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REVIEW

Observed and predicted impacts of climate change on the estuaries of south-western Australia, a Mediterranean climate region

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Abstract
Regions with a Mediterranean climate are generally predicted to become warmer and drier with climate change. Estuaries in these regions are influenced by a broad range of climate drivers and are particularly vulnerable to the effects of climate change. We examine observed and predicted effects of climate change on the estuaries of south-western Australia (SWA), where sustained warming and drying trends have caused dramatic declines in freshwater flows of up to 70% since the 1970s, as a case study of the impacts that might be expected in other Mediterranean regions. Current and projected impacts of climate change in SWA include progressive warming and 'marinisation' of estuaries; extended closure of periodically open systems; an increased frequency and severity of hypersaline conditions; enhanced water column stratification and hypoxia; and reduced flushing and greater retention of nutrients. We document the effects of these environmental changes on the habitats, biota and ecology of SWA estuaries, including phytoplankton, macrophytes, invertebrates and fish. For example, decreasing river flows will cause periodically open estuaries across SWA to remain closed for longer periods, inhibiting the extent to which marine taxa can access these systems, thus reducing species diversity, whereas marinisation of permanently open systems will increase species diversity. We discuss the broader relevance of our findings, placing them in a global context and highlighting implications for ecosystem services and human populations. Finally, we consider the adaptation options that could be implemented to reduce the impacts of climate change in Mediterranean climate regions.

Keywords Climate change · Estuary · Hydrology · Hypersalinity · Hypoxia · Phytoplankton

Introduction

Climate change, linked to anthropogenic increases in greenhouse gases, is proceeding at an unprecedented rate (IPCC—Intergovernmental Panel on Climate Change 2013), with measurable impacts on aquatic environments worldwide (Firth and Fisher 2012; Hoegh-Guldberg and Bruno 2010). Warming will increase throughout this century, leading to

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long-term, broad-scale changes in a suite of climate drivers, including air and sea surface temperatures (SST), rainfall patterns, sea level and extreme weather events (IPCC—Intergovernmental Panel on Climate Change 2013). Whilst global predictions of mean climate conditions are important, ecological impacts of climate change are more likely to be mediated by responses to extremes than changes in average conditions (Coumou and Rahmstorf 2012) and will exhibit great spatial variability as, for example, some regions become wetter and others drier (Durack et al. 2012; Hobday and Lough 2011).

Mediterranean climate regions, i.e. the Mediterranean Basin, central Chile, California and the Baja Peninsula, and parts of southern Australia and South Africa (Klausmeyer and Shaw 2009), are characterised by warm to hot, dry summers and mild to cool, wet winters (Belda et al. 2014). These regions are generally predicted to become warmer and drier (e.g. Giorgi and Lionello 2008; Trenberth 2011), with flow-on effects on their terrestrial and aquatic ecosystems (Klausmeyer and Shaw 2009; Thompson et al. 2015). The floristic diversity of Mediterranean climate regions has received much attention, yet they also support important land-sea connections, particularly through estuaries. Estuaries are highly productive and valuable aquatic ecosystems that provide a multitude of ecosystem services (Barbier et al. 2011; Costanza et al. 1997, 2014). As transition zones between marine, freshwater and terrestrial environments, estuarine ecosystems are particularly vulnerable to the effects of climate change (Poloczanska et al. 2007). Moreover, as they provide key locations for human settlements (Hallett et al. 2016b), many estuaries have been extensively impacted by pollution, habitat loss, altered hydrology and/or geomorphology, and overfishing (Kennish 2002), compounding the pressures associated with climate change.

Estuaries in the Mediterranean climate regions of Australia exemplify these climatic and non-climate stressors. Australia is the driest inhabited continent on Earth and Australian river flows are among the most variable in the world, reflecting both marked seasonality and inter-annual variability in rainfall (Finlayson and McMahon 1988; Hobday and McDonald 2014). The resulting hydrologic regime, i.e. the timing of flows of different magnitudes, is crucial in structuring the unique environments and biota of Australian estuaries, including those in south-western Australia (SWA; Online Resource 1). Moreover, like many such systems worldwide (Hearn 1998), estuaries in SWA are typically shallow and microtidal (tidal range < 2 m), with relatively long water residence times (Tweedley et al. 2016b).

This review examines observed and predicted effects of climate change on the estuaries of SWA, as a case study of the impacts that might be expected in other Mediterranean climate regions. We document the evidence for changes in climate drivers across SWA and evaluate their observed and potential effects on estuarine environments, their habitats, biota and ecology, supported by examples from other comparable regions worldwide. We then discuss the relevance of our findings in a global context, including the implications for human populations. Finally, we consider briefly the adaptation responses that can be implemented in these regions, noting the conflicting objectives of development and ecosystem protection that are often encountered.

Regional context

The Mediterranean climate of SWA (Online Resource 1) has up to 80% of annual rainfall from May to October (Hope et al. 2015a). The relative strength of waves, tides and freshwater flows determines the mouth status of estuaries (Heap et al. 2004); thus, wave patterns and rainfall variability are key drivers of estuarine morphology and ecology in this and other microtidal regions. Estuaries of SWA, as in other Mediterranean climate regions (Collins and Melack 2014; Cooper 2001; Tweedley et al. 2016b), can be classified as permanently open (PO) or periodically open. The PO estuaries in SWA are commonly maintained in an open state through human action, via dredging, removal of rock bars or construction of artificial entrance channels (Brearley 2005). Periodically open systems include those that are either intermittently open (IO), seasonally open (SO) or normally closed (NC), depending on whether and for how long they become separated from the ocean by the formation of a sand bar across their mouth (Chuwen et al. 2009b; Hodgkin and Hesp 1998). Indeed, some NC estuaries may open so infrequently, if at all, that they could be regarded as permanently closed, saline coastal lakes or lagoons (Hodgkin and Hesp 1998).

A key climatic feature of SWA is a gradient of increasing air temperatures and decreasing rainfall (and hence river flows) from the south-west corner to the South Australian border (Lester et al. 2014). This gradient not only influences the types of estuary found along the coast (Online Resource 1), their degree of connectivity to the ocean and thus their environmental conditions, flora and fauna, but also provides an opportunity to use a space-for-time approach to examine the changes that various estuaries across the region will experience with climate change (Lester et al. 2014). Moreover, the relatively rapid rate of change in the climate of SWA, including a recent record of anomalously warm and dry years, facilitates understanding of the longer-term impacts of climate change and offers lessons for slower warming regions.

The marine flora and fauna of the region are influenced by the Leeuwin Current (e.g. Ayvazian and Hyndes 1995), which flows southward along the Western Australian coast bringing warm water from the tropics. As a result, biological assemblages are characterised by temperate species, with a declining presence of subtropical and warm-temperate species from the north-west to the south-east corner of SWA (e.g. Hutchins 1994; Carruthers et al. 2007; Wernberg et al. 2013). The estuarine environments and biota of SWA estuaries also reflect the region's small tidal range (< 1 m). For example, the geographic extent of tidal marshes in SWA estuaries is limited; thus, these habitats are excluded from the current review.

Observed and predicted changes in the regional climate

The major climatic drivers that shape environmental conditions in estuaries include air temperatures, SST and rainfall (Poloczanska et al. 2007), as well as rising sea levels. Observed and predicted changes in the climate of SWA are summarised conceptually in Fig. 1.

Annual mean air temperatures for SWA rose by 1.1 °C from 1910 to 2013. By 2030, temperatures are predicted to be 0.5–1.1 °C above the 1986–2005 average, with respective increases of 1.2–2.0 and 2.6–4.0 °C by 2090 under moderate (representative concentration pathway; RCP4.5) and high (RCP8.5) emissions scenarios (Hope et al. 2015a). Rising mean air temperatures will be accompanied by a marked increase (> 150%) in hot (> 35 °C) and extreme (> 40 °C) temperature days. An increase in SST of 0.02 °C per year since the 1950s has been observed off SWA (Pearce and Feng 2007)—an ocean warming hotspot (Hobday and Pecl 2014). Increases in SST have been greatest in autumn-winter, with the peak in the seasonal temperature cycle shifting by 10–20 days from the 1950s to the 2000s (Caputi et al. 2009) as warmer SST persists later into the year. Across coastal waters of SWA, warming by 2090 is projected in the range of 1.5–3.9 °C for RCP8.5 (Hope et al. 2015a).

Winters in the region became 25% drier over the course of the twentieth century (Hughes 2003), including a 15–20% decline in late autumn-winter rainfall since the 1970s (Hope et al. 2015b) and a recent absence of very high rainfall years relative to much of the twentieth century. Decreases in future winter, spring and annual rainfall are projected with high confidence. By 2030, winter rainfall for SWA may change by − 15 to + 5%, and by 2090, these ranges are around − 30 to − 5% under RCP4.5 and − 45 to − 5% under RCP8.5 (Hope et al. 2015a). Despite these projected decreases, the intensity of heavy rainfall events across SWA is likely to increase. Although storms and cyclones may become less frequent across the region (Elsner et al. 2008), their severity may increase (Hughes 2003) and forecast changes in the temporal pattern of storms will intensify runoff profiles (Min et al. 2011; Wasko and Sharma 2015). In particular, very large fluctuations in summer rainfall intensity are predicted (Andrys et al. 2017), which will dramatically alter estuarine hydrology. The above changes in rainfall patterns largely reflect a progressive southward shift of winter storm systems and greater prevalence of high pressure systems (Hope et al. 2015a).

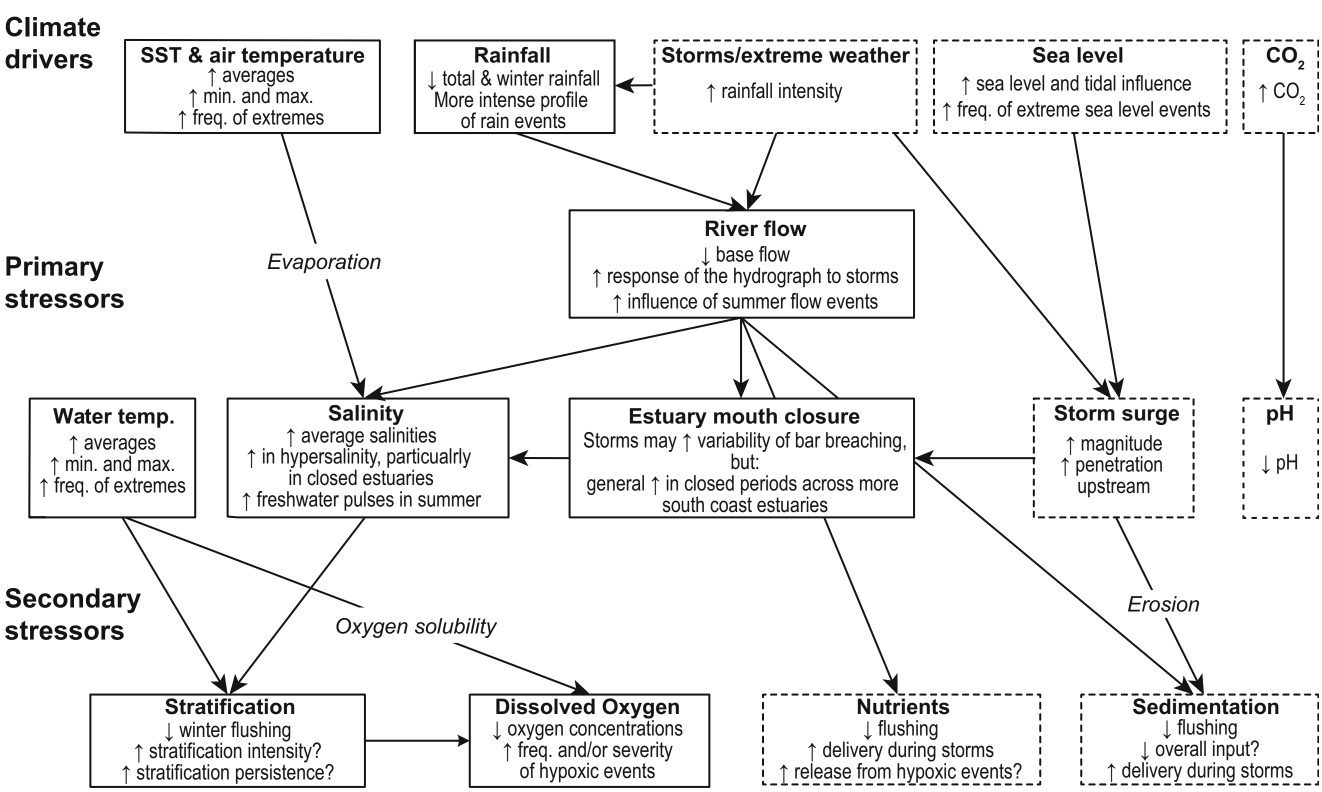

Fig. 1 Conceptual diagram of key climatic drivers across south-western Australia and their effects on the primary and secondary environmental stressors of estuaries in this region. (Dashed boxes indicate drivers and effects whose direction and/or magnitude of change is less certain or considered to be less significant)

Sea level at Fremantle has risen by an average of 1.4 mm per year from 1966 to 2009 and is predicted to increase by 7–17 cm by 2030, and 28–66 cm by 2090, under RCP4.5 (Hope et al. 2015a). Rising sea levels will increase the susceptibility of SWA estuaries to coastal flooding associated with extreme sea level and storm surge events. The frequency of these events has increased 3-fold since 1950 (Church et al. 2006) and is predicted to rise dramatically with climate change. For instance, a 50-cm rise in mean sea level will see a 100- to 1000-fold increase in the frequency of extreme sea level events in SWA (Braganza et al. 2014).

Finally, acidification of marine and estuarine waters will occur due to rising atmospheric CO_2 concentrations, e.g. ocean pH in SWA is projected to fall by up to 0.08 units by 2030, and by up to 0.15 (RCP4.5) to 0.33 (RCP8.5) by 2090 (Hope et al. 2015a). The latter values would represent an additional increase in acidity of 40 and 110%, respectively, imposing an additional environmental stressor on estuarine ecology.

Effects of climate change on environmental conditions

The above climate drivers are already modifying the environmental conditions in estuaries of SWA and will do so at an increasing rate if climate change follows a business as usual pathway (e.g. RCP 8.5). Such changes will reshape the environmental stressors to which estuarine flora and fauna are subjected (Fig. 1).

Increases in air temperature and SST contribute to warming of estuarine waters, especially as many estuaries are shallow and have a high surface area to volume ratio. This warming effect will be particularly marked in shallow, nearshore habitats (Oczkowski et al. 2015) and in periodically open systems when they become disconnected from the ocean (James et al. 2013). For example, water temperatures in the shallow distal portions of the Leschenault Estuary (Online Resource 1) regularly exceed 30 °C during summer (Veale et al. 2014).

Warming will also raise the salinity of estuarine environments through increased evaporation, contributing to 'marinisation' of PO estuaries over time and increasingly frequent and severe hypersaline conditions in some systems (Cyrus et al. 2011; Largier et al. 1997). Increasing salinities are evident in some PO estuaries of SWA (e.g. Valesini et al. 2017), although region-wide trends have yet to be effectively documented. As in several other Mediterranean climate regions (e.g. Webster 2010; Wooldridge et al. 2016), hypersalinity is prevalent among SWA estuaries, including both PO (Loneragan et al. 1987; Veale et al. 2014) and NC systems (Chuwen et al. 2009a, b; Hoeksema et al. 2006), primarily reflecting relatively low freshwater inputs and high rates of evaporation in summer. For example, salinities of 296 have been recorded in Culham Inlet during an extended closed period (Chuwen et al. 2009a). South coast estuaries will be most susceptible to hypersalinity (*see below*), some of which may become negative or inverse estuaries (sensu Largier et al. 1997) for longer periods due to climate change.

Changes to rainfall, and thus river flows, across SWA will exacerbate these increasing salinity regimes and lead to additional impacts. Observed changes in the timing and magnitude of rainfall, combined with increasing temperatures and evaporation and the clearing of 80–90% of native vegetation since European settlement (Halse et al. 2003), have had pronounced effects on freshwater flows (Petrone et al. 2010). Inflows to dams across SWA have declined by up to 70% since the mid-1970s (Barron et al. 2012), with total annual stream flow in 2010, the driest year on record for SWA, only ~5% of the long-term average (Silberstein et al. 2012). Further declines in annual flow of ~30% by 2030 are projected under a medium emissions scenario (Silberstein et al. 2012).

These changes will have significant secondary effects on multiple estuarine stressors, some of which may vary between estuary types and will be harder to predict due to complex interactions among climate drivers (Fig. 1). For instance, declining rainfall and river flows, rising sea levels and increased storm surge will increase the influence of the marine environment on PO systems and also alter erosion/deposition cycles. In the longer term, this will encourage the extended closure of numerous SWA estuaries; IO and SO systems will generally experience shorter open phases and longer periods between mouth openings, whilst NC estuaries in the drier east of SWA may 'evolve' towards a permanently closed, lagoonal state (Hodgkin and Hesp 1998). Such changes would in turn increase the likelihood of extreme temperatures and salinities in these systems (Chuwen et al. 2009a, b; Cyrus et al. 2011; Collins and Melack 2014). However, changes in the timing and intensity of storm events will also exert an influence on estuarine connectivity. As the influence of winter rainfall declines and that of summer storm events potentially increases into the future, estuaries that previously opened predominantly during winter may instead open during summer. This would lead to changes in the effects of opening on estuary hydrology, flushing and environmental conditions (e.g. Human et al. 2016).

Declining flows will also influence the dynamics of sedimentation, nutrients, stratification and hypoxia within SWA estuaries, although the direction and magnitude of these effects are less certain and likely to be context-dependent. Whilst decreasing annual flows will potentially deliver less sediment and nutrients to estuaries under baseflow conditions (Thompson et al. 2015), less scouring and flushing is also likely to occur, encouraging greater retention and internal cycling within estuaries (Statham 2012). Also, the growing influence of more intense summer storms will increase delivery of sediment and nutrients via high flow events, particularly if intense rainfall follows prolonged drought conditions that increase the erodibility of catchment soils (Thrush et al. 2004). Moreover, greater rates of erosion are associated with rising sea levels and increasing storm surge conditions (Eliot 2012).

Nutrient dynamics in estuaries are also influenced by, inter alia, dissolved oxygen (DO) concentrations in waters and sediments. As ammonium and phosphates are typically released from sediments under hypoxic to anoxic conditions (Middelburg and Levin 2009; Rabalais et al. 2010), oxygen availability influences the extent to which estuarine sediments are nutrient sinks or sources (Statham 2012). Climate change effects on DO in SWA estuaries are somewhat uncertain and likely to exhibit considerable spatial and temporal variability. Warmer estuarine waters will contain less oxygen due to reduced oxygen solubility and increased biological oxygen demand (Ficke et al. 2007). However, DO levels in these estuaries are also strongly influenced by water column stratification, with enhanced stratification leading to the development of hypoxic or anoxic conditions in the water column and sediments (Brearley 2013; Douglas et al. 1997; Kurup and Hamilton 2002; Tweedley et al. 2016a). The key question will be how changes in rainfall timing and magnitude influence stratification, oxygen availability and nutrient dynamics in different systems. Nonetheless, reduced flushing and enhanced stratification in middle to upper estuarine regions is expected with declining flows.

Impacts on estuarine habitats, flora and fauna

We synthesise and summarise the ecological impacts of climate change across different biotic groups and on various levels of biological organisation, i.e. biological performance, phenology, abundance and distribution, and community structure (see Koenigstein et al. 2016). Accompanying appendices (Online Resources 2, 3, 4, 5 and 6) detail the effects of climate change on phytoplankton, flora, invertebrates and fishes, including numerous examples of observed and predicted impacts from SWA and other Mediterranean climate regions.

Effects on biological performance

The biological performance of an organism is inextricably linked to its environment, mediated primarily through the energetic costs of homeostasis and adaptive responses to environmental stress. Effects of stress are manifested in an organism's molecular biology, physiology, behaviour, growth and reproduction and may ultimately determine their survival (Killen et al. 2013; Sokolova 2013). Climate change will therefore impact on estuarine biota by altering the abiotic stressors to which they are exposed.

Temperature is a key factor affecting the biological performance of organisms (Pörtner and Farrell 2008; Sokolova 2013). Increasing water temperatures may enhance the growth and/or reproduction of organisms that use estuaries, from phytoplankton to fish (Gillanders et al. 2011; Thomas et al. 2016). For example, elevated water temperatures will facilitate longer periods of growth of the Western school prawn (*Metapenaeus dalli*) and Blue swimmer crab (*Portunus armatus*) in SWA estuaries and enhanced recruitment of warm-temperate marine fishes (Online Resource 6). However, warming will negatively impact the physiology and performance of species that are close to their thermal maximum, particularly during their germination or larval stages (Andrews et al. 2014; Crisp et al. 2017; Madeira et al. 2016), and elevated temperatures may negatively impact the recruitment of cool-temperate marine fish. Mortality of seagrass associated with high temperatures has been observed in the Swan-Canning Estuary (Hoffle et al. 2012), and phytoplankton are predicted to exhibit a strong negative response to temperatures > 27 °C (Fig. 2; Online Resource 2).

Whilst metabolic demand increases with water temperature, warmer, saltier waters also hold less oxygen. Any decrease in oxygen availability, and particularly to an extent that results in environmental hypoxia, will potentially cause stress to biota. Hypoxia is a key stressor in many SWA estuaries, and particularly for benthic habitats. For example, sediment anoxia and associated sulfide intrusion are a major stressor of rooted macrophytes and infaunal communities (Online Resources 4 and 5). Hypoxia induces molecular stress responses that cascade through biochemistry and physiology to ultimately impact metabolism, behaviour and scope for growth/reproduction (Wu 2002; Spicer 2016). These effects vary markedly among taxa (Riedel et al. 2016) and will be greatest

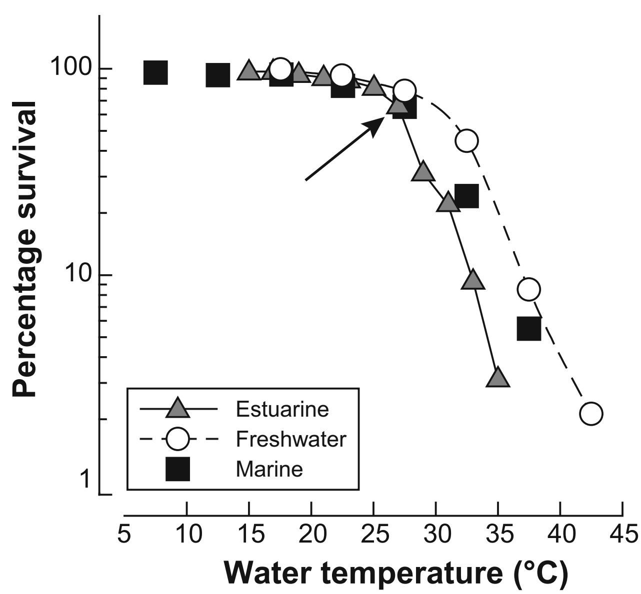

Fig. 2 Percent surviving from > 200 species and 439 strains of phytoplankton at different temperatures and from three different habitats (based on the analysis of data in Supplement, Appendix 2, of Thomas et al. 2016). Arrow highlights the marked decrease in survival at temperatures exceeding 27 °C

for species at their thermal tolerance limits (Koehn et al. 2011), particularly under increasingly frequent and extreme maximal water temperatures.

Rising salinities will place species that are close to their upper salinity limits under greater osmoregulatory stress, potentially altering their metabolism, activity, growth, spawning and development (Smyth and Elliott 2016; Whitfield 2015; Online Resources 2, 3, 4, 5 and 6). For example, most freshwater fish species, which lack chloride cells in their gill epithelia, will be unable to tolerate rising salinities (Whitfield 2015). If salinities exceed an organism's biological tolerance, mass mortalities may result. In the NC Culham Inlet (Online Resource 1) in 2001, hypersaline conditions (~ 85) caused the death of an estimated 1.3 million Black bream (Hoeksema et al. 2006).

Effects of estuarine acidification are less well understood, particularly for phytoplankton (Online Resource 2), but are likely to vary greatly among taxa (Sokolova et al. 2016). Decreasing pH will likely have positive effects on growth of seagrasses and fleshy macroalgae, but negative impacts on calcareous macroalgae (Online Resource 4). Invertebrate taxa exhibit widely varying responses to acidification, with recent studies documenting resistance to negative impacts among key groups (Online Resource 5). Impacts on fish are likely to be indirect given the relatively high tolerance of estuarine species to changes in water chemistry (Booth et al. 2011), for example, via a reduced ability of diadromous fish to detect and respond to olfactory cues from estuaries, and widespread trophic impacts associated with any disruption of calcification and subsequent loss from the diet of potential prey items including molluscs and diatoms (Gillanders et al. 2011).

Climate change will have both negative and positive effects on the survival, abundance, distribution and community composition of estuarine flora and fauna across SWA. However, in many cases, we do not know the environmental optima or physiological tolerance ranges of the flora and fauna of this region, and much work is needed to enable specific predictions of their responses to climate change. The potentially synergistic effects of interacting stressors represent a further significant gap in our understanding of climate change impacts (Brown et al. 2013a). For example, acidification may narrow the thermal tolerances of marine invertebrates (Whiteley and Mackenzie 2016), and elevated temperatures can decrease the survival times of marine benthos during hypoxic events by up to 74% (Vaquer-Sunyer and Duarte 2011). In such cases, the costs of responding to one stressor may compromise an organism's ability to cope with an additional stressor, increasing the allostatic load on the organism and impacting its fitness (Schulte 2014).

Effects on phenology

Understanding of phenological responses to climate change varies widely among both geographic regions and taxa (e.g. Gallinat et al. 2015; Ovaskainen et al. 2013; Poloczanska et al. 2013). Relatively little is known regarding the phenology of estuarine organisms (Testa et al. 2016), particularly in the southern hemisphere (Beaumont et al. 2015). This represents a significant research gap that must be addressed to enable robust predictions of future climate change effects on the ecology of SWA and other Mediterranean climate regions. Nonetheless, some future changes to estuarine phenology are likely, based on extrapolation of observed trends.

The seasonality of SWA rainfall has already shifted, with autumn and winter becoming significantly drier, and the trend of a southerly contraction in the SWA Mediterranean climate region is forecast to continue (Klausmeyer and Shaw 2009). Changes in temperatures and the timing of rainfall and river flows are expected to stimulate phenological shifts among estuarine flora and fauna. Typical 'summer' conditions, i.e. low freshwater flows coincident with high temperatures, insolation and evaporation (Hope et al. 2015a), will develop earlier and be maintained longer into autumn. Earlier springs and longer summers alter the timing of spawning, larval release and the movements of marine organisms (Poloczanska et al. 2013), and similar responses are likely in estuaries. For example, less frequent freshwater pulses may reduce the cues and hence success of macrophyte germination (Kim et al. 2013; Stafford-Bell et al. 2016). Extended periods of elevated salinities will influence the seasonal succession of phytoplankton (Online Resources 2 and 3) and the timing of reproduction and recruitment among invertebrates and fishes (Online Resources 5 and 6).

Effects on abundance and distribution

Freshwater flows exert significant influence on the abundance and distribution of estuarine biota via their effects on water column stratification, residence time, nutrient concentrations and turbidity, which in turn control estuarine productivity and the availability of suitable environmental conditions and habitats (Cloern et al. 2014). River flow is the dominant driver of phytoplankton biomass in the PO Swan-Canning Estuary (Chan and Hamilton 2001), and chlorophyll *a* increases in the upper reaches of this system during dry winters (Thompson et al. 2015). Continuing declines in freshwater flows across SWA will increase water residence times and nutrient retention in estuaries, whilst summer storms are predicted to increase allochthonous nutrient delivery (Fig. 1). These changes will likely increase phytoplankton biomass, with potential effects on secondary production via trophic cascades.

Biotic responses to reduced freshwater flows will vary markedly among estuaries of different types (i.e. PO, IO, SO, NC), reflecting the effects of local flow regimes on estuarine connectivity, habitat availability and environmental conditions, and how these in turn influence the distributions, reproduction and recruitment of various taxa (Online Resources 2, 3, 4, 5 and 6). The loss or contraction of particular habitats due to climate change will alter the abundance and distribution of fauna with strong affinities for those habitats. For example, changes in the distribution and biomass of seagrass and macrophytes will impact vegetation-associated fishes (Online Resource 6). Declines in the abundances of such fish species coincided with a marked decrease in macroalgal growth in the Peel-Harvey Estuary following the construction of an artificial opening designed to improve tidal flushing of that highly eutrophic system (Young and Potter 2003a, b). More broadly, the abundance and distribution of biota will be influenced by the degree to which prevailing abiotic conditions align with their environmental tolerances. Declining freshwater flows across SWA have already led to increasingly saline conditions in SWA estuaries, causing the distribution of freshwater fish species to contract upstream and allowing more marine species to penetrate further into estuaries and remain there for longer periods (Potter et al. 2016; Valesini et al. 2017). Similarly, shifts in the distributions of seagrass species have been observed in SWA estuaries as saline waters penetrate further upstream (Online Resource 4).

At a regional scale, poleward range extensions will occur among tropical and sub-tropical species of flora and fauna (Booth et al. 2011; Hyndes et al. 2016) as warming marine waters enable some species to overcome overwintering bottlenecks (Figueira and Booth 2010) and move between estuaries. For example, the (sub)tropical atherinids *Craterocephalus mugiloides* and *Atherinomorus vaigiensis* colonised and became abundant in the Leschenault Estuary between 1994 and 2008–2010 (Veale et al. 2014) and have since further extended their distribution southward to the Vasse-Wonnerup system (Online Resource 1). Similar range extensions have been documented among tropical crab species, with Mud crabs (*Scylla serrata*) and Coral crabs (*Charbydis ferriata*) reaching the temperate Swan-Canning Estuary following a period of elevated water temperatures in 2010/2011 (Caputi et al. 2014). Increasing temperatures will thus lead to a progressive 'tropicalisation' of estuarine biota (James et al. 2013), mirroring the process that is occurring in the marine environment of WA (Cheung et al. 2012).

Effects on community structure

The aforementioned effects of climate change on biological performance, abundance, distribution and phenology will combine to modify the structure of floral and faunal communities in SWA estuaries. Changing abiotic conditions will act as environmental filters when they exceed the tolerances of organisms, playing a direct role in controlling community assembly and disassembly (Kraft et al. 2015). More subtly, changing environmental conditions will also influence the biological interactions among species, e.g. elevated water temperatures may favour faster-growing macroalgae over seagrasses, and increased stratification will enable dinoflagellates to outcompete less motile phytoplankton taxa (Online Resources 2, 3 and 4). For higher taxa, effects of climate change stressors on biotic habitats such as macrophytes are likely to be important, given that they not only provide physical structure but also affect ecosystem productivity and physicochemical variables such as turbidity and oxygen concentrations (Morgan et al. 2016), which in turn influence community assembly.

Community-level responses to freshwater inputs will be context dependent, differing among species and in relation to the characteristics of each estuary and the timing and magnitude of flows (Whitfield 2005; Dolbeth et al. 2010; Gillson 2011). Marinisation may increase the species richness and taxonomic diversity of estuarine faunal communities, particularly in PO systems, due to enhanced estuarine use by marine taxa, whereas freshwater species will become less prevalent as their distributions contract upstream (Online Resources 5 and 6). However, decreasing river flows will cause more periodically open SWA estuaries to remain closed for longer periods. This will reduce the extent to which marine taxa can access and use these systems (Gillanders et al. 2011), thereby altering their community composition and reducing diversity (Online Resources 5 and 6).

Extreme environmental conditions will have increasing impacts on estuarine communities, the nature of which will reflect differences in environmental tolerances among species. For example, protracted periods of bottom-water hypoxia cause marked shifts in the composition of benthic macroinvertebrate communities in SWA estuaries. Responses include decreases in species richness, diversity and the abundances of more sensitive taxa such as small crustaceans, with the remaining assemblage comprising predominantly small-bodied annelids (Tweedley et al. 2016a). Similarly, increasing hypersalinity will have negative effects on biological communities, leading to e.g. reduced phytoplankton biodiversity, with a likely increase in the proportion of cyanobacteria but vastly fewer species across the other major taxonomic groups (Online Resources 2 and 3). Extreme hypersalinity will cause mass mortalities of flora and fauna (Hoeksema et al. 2006; Kim et al. 2013) and the dramatic simplification of community structure and composition (Veale et al. 2014; Dittmann et al. 2015).

Water column stratification and microalgal blooms exert significant influence over environmental conditions—particularly DO concentrations—and the ecology of faunal communities in many SWA estuaries. Ongoing declines in river flows across SWA will encourage increased stratification, lower DO, longer water residence times and increased nutrient retention in estuaries (Thompson et al. 2015; Tweedley et al. 2016b). Such conditions will favour vertically migrating dinoflagellates (Horner Rosser and Thompson 2001; Jephson et al.

2011) and other bloom-forming phytoplankton (Online Resource 2). Future effects of climate change on stratification and algal blooms are difficult to predict and will be strongly influenced by the timing and magnitude of river flows and the geomorphology of each particular estuary-catchment system. However, any increase in the prevalence or severity of hypoxia/anoxia, associated with greater stratification and/or microalgal blooms, would significantly impact the behaviour and biological performance of estuarine fauna. In the Swan-Canning Estuary, for example, stratification-induced hypoxia and algal blooms have dramatic effects on fish movements, abundance and community composition, and reduce the ecological health of the system (Hallett et al. 2016a).

Knowledge gaps and uncertainties

As detailed above and summarised in Fig. 3, climate change will alter environmental stressors and thereby impact the flora and fauna of permanently and periodically open estuaries in SWA, at levels of biological organisation from molecules to communities.

We acknowledge that ecological responses to climate change will be more complicated than we can currently envisage, including unforeseen impacts of disease (Altizer et al. 2013) and the complex, indirect effects of altered phytoplankton and macroalgal blooms (Hallett et al. 2016a; Hoffle et al. 2012). Indeed, this review highlights key gaps in our understanding of SWA estuaries and the likely impacts of climate change on their biota. Most notably, our understanding of the biology of many estuarine species, including their environmental tolerances, is relatively poor. This is particularly true for species that are commercially unimportant. Moreover, we have limited understanding of the ecological interactions, including competitive and trophic relationships, among estuarine biota. Together, these factors preclude more specific predictions of ecological responses to climate change and inhibit our ability to implement directed adaptation measures (e.g. Hobday and Pecl 2014; Pratchett et al. 2017; see "Possible adaptation responses" section). Another significant gap concerns the potentially synergistic effects of interacting stressors on estuarine ecology. For example, changes in stratification and hypoxia may reduce the suitability of deeper habitats as thermal refugia for fish, and increased hypoxia will enhance ammonia release from sediments, exacerbating the physiological stressors to which organisms are exposed (Middelburg and Levin 2009).

However, it is important to note that the rivers and estuaries of SWA, like those of other Mediterranean climate regions, are characterised by highly variable flows to which their fauna are adapted. Aquatic environments with high variability tend to be dominated by generalist and/or *r*-selected species that can exploit a wide array of resources and tolerate changing environmental conditions (Ficke et al. 2007; Steffen et al. 2009). The evolutionary adaptation of the estuarine biota of SWA to variable environmental conditions may confer a degree of resilience to the impacts of climate change, although the rate and magnitude of future change (and particularly the range of associated extreme conditions) may exceed the adaptive capacity of species (Morrongiello et al. 2011).

The future of Mediterranean climate estuaries

The Mediterranean climate region of SWA is a climate change hotspot that is predicted to become considerably drier and warmer in coming decades. Effects of climate change on the environments, habitats and biota of estuaries across SWA (Fig. 3) provide insights into the future impacts of climate change in other comparable regions. These impacts will have significant repercussions for the human uses and benefits that estuaries provide, and will require potentially complex and costly adaptation responses if maintaining these environments is a societal objective.

Global context

Several of the trends and impacts described for SWA are evident in other Mediterranean climate regions. Widespread increases in SST and more frequent marine heatwaves are driving the tropicalisation of temperate marine ecosystems worldwide as (sub)tropical species extend their ranges into higher latitudes, the consequences of which can include ecological regime shifts and significant fisheries impacts (Vergés et al. 2014; Wernberg et al. 2016). Similar climate-driven range extensions have also been documented among the estuaries of Mediterranean climate regions in South Africa (James et al. 2013; Potts et al. 2015; Whitfield et al. 2016) and Europe (Nicolas et al. 2011; Baptista et al. 2015).

Combined warming and drying are driving the marinisation of estuarine ecosystems across southern Europe (Chaalali et al. 2013; Chevillot et al. 2016; Pasquaud et al. 2012; González-Ortegón et al. 2015). Moreover, Chevillot et al. (2017) recently documented the earlier onset of 'spring' conditions in the Gironde Estuary, France, in response to warming temperatures and altered river flows, highlighting the potential ecological implications of the resulting phenological mismatch in abundances of key fish species and their zooplankton prey. Increasing salinity regimes are also an increasingly important driver of ecological changes among estuaries of South Africa (James et al. 2013) and South Australia (Zampatti et al. 2010). Californian estuaries such as San Francisco Bay will experience similar trends to those in SWA, i.e. increased water temperature, elevated salinity and sea level, and decreased precipitation and river flows (Cloern et al. 2011; Feyrer et al. 2015), leading to significant impacts on their ecology (Brown et al. 2013b; Lehman et al. 2013).

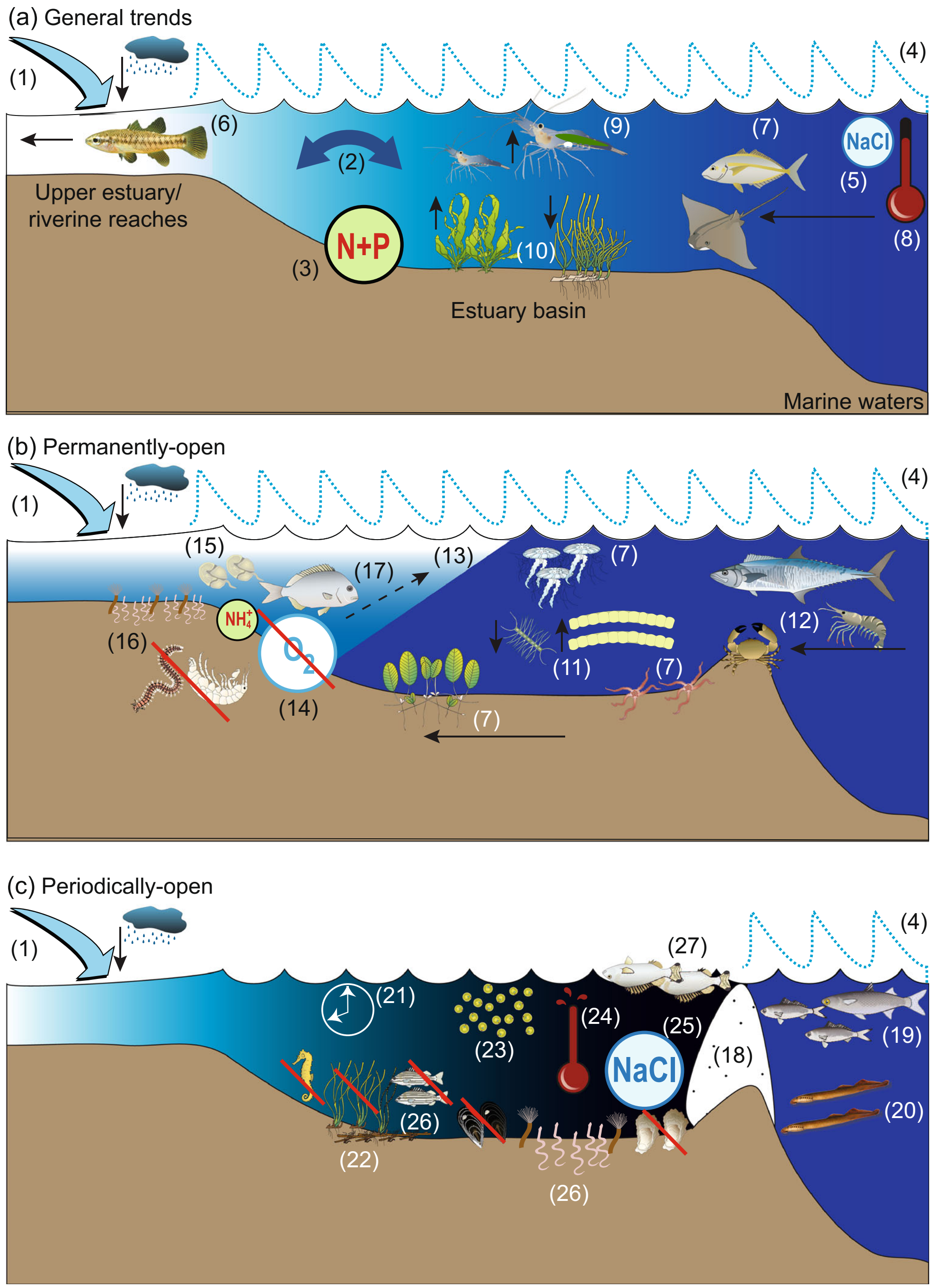

Fig. 3 Conceptual summary of predicted environmental and ecological impacts of climate change on estuaries of south-western Australia. (Images courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science [ian.umces.edu/symbols/]). **a** Across estuaries in general, (1) declining rainfall ➔ (leads to) decreased freshwater flows ➔ (2) reduced riverine flushing of estuaries ➔ (3) increased retention and internal nutrient cycling. (4) Increased sea level and storm surge ➔ (5) enhanced marine influence and increased salinities ➔ (6) upstream contraction of freshwater species distributions and (7) expanded marine species distributions. (8) Increasing water temperatures ➔ (9) increased growth of ectotherms and (10) growth of macroalgae is favoured over seagrasses. **b** In permanently open estuaries, (1) decreased freshwater flows ➔ marinisation ➔ (7) greater penetration of marine species and (11) salinity-induced shifts in community structure. Increasing water temperatures ➔ (12) range extensions of tropical species. Declining flows also cause (13) increased stratification in middle-upper estuary ➔ (14) increased hypoxia ➔ (15) shift in phytoplankton community composition, e.g. greater dominance by dinoflagellates, (16) simplification of infaunal communities and (17) emigration of mobile fish species to refuge areas. **c** In periodically open estuaries, (1) decreased freshwater flows ➔ (18) protracted closure of entrance by sand bars ➔ impedes (19) entry of marine species and (20) migration of diadromous species. Increased temperatures, salinities and (21) water residence time ➔ (22) loss of macrophytes and (23) altered phytoplankton community composition. (24) More extreme water temperatures and (25) hypersalinity ➔ (26) simplification of communities and (27) mass mortalities

Decreased precipitation and river flows are also prolonging the closure of periodically open estuaries in several Mediterranean climate regions, influencing their faunal richness and diversity (James et al. 2013; Pasquaud et al. 2015). In many cases, the extended closure of these estuaries increases their susceptibility to hypersalinity and/or hypoxia, potentially resulting in the extirpation of fauna (Collins and Melack 2014; Mikhailov and Isupova 2008; Wooldridge et al. 2016). Droughts are becoming more frequent and/or severe in many Mediterranean regions of the world (Diffenbaugh et al. 2015; Vicente-Serrano et al. 2014), and the extreme environmental conditions generated by these events are thus likely to play an increasing role in shaping estuarine ecology in these systems (e.g. Dittmann et al. 2015; Lehman et al. 2017). This is particularly true in regions such as California and South Australia, where societal demands for water abstraction are high.

Climate change and other anthropogenic pressures

Estuaries worldwide are subjected to anthropogenic pressures including hydrological modification, habitat loss, chemical pollution and nutrient enrichment, overfishing and introduced species (Kennish 2002; Jennerjahn and Mitchell 2013). In many cases, climate change impacts on estuaries will be exacerbated by the synergistic effects of these anthropogenic pressures. Intensifying urbanisation will accelerate the delivery of nutrients and pollution to estuaries during extreme storm events (Beck and Birch 2012), and declining flows will increase the residence times, stratification and susceptibility of many estuaries to cultural eutrophication and harmful algal blooms (Rabalais et al. 2010). Furthermore, widespread loss of riparian vegetation will reduce shading, increasing the frequency and severity of extreme water temperatures; heightened effects of hypoxia will be seen in anthropogenically degraded, sulfidic sediments (Vaquer-Sunyer and Duarte 2010), and many pollutants will exhibit increased toxicity at higher temperatures (Ficke et al. 2007).

Perhaps most critically for estuaries in Mediterranean climate regions, the ecological effects of declining freshwater flows under a drying climate will be aggravated by increasing water extraction for human use (Vörösmarty et al. 2000). In South Australia, for example, upstream diversion of water in the Murray-Darling Basin magnifies the effects of drought in the Ramsar-listed estuary and wetlands of the Coorong, Lower Lakes and Murray Mouth (Kingsford et al. 2011). Similarly, the upstream consumption or diversion of 39% of unimpaired runoff to the San Francisco Bay Estuary has significant ecological impacts on biotic communities ranging from phytoplankton to fish (Cloern and Jassby 2012). The interaction of these pressures will have profound repercussions: climate change and human development will drive an increasingly rapid pace of change in estuaries (Cloern et al. 2016), shifting the baselines against which their health is measured and forcing us to reconsider how we use and manage them into the future (Duarte et al. 2013; Kopf et al. 2015).

Effects on ecosystem services and human populations

Ecosystem services, derived from the healthy functioning of ecosystem structure and processes, provide a host of direct and indirect societal benefits (Costanza et al. 1997; Barbier et al. 2011; Turner et al. 2015) which are commonly categorised as either provisioning (e.g. food), supporting (e.g. primary production), regulating (e.g. waste burial) or cultural (e.g. recreation) (Millennium Ecosystem Assessment 2005). Estuaries are widely recognised as among the most vital ecosystems globally for providing such services and benefits (Barbier et al. 2011; Wetz and Yoskowitz 2013).

The cumulative impacts of climate change on the ecosystem structure and processes of Mediterranean and more particularly SWA estuaries described in preceding subsections will naturally translate into differences in their ability to deliver ecosystem services and subsequent human benefits. However, as outlined below, such trends are likely to be complex, non-linear and spatially and temporally dependent (Wetz and Yoskowitz 2013; Pinto et al. 2014). For example, in the upper, deeper reaches of these systems and/or those that become closed to the sea, it may be expected that the various negative impacts on water and sediment quality resulting from reduced riverine flushing, increased stratification and warmer temperatures ("Effects of climate change on environmental conditions" section) will compromise delivery of many ecosystem services. In contrast, the lower reaches of PO systems will experience greater tidal flushing with rising sea levels, which could in turn improve habitat quality, area and/or diversity for marine species.

For obvious *provisioning* services such as targeted fish and shellfish stocks, the above-described effects in upper and/or periodically open Mediterranean estuaries have been well documented with respect to major mortality events (e.g. Hoeksema et al. 2006), chronic reductions in growth and productivity (e.g. Cottingham et al. 2014) and loss of nursery habitat (e.g. Hughes et al. 2015). Conversely, increased tidal incursions have been linked to improved fisheries in the lower-middle reaches of some estuaries, not only through greater marinisation and ocean connectivity, but also through accompanying increases in marine seagrass and mangrove habitats and their associated trophic and nursery functions (e.g. Boon et al. 2016). Changes in estuarine macrophyte habitats, either via progressive shifts from fresh/brackish water to marine species (e.g. Boon et al. 2016) or loss of biomass/diversity in response to greater salinisation, tidal inundation and sediment erosion expected with climate change (Craft et al. 2009; Grenfell et al. 2016), will in turn signal shifts in the ability of estuaries to deliver *supporting* ecosystem services such as primary production and nutrient cycling and *regulating* services such as natural flood protection and waste removal. The latter type of services also includes climate regulation (Heckbert et al. 2011), which occurs via processes such as carbon sequestration/release and evapotranspiration (Gattuso et al. 1998; Chen and Borges 2009; Heckbert et al. 2011; Duarte et al. 2013). Estuaries are typically sources of carbon dioxide and other greenhouse gases given their extensive biotic respiration and decomposition of organic matter, and these emissions are likely to increase under projected climate conditions such as warmer temperatures (enhancing decomposition), more frequent storms (increasing pulses of nutrients and organic matter) and increased hypoxia (influencing carbon dioxide flux at the air-water interface and biogeochemical processes such as denitrification) (Gattuso et al. 1998; Chen and Borges 2009; Heckbert et al. 2011). However, microtidal and highly stratified estuaries, common in SWA and other Mediterranean regions, can be net carbon sinks due to their long residence times and lack of mixing, which promotes carbon sedimentation (Chen and Borges 2009; Koné et al. 2009).

Several of the above ecosystem shifts anticipated with climate change will have obvious impacts on societal perceptions and thus *cultural services* provided by these estuarine environments, including recreation, aesthetic benefits and spiritual connection (Pinto et al. 2014; Boon et al. 2016). Many also have clear economic impacts via industry development and sustainability, including food production (e.g. Pinto et al. 2010; Hughes et al. 2015) and tourism (e.g. Pinto et al. 2010).

Much work is still required, however, to develop quantitative impact pathways that connect stressor effects, including both climate-related and other anthropogenic pressures, to estuarine ecosystem service delivery (Mach et al. 2015). This will be imperative for understanding how vital services might be impacted under anticipated future scenarios and improving adaptation responses to sustain the societal benefits they generate.

Possible adaptation responses

Adaptation responses implemented by humans are designed to decrease system vulnerability due to climate change (Adger et al. 2005). A common model of vulnerability (Hobday et al. 2016; IPCC—Intergovernmental Panel on Climate Change 2014) is defined by three components: exposure, sensitivity and adaptive capacity. Proactive or reactive adaptation actions can decrease the exposure to climate effects, decrease the sensitivity or increase the adaptive capacity of species (e.g. Alderman and Hobday 2016; Foden et al. 2013; Williams et al. 2008) but have received limited attention at a habitat scale (see Thresher et al. 2015). We describe a broad spectrum of options here for estuaries in Mediterranean climate regions, building on Sheaves et al. (2016), and noting that in many cases these options may not yet be technically, socially or legally possible. We also discuss the possibility of negative consequences from an intervention (maladaptation; Magnan et al. 2016) on other parts of estuarine systems or to the climate system in general. The outcomes and relative expense of proactive and reactive interventions could be investigated in simulation models, even if technical or legal barriers exist.

Firstly, *exposure* of estuaries in Mediterranean climate regions to reduced rainfall and increased salinity might be reduced by artificially increasing water flows, perhaps via cloud seeding, inflows from dam storages, or supplementation from artisanal bores. These adaptation options can be applied in a proactive fashion (e.g. riparian enhancement to increase shading and hence reduce water temperatures in upper estuarine reaches; Ghermandi et al. 2009) or reactive (e.g. artificial oxygenation to alleviate stratification-induced hypoxia; Hipsey et al. 2013). Options such as covering the surface of estuaries to reduce evaporation with flocculants or covers, as used at smaller scales on water storage dams on farms (Hassan et al. 2015), might interfere with a range of species that depend on estuaries, and represent a maladaptive response.

Developing adaptation options to decrease the *sensitivity* of estuarine systems to climate change—whereby they experience the warmer, drier conditions but are less affected—is more difficult. Options to remove introduced species, manage bar openings, reduce nutrients and mitigate algal blooms to lessen the stress on estuaries may reduce their sensitivity. Channel deepening, which will allow more water mixing and result in cooler water in deeper locations, may reduce the impact of atmospheric heating on these estuaries. This approach carries a risk of maladaptation, as deeper waters may become deoxygenated. Reactive strategies to reduce the sensitivity of estuarine systems following a climate-related extreme are also possible. Real-time monitoring and reporting to inform management of estuaries may offer benefits, such as facilitating risk-based decision-making for artificial mouth opening to prevent hypoxia (Twomey and Thompson 2001; Human et al. 2016). Finally, other options to reduce sensitivity may need to be implemented in the estuary catchment, such as measures to reduce nutrient inputs from both diffuse (e.g. agricultural) and point sources (e.g. septic tanks). For example, back-up generators could prevent the dumping of sewage into estuaries following storm-induced power failures at treatment plants, as occurred in the Swan-Canning Estuary in 2010.

Increasing *adaptive capacity*, to allow estuaries in Mediterranean climate regions to cope with increased temperatures and lower rainfall, is possible via protective measures that enhance natural processes. For example, a proactive strategy of maintaining natural water flows and decreasing water removals represents a robust approach to reducing vulnerability (Palmer et al. 2008). Similarly, ecosystem restoration is possible, and usually has few side effects, but must be implemented at a suitably large scale to be effective. These approaches can be difficult to implement in highly modified landscapes where there are competing demands for water, or modifications to geomorphology have occurred.

Overall, the need for adaptation is increasingly critical given the continuing failure to effectively address the causes and thus mitigate the effects of global warming. Loss of ecosystem services will mean that proactive adaptation is likely to be more cost-effective than reacting once impacts are established. To implement some of these options, new or revised governance frameworks across sectors may be needed, the establishment of which represents an additional adaptation challenge (Hallett et al. 2016c).

Conclusions

The natural features of estuaries in Mediterranean climate regions make these systems particularly vulnerable to long-term drying and warming trends. These features include their generally shallow nature, relative lack of tidal influence, significant seasonal and inter-annual hydrological variability and, in many cases, their periodic closure by sand bars. As a result, many such estuaries tend to be poorly flushed for much of the year, encouraging the retention of organic material and nutrients and the development of stratified conditions, algal blooms and environmental hypoxia. The interacting pressures of climate change and human development will profoundly affect the environments and ecology of estuaries in Mediterranean climate regions worldwide and the societies and ecosystem services that they support. The key challenge is determining how best to manage and adapt our use of these systems to make them less sensitive and more resilient to the effects of future pressures, including climatic extremes.

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