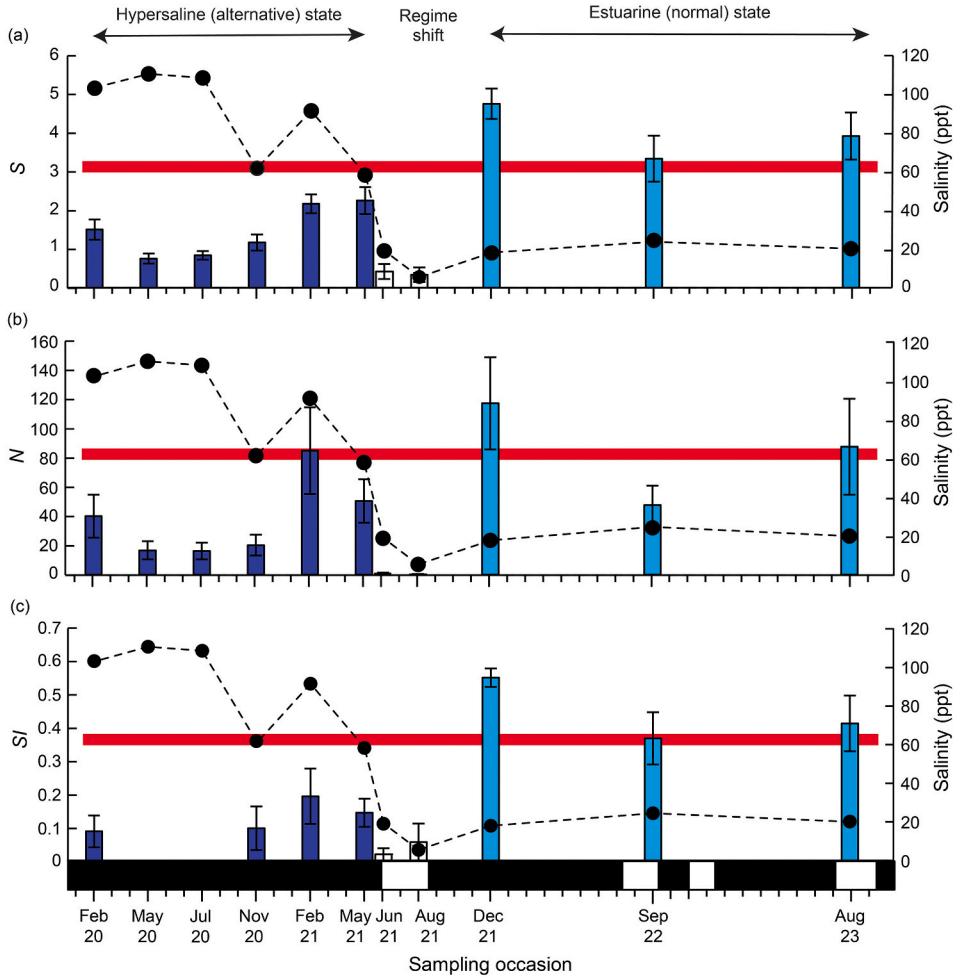

Fig. 3. Means (±1 standard error) of the (a) number of taxa (*S*), (b) total number of invertebrates (*N*, inds. 100 cm^{-2}), and (c) Simpson's index (*SI*). Mean salinity (ppt; dashed line) is also provided together with a salinity threshold (red line) of 60–65 ppt (Dittmann et al., 2015; Wooldridge et al., 2016). Black and white shading along the x-axis denotes the approximate times the estuary was closed and open, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the sporadic presence of a single amphipod species (either *Grandidierella* sp. or *Corophium minor*). The dominant species was the non-biting midge *Tanytarsus barbitarsis*, whose larvae are among the most salt tolerant found in salt lakes globally (Paterson and Walker, 1974; Shadrin et al., 2017). The detritus-feeding larvae of *T. barbitarsis* survive hypersaline conditions by maintaining the salt concentration of their haemolymph at 10 g L^{-1} by continuously drinking water and excreting salt (0.3 osmol kg^{-1}; Kokkinn, 1986; Bradley, 2008). Despite its impressive osmoregulation, the lethal concentration of salinity at which 50 % of a population dies is 94 g L^{-1} (Kokkinn, 1986). This limit was surpassed in Beaufort Inlet in the first three sampling occasions (salinity >100 ppt) when a low number of invertebrates was recorded. Similarly to salt lakes in Crimea and Bolivia (Dejoux, 1993; Shadrin et al., 2017), larvae of the halotolerant Ceratopogonidae (biting midges) sporadically occurred alongside *T. barbitarsis* in Beaufort Inlet. When salinity declined to ~60 ppt following seasonal rainfall and riverine inflow in November 2020 and May 2021, while the bar remained closed, *T. barbitarsis* abundances increased and larvae of various Trichoptera (caddisflies) emerged (e.g. *Notoperata* sp. 1 and 2, *Triplectidina* sp.). While caddisflies are often used as indicator species in freshwater environments, their occurrence under hypersaline conditions is unexpected. Instead, they tend to disappear with saltwater intrusion in freshwater environments in India and have a low tolerance for salinity in Australia (Benchamin and Kurup, 2023; Chessman, 2023). In contrast, giant ostracods are common salt lake fauna (Lawrie et al., 2021), with a few individuals of the halophilic *Mytilocypris ambiguosa* recorded in November 2020. Overall, the benthic community of the estuary during its hypersaline state was mainly populated by terrestrial insects adapted to living at nearby salt lakes, a terrestrial subsidy that was likely crucial to maintaining an invertebrate community during this time.

Relying on a subsidy of insects from fringing terrestrial ecosystems raises the question as to whether this community state can be considered self-sustaining (i.e. successfully reproducing in that environment), prerequisite evidence for an alternative stable state (Connell and Sousa, 1983; Peterson, 1984; Petraitis and Dudgeon, 2004). As the insects recorded do not actively reproduce *within* the estuary, their populations are externally maintained by terrestrial adults. Yet these insects are dependent on water bodies, with their aquatic larvae inhabiting a benthic niche in which they grow, moult and metamorphose (Bradley, 2008). Considering that the generation time of *T. barbitarsis* is typically 30 days (Paterson and Walker, 1974; Kokkinn, 1986), and that the species consistently occurred over the 1.5 years of sampling during the estuary closure, multiple turnovers of the population have occurred. Although dipteran insects temporarily leave the water as adults to reproduce, their abundance declines with distance from a water source (Delettre and Morvan, 2000), exhibiting their reliance on aquatic environments due to an obligate, aquatic developmental stage. Moreover, chironomids spend the majority of their life in their aquatic larval stage, in which time they acquire most of the energy needed to complete their life cycle (Tokeshi, 1995). As such, an invertebrate community

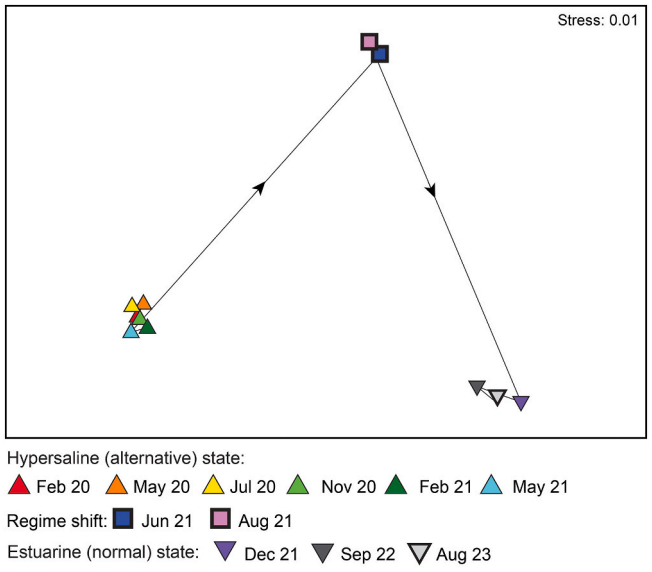

Fig. 4. A non-metric multidimensional scaling plot of the group centroids of benthic invertebrate samples from each sampling occasion in Beaufort Inlet, south-western Australia. Samples with think black lines were collected when the estuary was open. The trajectory depicts invertebrate composition change over time.

composed primarily of semi-aquatic insects can also be considered self-sustaining and highlights an intricate link between terrestrial and aquatic ecosystems.

In contrast to a terrestrially-subsidized community, typical estuarine invertebrate communities are highly adapted to ensure their populations are self-sustaining and in a stable state. As inhabitants of environmentally variable ecosystems, estuarine invertebrates withstand inherent stresses and capitalize on conditions (e.g. reduced species competition) that stem from changing salinities, water temperature, hypoxia (exacerbated by eutrophication), current speeds and sediment movement, which occur over various timescales (Elliott and Quintino, 2007). For example, fossorial amphipods and bivalves in Chesapeake Bay (United States) withstand sediment burial at varying pressure stress levels (Hinchey et al., 2006). Furthermore, palaemonid shrimp in the Guadalquivir Estuary (Spain) are more capable of maintaining metabolism when experiencing hypoxia over various environmental gradients than their freshwater and marine counterparts (González-Ortegón et al., 2013). The adaptation of estuarine invertebrates to fluctuating environmental conditions has also made them resistant to large-scale climatic events, with community recovery observed in less than a year following a hurricane in San Antonio Bay (United States; Montagna, 2023). Sandbar breaching in TOCEs can result from major climatic events, such as hurricanes or cyclones, or from artificial breaching, with both benthic and hyperbenthic communities being resistant to its effects (Gladstone et al., 2006; Lill et al., 2013; Wooldridge and Bezuidenhout, 2016). Their adaptations also extend to their reproduction, with serpulid polychaetes that inhabit hypersaline estuaries in the southern United

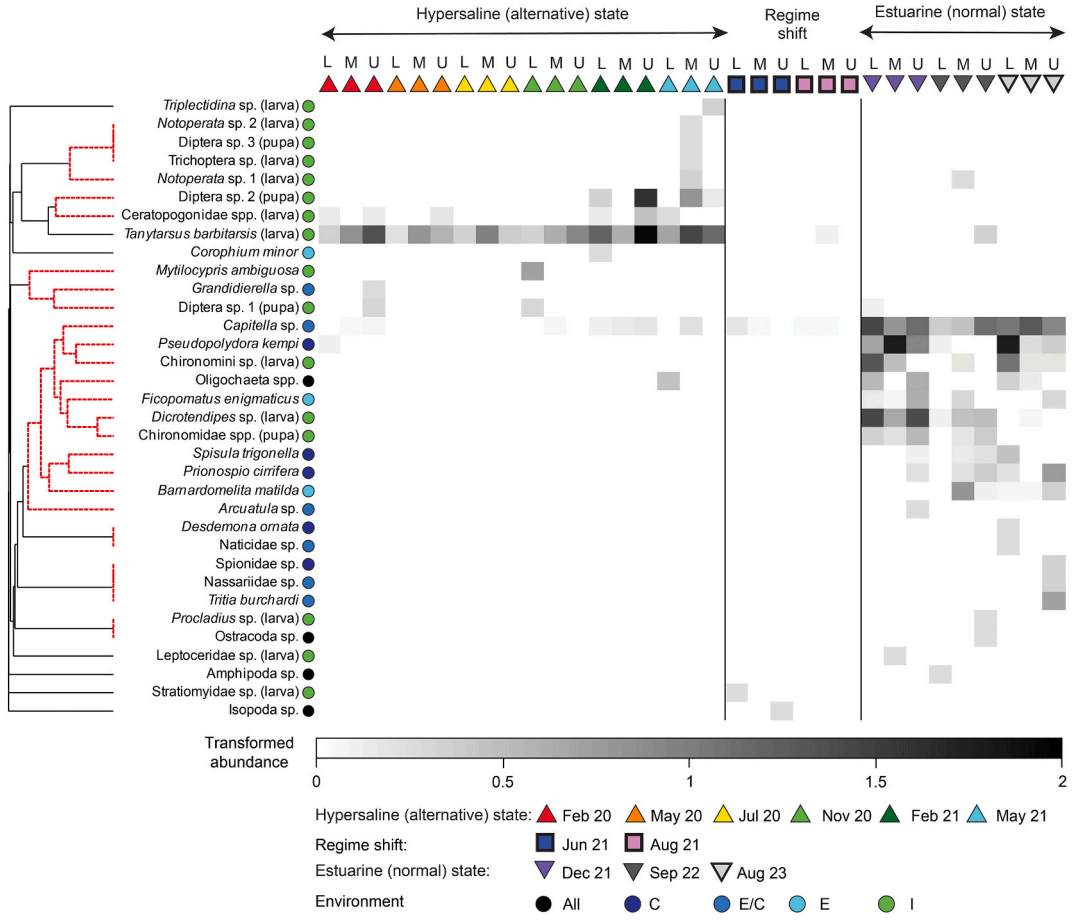

Fig. 5. Shade plot of the pre-treated, average abundance of invertebrates caught in each region of Beaufort Inlet, south-western Australia. Sample labels denote the estuary region, i.e. L, lower; M, middle; U, upper). Taxa names are coded according to the aquatic environment(s) they predominantly inhabit (All; C, coastal; E, estuarine; I, inland). The grey shading is proportional to taxon abundances and the cluster dendrogram distinguishing taxa with significantly distinct (black) and non-distinct (red) spatio-temporal patterns of abundance.

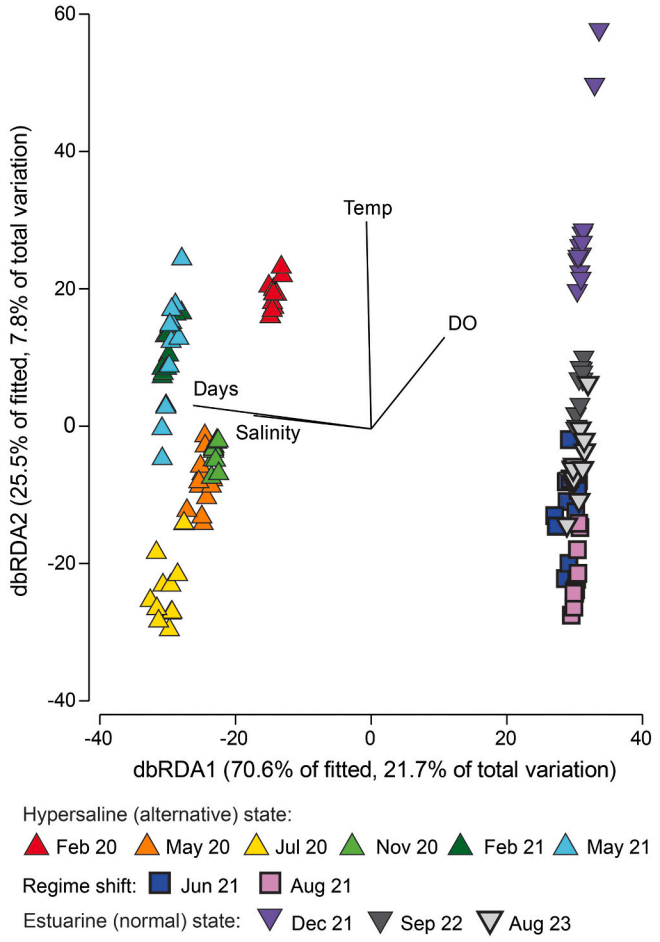

Fig. 6. A distance-based redundancy analysis (dbRDA) plot of invertebrate community composition for each sample taken from Beaufort Inlet, south-western Australia. The plot is overlayed with vectors for each environmental variable, with the length of the vector denoting the strength of influence that variable had on dbRDA axes 1 and 2.

States and Australia undergoing a protracted spawning period in which pelagic larvae are released to ensure continued recruitment and species persistence (Dittmann et al., 2009; Breaux et al., 2023). Other species in south-western Australian estuaries, such as the spionid *Dipolydora socialis* or the pea clam *Arthritica semen*, have 'opted out' of pelagic larval stages and maintain juveniles within their tubes and shells, respectively, presumably to protect these early life stages from the natural stress encountered in these estuaries (Warwick et al., 2018; Rose et al., 2019). Indeed, *Capitella* sp. was the only polychaete to endure the extreme hypersaline conditions in Beaufort Inlet and is a species that utilises this benthic brooding strategy. A variety of such self-sustaining traits are important attributes of species that contribute to the community composition of alternative stable states (Peterson, 1984).

In addition to self-sustaining biological traits, each stable state should exhibit positive feedback loops among the physical, chemical and biological components of the system that tend to stabilize the state itself (Scheffer et al., 2001; Hölker et al., 2015). Such interconnected cycles in a normal, estuarine state create 'helpful resilience', aiding in maintaining the community in its state, while those in a hypersaline, alternative state spur 'unhelpful resilience', as the feedbacks make it increasingly difficult to restore the ecosystem to the estuarine state (Standish et al., 2014). For benthic environments, positive feedbacks often involve the functional actions of invertebrates (e.g. burrowing) that manipulate sedimentary properties (e.g. oxygenation, particle size distribution), thereby maintaining sediments in a suitable form for continued habitation (Peterson, 1984; Petraitis and Dudgeon, 2004). In freshwater lakes experiencing eutrophication, chironomids may indirectly support the feedback loops maintaining both the clear (i.e. macrophyte dominated) and turbid (i.e. phytoplankton dominated) stable state (Hölker et al., 2015). It is thought they influence nutrient competition dynamics among plants via their bioturbation impact on nutrient fluxes at the sediment-water interface in either state or that they favour the clear water state simply by exporting nutrients from the system entirely once the adult life stage is reached (Hölker et al., 2015). For invertebrates that preferably inhabit nutrient-poor, sandy sediments, their burrowing action facilitates denitrification, a microbial process that removes bioavailable nitrogen. Bioturbation that enhances denitrification may, in turn, help to maintain the sediments in an unenriched state, thereby indirectly maintaining the benthic environment in their preferred state. Indeed, invertebrates in the nearby Swan-Canning and Peel-Harvey estuaries of south-western Australia enhance denitrification in the sandy sediments they inhabit (De Roach et al., 2002; Cronin-O'Reilly et al., 2022). For an alternative, hypersaline state comprising insect larvae, as documented in the current study, such positive feedbacks are less obvious. However, hypersalinity acts like other stressors and favours the persistence of short-lived, small-bodied species (Boltt, 1975; Breaux et al., 2019), which have a restricted bioturbation impact due to their reduced biomass (Cronin-O'Reilly et al., 2022). As hypersalinity supports communities of superficial bioturbators, the sediments remain inhospitable from the salts and sulphides they contain, which could otherwise be remediated if larger, bioturbating estuarine species (e.g. the nereid *Simplisetia aequisetis*) were present (Lam-Gordillo et al., 2022). The hypersaline state is thus partly maintained via the continued hostility of its sediments due to the sole occurrence of superficial bioturbators.

4.2. *Thresholds for regime shifts*

Alternative stable states are typified by the occurrence of an external and/or internal event(s) that cause a regime shift between two states, that is, to tip the ball over the bifurcation fold from one cup into another (Scheffer et al., 2001; Petraitis and Dudgeon, 2004). A regime shift encapsulates an ecological threshold being surpassed, at which point a non-linear shift in community structure occurs (Beisner et al., 2003; Suding and Hobbs, 2009). For the alternative, hypersaline state to occur, a regime shift was caused by an external climate of low rainfall that manifested in reduced riverine inflow (of which, if any, was saline), a prolonged estuary closure, and evaporation that resulted in salinity concentrations that exceeded those tolerated by the estuarine community. Salinity increases can sometimes cause linear declines in species richness of both fish and invertebrate communities (Whitfield et al., 2006; Dittmann et al., 2015; Getz and Eckert, 2023), providing contrasting evidence of a regime shift. However, non-linear shifts of invertebrate diversity have also occurred in Rincon Bayou (United States) where diversity initially increased as salinity increased, and then declined when salinities fell outside the normal salinity range (0–40 ppt) of an estuary (Montagna et al., 2002). Additionally, a sharp, non-linear shift in invertebrate community composition to an insect-dominated assemblage occurred in the Coorong (South Australia) when salinity reached 64 ppt (Dittmann et al., 2015). We might then expect both linear (e.g. using DISTLM) and non-linear (e.g. using Bio-Env) relationships to be detected under various scenarios (Clarke and Warwick, 2001), with strong non-linear correlations expected when a threshold is surpassed. In this study, the salinity threshold had already been surpassed prior to sampling, as sampling commenced at salinities of >100 ppt. Both DISTLM and Bio-Env test correlations between explanatory variables and community composition were also relatively low, indicating a large amount of variability present, the potential influence of unmeasured variables, and/or the community's independence from the measured environmental variables as garnered from their adaptation to a dynamic ecosystem (Elliott and Quintino, 2007; Elliott and Whitfield,

2011; Pillay and Perissinotto, 2013). Correlations may also have been reduced due to additional bar breaching events that occurred between later sampling occasions. Despite this, the number of days the estuary remained closed and salinity were the most influential drivers of community composition, with the dbRDA plot separating invertebrate samples into two broad groups according to these variables. These findings further illustrate the coupled driving force of estuary closure and salinity on determining the communities present (Pillay and Perissinotto, 2013).

In terms of alternative stable state theory, a regime shift is a period when the ecosystem is considered relatively unstable (Scheffer et al., 2001). Interestingly, our study captured a regime shift to a normal, estuarine state, which was triggered by heavy rainfall in the winter of 2021 that led to the sandbar breaching in June of that year. During the regime shift, the invertebrate community was depauperate and relatively unstable as 66 % of samples were azoic for <three months. Severe scouring of the sediment likely occurred, with epifauna flushed from the system while the infaunal polychaete *Capitella* sp. remained. Sediment scouring is an effect of the floods needed to breach estuarine sandbars (Van Niekerk et al., 2020), which can reduce invertebrate numbers and diversity in the process, as was observed in the nearby Swan-Canning Estuary (Kanandjembo et al., 2001). Alternative stable state theory postulates that the energy required to return an ecosystem to the 'previous' or desired state is likely substantially more than is needed to tip it into the undesired state, and it may need to reset the system to a time prior to the development of the desired state in order to do so (i.e., hysteresis; Suding and Hobbs, 2009). Sand bar breaches in estuaries are events that take an enormous amount of physical force to incite. In TOCEs in south-western Australia, they usually occur following high volumes of river discharge in winter, or, to a lesser extent, atypical summer storms (Hoeksema et al., 2018). They may also be influenced by long-term climate oscillations such as the Indian Ocean Dipole, which affects rainfall and river flow in the region (Hameed et al., 2011), yet direct links to bar breaching have yet to be made. For St Lucia Estuary (South Africa), it was wave action driven by a cyclone that finally breached the sandbar after ~5 years of closure, allowing marine fishes to enter the estuary, and some invertebrates to increase in abundance (Vivier et al., 2010; Pillay and Perissinotto, 2013). Our study suggests that climatic events that cause sandbar breaching may be a phenomenon that triggers a regime shift 'back' to an estuarine state. However, not every breach prompts a regime shift between states as they are a natural feature of these estuaries (Gladstone et al., 2006; Lill et al., 2013; Wooldridge and Bezuidenhout, 2016). Indeed, the estuarine invertebrate community of Beaufort Inlet remained relatively stable following three sandbar breaches between 2021 and 2023. The only potential evidence of further breaching was a reduced richness and abundances of invertebrates observed in September 2022 following a breach two months prior.

An apparently strict condition of alternative stable states is that the community change is irreversible (i.e. permanent) following a surpassed threshold and lessoning of the pressure (Mac Nally et al., 2014; Capon et al., 2015). As such, the return of an estuarine community following the initial sandbar breach may not be considered an alternative state. We did observe the return of many species that are typical of an estuary in this region, such as the spionids *P. cirrifera* and *P. kempi*, the bivalve *S. trigonella*, and the amphipod *B. matilda* (Platell and Potter, 1996; Kanandjembo et al., 2001; Cronin-O'Reilly et al., 2022). However, there were also notable species absences such as the polychaetes *S. aequisetis*, *Scoloplos normalis*, and *Marphysa* sp., and the pea clam *Arthritica semen*, which previously occurred in the estuary (Hodgkin and Clark, 1988). Given their wide distribution across southern Australia (Hastie and Smith, 2006; Dittmann et al., 2015), the benthic brooding strategy utilised by some species (Rose et al., 2019), and the nearest estuary being >40 km away, their recovery may just be slow, as it was for the Coorong (Dittmann et al., 2015). The further opening and closing of the estuary that occurred may have also affected recovery, via flushing or restricting ocean connectivity. Alternatively, they may have been locally extirpated due to a lack of refuges during the prolonged estuary closure, and we are observing a 'shallowing' of the estuary cup, whereby the resilience of the estuary is reduced through the loss of key estuarine species that interact with and stabilize the 'landscape' of the estuarine state (Peterson, 1984; Beisner et al., 2003). With hypersalinity anticipated to increase in severity and frequency under a drying climate (Hallett et al., 2018), successive state shifts may further erode the system's resilience due to an insufficient time for species recovery between disturbances, as the outcome heavily relies upon site history (Petraitis and Dudgeon, 2004). We thus observed incomplete recovery of the estuarine state. As displayed in the conceptual model (Fig. 7), the estuarine state is clearly healthier given its increased species diversity, invertebrate numbers, and as a consequence, structural complexity (Costanza and Mageau, 1999). A lessening of the resilience of the estuarine state, as driven by extreme hypersaline conditions and successive state shifts, could justify artificial sandbar breaching as a pragmatic management action to maintain the estuarine state.

It remains to be seen if Beaufort Inlet in south-western Australia is an anomaly among TOCEs, in that it harboured a suite of natural characteristics that made it the ideal ecosystem to tip into an alternative state, or if it a 'canary in the coalmine', indicating to a wider problem that may affect other types of low-inflow estuaries in arid, semi-arid, or seasonally arid climates with escalation of the climate crisis. It could potentially occur in low-inflow estuaries that become hypersaline despite being permanently open to the ocean (Largier, 2023). For example, there is evidence that four ecological configurations occur within one hypersaline state following extended periods of low inflow to the Coorong (Lester and Fairweather, 2011). For south-western Australia, winter rainfall is declining and exceptionally wet winters that are more likely to cause bar breaches are expected to be scarcer from 2023 onwards (Rauniyar et al., 2023). These model predictions suggest that Beaufort Inlet, and other estuaries in the region, will remain closed for extended periods, isolating them from a replenishing source of marine water and species recruitment, and causing hypersalinity. The hypersaline state will then become more common, further eroding the resilience of the estuarine state by impeding complete species recovery after the system-wide disturbance temporarily ceases. This work provides an insight into new challenges faced by estuaries under human-induced climate change and supplies essential information for discerning a planetary tipping point of salt concentrations in Earth's ecosystems (Kaushal et al., 2023).

4.3. Conclusion

Our findings provide compelling evidence that estuaries, as highly dynamic ecosystems, can tip into alternative stable states. For Beaufort Inlet, it was a prolonged estuary closure that, coupled with low freshwater inflow, created severe hypersaline conditions that were lethal to the resident estuarine community present. The estuary was dominated by halotolerant insects from nearby, inland waters in its closed, hypersaline state, a terrestrial subsidy which was likely crucial to maintaining some ecosystem structure. The system then underwent a regime shift to an estuarine state following heavy winter rainfall that breached its sandbar, and contained polychaete, mollusc and amphipod species typical of an estuary. However, recovery was incomplete, with key estuarine species missing. It is possible that low-inflow TOCEs possess a set of inherent characteristics that make them prone to extreme environmental shifts that fall outside the 'normal', variable state of an estuary. More work is needed to discern whether this is a phenomenon unique to estuaries in the region or if it applies to drying climates elsewhere, and to further disentangle the positive feedback loops that help to maintain the system in either state.

CRediT authorship contribution statement

S. Cronin-O'Reilly: Writing – review & editing, Writing – original

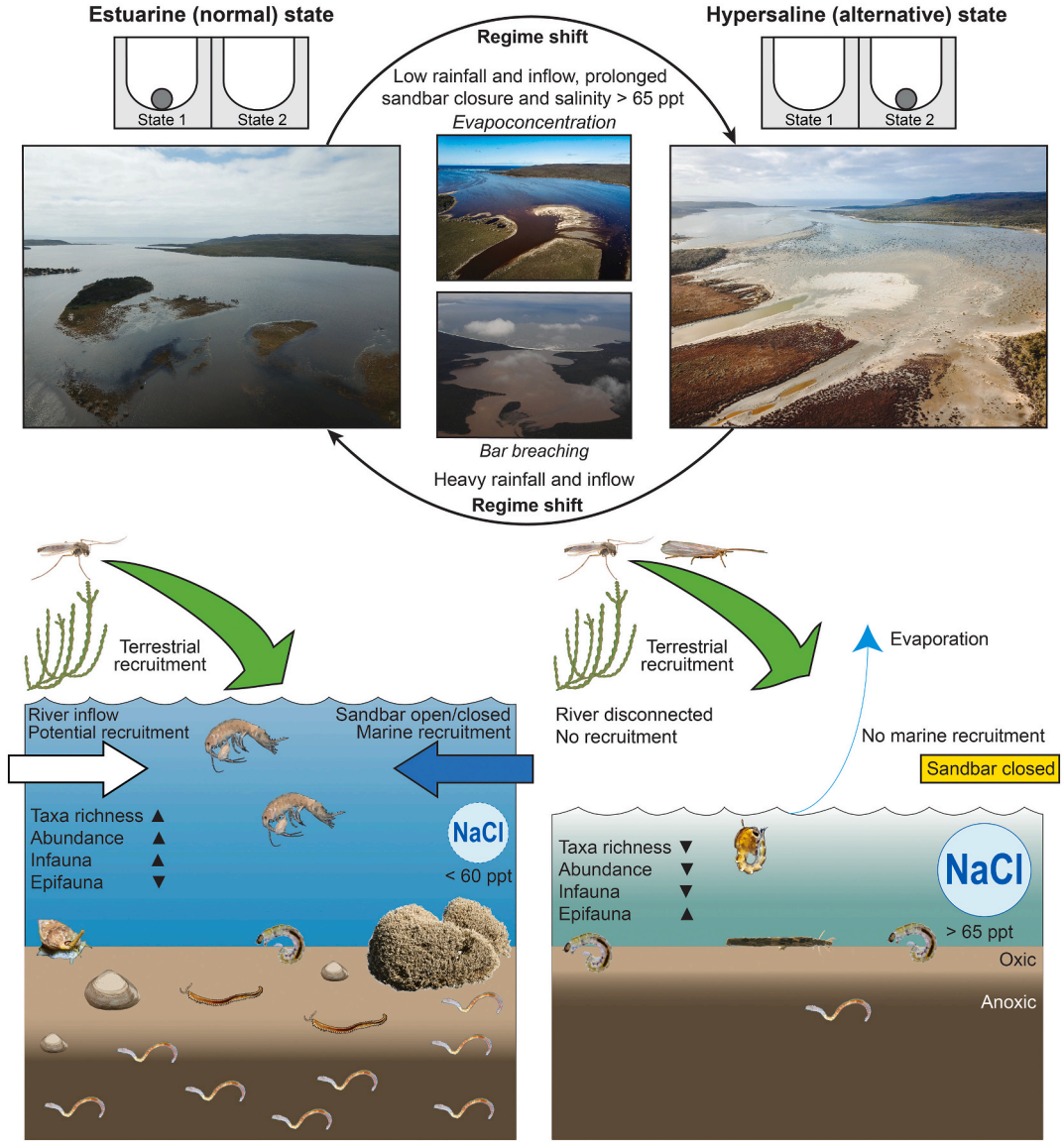

Fig. 7. A conceptual model depicting the estuarine and hypersaline stable states, the main physical drivers that trigger regime shifts between the states, and the ecological configuration of the invertebrate communities of each state. The size of the salinity (NaCl) symbol indicates the amount of salt present, and triangles indicate whether levels of diversity, abundance and invertebrate groups are higher (triangle) or lower (inverted triangle) in each state. Images were made using photographs sourced from Wikimedia Commons (see acknowledgements) and symbols are from the Integration and Application Network (ian.umces.edu/media-library).

draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **K.N. Krispyn:** Writing – review & editing, Methodology, Investigation, Conceptualization. **C. Maus:** Writing – review & editing, Investigation. **R.J. Standish:** Writing – review & editing, Writing – original draft, Conceptualization. **N.R. Loneragan:** Writing – review & editing, Resources, Methodology, Conceptualization. **J.R. Tweedley:** Writing – review & editing, Visualization, Supervision, Resources, Project administration, Methodology, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data statement

Data will be made available on request.

Acknowledgements

Our sincere thanks to Katy Fannei, Max Fabry and community members of the Little White Whale Project for supplying weekly sandbar status updates, and to Frank Thygesen for providing sandbar updates, site access and remote sampling support. We would also like to express our gratitude to Dillon Newman, Caitlan Davis, Oliver Loffelman, Brian Poh, Mitchell Spurling, Todd Cowdrey, Michael Taylor, Amy Carmignani, Billy Bowe, Ben Roots, and Steph Fourie for sampling support. We thank Dr. Holly Emery-Butcher for her guidance on chironomid larval identification. We thank Michael Moir for supplying aerial photographs of the estuary and Wikimedia Commons contributors for their photographs of invertebrates that we modified to make vectors for our conceptual model (see Table A.9 for full contribution list). The two

anonymous reviewers are thanked for their insightful comments that greatly enhanced our manuscript. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors. Sampling was conducted under Department of Primary Industries and Regional Development exemptions 3539 and 251017722.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.176356.

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