Macrobenthic invertebrates of the Coorong, Lower Lakes and Murray Mouth Ramsar Site: A Literature Review of Responses to Changing Environmental Conditions

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1. Executive Summary

- The Coorong, Lower Lakes and Murray Mouth (CLLAMM) region is listed as a wetland of international importance under the Ramsar Convention and recognised as an Icon Site under the Living Murray Initiative of the Murray-Darling Basin Authority. Yet over the past five years the region has been subject to a significant reduction in freshwater flows from the River Murray as a result of drought and the over allocation of water resources. The lack of freshwater flow across the barrages has led to a severe salinity increase in the Coorong and saltwater seepage into the Lower Lakes. This, coupled with lowered water levels in the Lower Lakes and the subsequent exposure of acid sulfate soils, has had a significant effect on the ecology of the region.

- Present and future management decisions need to consider how these changing environmental conditions will continue to affect the aquatic biota within the region. Macrobenthic invertebrates are important for food webs and productivity in estuaries, and can be used as bioindicators of certain environmental conditions and contamination loads.

- Significant changes in macroinvertebrate distributions have been observed since 2006, with many of the more salinity tolerant species now present in Lake Alexandrina following seawater intrusion. If salinities continue to increase throughout the lakes, they provide suitable habitats for many of estuarine macroinvertebrate species, while the distribution and abundance of freshwater species will decrease. In the Murray Mouth, salinity has increased to hypersaline conditions, and abundances and biomass of macroinvertebrates decreased substantially since the last water release in 2005.

- Benthic communities are regulated by a combination of interactions with environmental factors (salinity, temperature, nutrient availability and pH) and other biota (such as predation and competition). No factor or process can be seen in isolation, as responses to one factor can vary subject to the level of another. For example, tolerance to very low oxygen concentrations can vary in the presence of sulphide in the sediments, and pH can affect the toxicity of metals for macroinvertebrates. This complexity prevents the simple identification of thresholds for macroinvertebrate responses.

- The occurrence of acid sulfate soils means that acidification and the release of metals into water bodies is likely. While pH tolerance ranges for particular macroinvertebrate species in the CLLAMM regions are largely unknown, literature records on related species indicate that reduced growth rates and mortality starts at pH 7, with no macrobenthos able to exist in sediments with a pH <5. Thus, acidification will be very detrimental to the macroinvertebrates, with follow-on effects on their predators and lost ecosystem functions (e.g. bioturbation).

- Most benthic macroinvertebrates take up heavy metals released by acidification through the body wall or their diet, and can accumulate metals in contaminated sediment. As many macroinvertebrates are important prey for both birds and fish, bioaccumulation may lead to toxic effects in higher trophic levels.

- Knowledge gaps regarding macroinvertebrates within the CLLAMM region include tolerance ranges of the species and populations occurring in the region, recruitment and recolonisation potential in response to changing habitat conditions, and population connectivity to other estuaries. Furthermore, the benthic fauna in the sediments of the deeper parts of the CLLAMM region is largely unknown.
2. Introduction

Estuaries worldwide suffer from high levels of contamination from urbanisation or industrialisation, and habitat degradation and land reclamation is increasing, particularly as a result of population increases, manipulation of river flow and land use practices in the catchment (Wolff 1990, Wilson 2005, Valiela 2006, Cyrus et al. 2010). Despite such pressures, estuarine habitats contribute to ecosystem health (for example by trapping contaminants in sediment) whilst also providing nursery grounds for fish and feeding grounds for migratory birds (Raffaelli 1999, Elliot & McLusky 2002, Cyrus et al. 2010).

Macrobenthic invertebrates are important in estuarine and lagoon systems as they process a significant proportion of primary production, thus potentially reducing eutrophication, and provide vital food sources for crustaceans, fish and birds as well as human harvest (Rainer 1982, Boucher & Clavier 1990, Kalejta & Hockey 1991, Herman et al. 1999, Attrill et al. 2009, Lloret & Marin 2009).

Whilst providing such important ecosystem services, macrobenthic invertebrates can also be used as bioindicators of a defined set of environmental conditions, contaminant loads on the system, overall system health (Wilson 1994, Summers et al. 1997) or to predict effects of climate change (Hewitt & Thrush 2009).

The Coorong, Lower Lakes and Murray Mouth are a wetland of international significance for migratory birds (Phillips and Muller, 2006). Unlike some bird and fish species, no macrobenthic invertebrates are listed under the Ramsar Convention or the Environmental Protection and Biodiversity Conservation Act 1999. Nor are any macrobenthic invertebrates listed as species of National Environmental Significance. Therefore it is not possible to categorise macroinvertebrate species according to any of the above legislative schemes.

The current ecological state of the Coorong can be described as degraded (Lester & Fairweather 2009). In the 1930s, five barrages were built to prevent seawater intrusion into the freshwater environment of Lakes Alexandrina and Albert (Shuttleworth et al. 2005), creating a freshwater lake system with water levels elevated to between 0.5 and 0.8 m AHD (Australia Height Datum) (Phillips and Muller, 2006). Over allocation of water resources and water requirements of an increasing population coupled with a long-term drought have reduced mean flow through the Murray Mouth from an average of 12,233 GL year\(^{-1}\) to 4,733 GL year\(^{-1}\), and increased the incidents of no flow at the Murray Mouth from 1 % to 40 % of the time (Goss 2003, CSIRO 2008, Brookes et al. 2009), leading to sediment deposition at the Murray Mouth causing almost-complete closure in 1981 and 1999 (Walker 2002, Shuttleworth et al. 2005). A sand-pumping project began in October 2003 to maintain connectivity with the southern ocean and is currently ongoing.

The reduction of flows from the River Murray into the Lower Lakes has led to a drop in water levels, exposing large areas of Acid Sulfate Soils (ASS) which are a threat to the ecological health of the system (Powell & Martens 2005, Fitzpatrick et al. 2008). As water levels recede, surface soils may dry out, desiccate and crack, exposing deeper soils to air and drying. Such exposure of ASS leads to the oxidation of soil constituents, such as sulfide, which release acidity and cause significant decreases in pH (Simpson et al. 2008). Acid sulfate soils may contain sulphuric acid (sulfuric material), have the potential to form sulfuric acid (sulfidic material), cause deoxygenation (monosulfidic black ooze) or release contaminants when the sulfide materials are exposed to oxygen (Fitzpatrick et al. 2009).

Fitzpatrick et al. (2008) found that more than 70% of soil profiles investigated exceeded a moderate risk of acidification. Subsequent rewetting of dried and oxidised ASS may result in high concentrations of trace metals being dissolved and released into waterways (Cook et al. 2000, Green et al. 2006,
Nordmyr et al. 2008, Simpson et al. 2008). This review therefore includes considerations of pH tolerances and bioaccumulation of heavy metals.

One of the discussed remediation strategies to prevent further acidification is introducing seawater into the Lower Lakes. The bicarbonate and carbonate present in seawater provide a natural buffering capacity, and tidal exchange after floodgate opening can decrease acidity and improve water quality, with more stable improvements achieved by prolonged and frequent tidal exchange (Indraratna et al. 2002, Johnston et al. 2005). Restoration of tidal exchange has significantly increased pH in ASS of a trial section of Trinity Inlet, Queensland, indicating that marine tidal inundation may be a suitable remediation strategy (White et al. 1997, Johnston et al. 2009). Thus, this review is also looking at tolerances of estuarine macroinvertebrates towards changes in salinity and other water quality parameters.

The objectives of this literature review are to compile knowledge on the main drivers of macroinvertebrate distributions in estuaries and examine how macroinvertebrates in the CLLAMM region respond to changing environmental conditions. Invertebrate tolerances to salinity and pH were of particular interest. Knowledge gaps emerging during the review are also identified. The review concentrates on brackish and marine invertebrate fauna, yet includes some aspects of the freshwater bivalve *Velesunio ambiguous* found in the lakes. The information reviewed will contribute to further risk assessments by government agencies in their decision process for a strategy to solve the environmental problems of the Coorong, Lower Lakes and Murray Mouth. To assist this process, some conceptual models on the main interactions and processes are provided.

3. Underlying Drivers of Macrobenthic Invertebrate Communities in Estuaries

Macrobenthic invertebrate distributions are influenced by a combination of multiple biotic processes and abiotic factors operating on different scales (Snelgrove & Butman 1994, Thrush 1999, Widdows & Brinsley 2002, Ysebaert & Herman 2002, Dye 2006b, Mackay et al. 2010) as illustrated comprehensively in Appendix 1. Figure 1 provides a highly simplified representation of this information and aims to highlight the key drivers and stressors which impact macrobenthic invertebrate communities. Biotic processes include for example predation, competition and mutualism as well as life history processes, whilst physical factors include for example water depth, sediment characteristics (grain size, nutrient and metal load) and salinity. These factors and processes occur concurrently, but may affect different life stages of macroinvertebrates differently. The composition of a benthic community is hence the result of interactions happening over longer time periods (such as sediment characteristics, competitive interactions) as well as short-term (such as inundation, predation).

Subsequently, macrobenthic invertebrate distribution often exhibits high spatial variability, particularly with regards to salinity gradients in estuaries (Jones et al. 1986, Mannino & Montagna 1997, Ysebaert et al. 1998, Dittmann et al. 2006c, Mackay et al. 2010). Water inundation periods, driven by the combined effects of tides and wind, also determine macroinvertebrate survival, abundance and distribution (Hummel et al. 1986, Hummel et al. 1988, Forbes & Cyrus 1993, Millet & Guelorget 1994). The combination of longer exposure and higher temperatures increases mortality, in particular of smaller sized macroinvertebrates such as small polychaetes (Hummel et al. 1988). Anthropogenic activities causing pollution, habitat destruction or depletion of certain species by fisheries can affect both abiotic and biotic interactions in estuaries and thus modify the natural patterns of distribution and
community structure. This is included in the following overview on the various drivers of benthic community regulation.

![Simple conceptual model of drivers and stressors which impact macrobenthic invertebrates.](image)

**Figure 1** Simple conceptual model of drivers and stressors which impact macrobenthic invertebrates. Blue boxes indicate the hydrological drivers of the systems with stressors (biotic and abiotic) in yellow boxes. The hydrological drivers act on each of the stressors. The green hexagons illustrate the different biotic groups that interact with the invertebrate communities. Lines connecting shapes indicate some type of interaction between the biota. The large circle illustrates that the stressors are operating within the hydrological environment and are interrelated. The dotted lines differentiate those processes or biological associations that operate primarily within, but are not limited to, the sediment of the ecosystem and the water column.
3.1 Abiotic factors

Within estuaries, the interface of marine and freshwater drives the dynamic nature of abiotic variables such as salinity and sediment characteristics, resulting in highly variable patterns of species diversity and abundances within and between transition zones (Attrill & Rundle 2002, Dye 2006a, Gilberto et al. 2007). Macrobenthic assemblages can frequently be classified into three separate communities along the estuarine salinity gradient: a marine community in the polyhaline zone; a brackish community in the mesohaline zone; a third community in the oligohaline and freshwater zones (Mannino & Montagna 1997, Ysebaert et al. 1998, Gilberto et al. 2007). Within these zones, species’ distributions are not static as the zonal boundaries fluctuate in time and space, particularly within the mesohaline and oligohaline zones (Chapman & Brinkhurst 1981, Ysebaert et al. 1998, Ysebaert & Herman 2002). However, the rate and magnitude of a salinity change may be a more important factor than the salinity gradient itself in driving macrobenthic invertebrate community composition (Sanders et al. 1965).

Salinity as well as recruitment patterns and species' survival are reliant on whether the entrance of the estuary is open or intermittently closed (Matthews & Fairweather 2003, Hirst 2004, Dye 2006a, Hastie & Smith 2006, Matthews 2006) and on the level of freshwater flow into the estuary (Forbes & Cyrus 1993, Attrill et al. 1996, Attrill & Power 2000, Gordon 2000, Kanandjembo et al. 2001). Estuarine fauna is thus dependent on the size and ecological state of the catchment and the connectivity between catchment and the ocean (Edgar & Barrett 2000, Hastie & Smith 2006, Valiela 2006). Comparing intermittent estuaries with permanently open estuaries revealed that elevated salinities favoured an increase in marine fauna and a simultaneous decline in some non-marine species (Teske & Wooldridge 2001, Dye & Barros 2005, Hastie & Smith 2006). In estuaries where physiochemical and morphological characteristics vary widely, the benthic macroinvertebrate fauna is frequently dominated by very few species (Kanandjembo et al. 2001, Currie & Small 2005). A reduced tidal gradient, such as caused by the construction of a storm-surge barrier, has been shown to affect particularly those amphipods and polychaetes (Nephtyidae) living in the upper and lower tidal zones respectively (van der Meer 1999). Physical barriers restrict movement, tidal exchange, and change habitat characteristics, thus leading to different communities (Ritter et al. 2008). Geomorphological changes to estuaries and inhibition of connectivity to either the catchment or the sea are thus causing major disturbances for the ecosystem and the macroinvertebrates within.

Seasonal changes in estuarine hydrology can greatly affect the dominant macrofauna (Kalejta & Hockey 1991, Kanandjembo et al. 2001), with changes in biomass being more pronounced than changes in community composition (Rozas et al. 2005). Low freshwater inputs can have detrimental effects on the macrobenthic community structure (Attrill et al. 1996, Attrill & Power 2000), and drought may cause severe and long term effects on aquatic invertebrate species, resulting in limited gene flow and dispersal causing population bottlenecks (Humphries & Baldwin 2003). Low water flow also prevents movements of invertebrates and fishes between the estuarine and upstream sections of the river (Flannery et al. 2002). In the St Lucia estuary, South Africa, low flow periods during a drought led to distinct macrobenthic invertebrate communities existing between regions and habitats, as restricted planktonic exchange and thus limited larval dispersal prevent connectivity between physically separated habitats (Pillay & Perissinotto 2008).

Although organic content, microbial content, food supply and trophic interactions, as well as sediment grain size, affect species distributions, no single parameter has been shown to explain patterns of infaunal species across many different environments (Jones et al. 1986, Snelgrove & Butman 1994). It is the combination of salinity and various sediment parameters, including mud content, organic matter, chlorophyll-a, water levels and redox-profile, nutrient concentrations and pH that determines spatial

For estuaries, the nutrient loads carried by rivers are vital, with some rivers contributing up to 95% of an estuary’s nitrogen load (Raffaelli 1999). Yet, discharges from urban or industrial sources frequently have elevated levels of nutrient and organic content in coastal waters and sediments to above natural levels. This can create an unbalanced ecosystem with high environmental stress and defined macrobenthic response (Pearson & Rosenberg 1978, Heip 1995). The effects of elevated nutrients, in particular as a result of sewage disposal, on marine populations have been studied world-wide, supporting the model by Pearson & Rosenberg (1978) (Reish 1986, Tsutsumi 1990, Morris & Keough 2001, 2002, Bishop et al. 2006).

Pearson & Rosenberg (1978) showed that along a gradient away from the source of organic enrichment, the benthic community changes from (a) species poor with few individuals as environmental conditions are intolerable; to (b) species poor but high abundance of small-sized opportunistic macroinvertebrates, such as Capitella, tolerant of anaerobic conditions (Tsutsumi 1990, Morris & Keough 2002, Norkko et al. 2006); and finally (c), a species-rich community of larger sized macroinvertebrates constituting higher biomass and dwelling deeper into the sediment layers (Pearson & Rosenberg 1978). Yet, macroinvertebrates also respond to environmental changes induced by further factors such as turbidity, regional rainfall, freshwater inflow and chlorophyll a concentrations (Currie & Small 2005, 2006). Thus, in estuaries the ecological effects of excessive nutrient levels are often difficult to distinguish against the normally high variability and dynamic nature of environmental conditions, and eutrophication effects are often only recognised towards the end-point of the process when changes are obvious and dramatic (Raffaelli 1999).

Hypoxic conditions, which can occur for example after severe eutrophication events, impact on macroinvertebrates, which has been shown to be species-specific and subject to the physiological tolerance to hypoxia (Diaz & Rosenberg 1995, Montagna & Ritter 2006). Organic enrichment can lead to dystrophic situations in lagoons, exceeding even the tolerances of opportunistic macroinvertebrates (Grizzle 1984, Lardicci et al. 1997). Yet, the responses of macroinvertebrates to changing environmental conditions can be inconsistent, and understanding benthic distribution patterns needs to include linkages between physical and ecological processes (Dye 2006b).

### 3.2 Biotic Interactions

Predation, competition and mutualistic relationships, individually and collectively, influence macrobenthic invertebrate communities in soft sediment environments (Peterson 1979, Reise 1985, 2002). In soft-sediments, competitive interactions are not as important as on rocky shores, where resources like space are limited (Black & Peterson 1988, Peterson 1991). Instead, positive interactions modulated by biogenic structures enhancing the microhabitat use are much more prominent in soft sediments, where larger ecosystem engineers often constitute particular associated faunal assemblages (Reise 2002). Bioturbation by burrowing infauna further contributes to the flux of dissolved nutrients over the sediment/water interface, fuelling the productivity in estuarine systems (Lohrer et al. 2004).

Three general categories of predators are recognised in soft sediment habitats: epibenthic predators (e.g. birds, fish), infaunal predators (e.g. polychaete worms, nemerteans) and sub-lethal browsers (e.g. fish feeding on bivalve siphons or polychaete appendages). Each of these exert different pressures on macrobenthic organisms, but all predators potentially reduce macrobenthic densities and thus affect the structure and dynamics of benthic communities (Thrush 1999). Predator diversity has
also been shown to enhance the secondary production and decrease the likelihood of trophic cascades (O'Gorman et al. 2008).

Most attempts to assess predation pressures on soft-sediment communities have involved the exclusion of predators using cages, allowing comparisons with unmanipulated areas. However, cages can affect currents, sedimentation rates and phytoplankton supply, thus producing artefacts that limit the application of results (Hulberg & Oliver 1979, Wilson 1991, Thrush 1999). Furthermore, many investigations to assess the effect of predation on macroinvertebrates using exclusion experiments are based on relatively modest sample sizes and small experimental areas. As such, the full effects of predation on benthic communities are difficult to assess in field experiments (Rosa et al. 2008). For example, Rosa et al. (2008) found that fish and bird predation had significant effects on prey density, but they were unable to dismiss the possibility that exclusion cages themselves had favoured polychaete populations.

### 3.3 Recruitment and colonisation

Seasonal variability in macrofaunal densities is also related to recruitment dynamics (Millet & Guelorget 1994, Qian & Chia 1994, Strasser et al. 2001). Life history processes are not only essential for recruitment, but larvae and juveniles constitute the more mobile life stages able for dispersal and colonisation (Smith & Brumsickle 1989, Günter 1992, Whitlatch et al. 1998). Life history traits and dispersal abilities are thus essential for recovery processes (Thrush & Whitlatch 2001, van Colen et al. 2008) and the resilience of benthic communities in intertidal ecosystems has been shown to depend on the recruitment and dispersal of the macroinvertebrates (Dittmann et al. 1999, Grimm et al. 1999, Thrush et al. 2009).

In estuaries which can be periodically closed, populations inside the estuary and lagoon may become disconnected from source populations outside the particular system, unless they are self-recruiting (Mackay et al. 2010). Colonisation of different regions within an estuary is also dependent on the salinity tolerances of larvae (Bochert et al. 1996). Recruitment is subject to processes affecting pre- and post settlement life stages, which includes various abiotic factors as well as biotic processes (Olafsson et al. 1994, Archambault & Bourget 1999). Larvae of the opportunistic polychaete Capitella, which dominates organically enriched sediments, were not attracted to higher hydrogen sulphide concentrations, yet may be more tolerant to higher sulphide and hypoxic conditions than larvae and adults of other benthic species (Dubilier 1988). Sediment properties alone are thus not sufficient to explain benthic recolonisation or distribution patterns, as different species respond differently and the colonising benthos itself can modify the sediment (Wu & Shin 1997, Montserrat et al. 2008).

Yet, succession in a tidal mudflat is a dynamic process and not only determined by life history traits, but also by resource availability, temporal variation and the bio-engineering capacities of colonising species (Zajac et al. 1998, Beukema et al. 1999, Rosenberg 2001). Seasonal variability in the availability of larvae may cause varied responses to disturbances (Zajac 1991). Furthermore, whether colonisation can take place and the course of recovery are determined by the scale and frequency of a disturbance (Norkko et al. 2006). Frequent salinity disturbances in particular interfere with the succession of macrobenthos to a more mature community (Ritter et al. 2005). If areas in an estuary have been affected by hypoxia and organic enrichment, colonisation occurs if species tolerant to such conditions occur in nearby unaffected areas and have the dispersal means and life history strategies to reach and establish populations in the previously defaunated areas (Boltt 1975, Gamenick et al. 1996)
4. Temporal and Spatial Distribution of Macroinvertebrates in the CLLAMM Region

No historic data are available on macroinvertebrate fauna prior to construction of the barrages in the Murray Mouth, and the first benthic studies in the Coorong were carried out in the 1980s (Geddes & Butler 1984, Kangas & Geddes 1984). The more recent macrobenthic invertebrate studies in the Murray Mouth and Coorong focussed on effects of water release, annual condition monitoring (Geddes 2003, 2005a, b, c, Dittmann et al. 2006a, Dittmann et al. 2006b, Dittmann et al. 2006c, Dittmann & Nelson 2007, Dittmann et al. 2008a) and the recent CLLAMMecology research cluster (Rolston & Dittmann 2009). The modified hydrodynamics led to a loss of the estuarine character of the CLLAMM region, affecting all ecosystem components including benthic invertebrates. The deterioration of the Murray Mouth and Coorong lagoons in the past five years has been reflected in a decline of macrobenthic abundances and a changed community structure (Baring et al. 2009), corroborating the suitability of macroinvertebrates to assess the health of an estuarine ecosystem (Wilson 1994).

In 1982 no outflow occurred over the barrages, and salinities reached a maximum of 80 g/ml (ppt) at the southerly sites of the North Lagoon, and ranged between 90-100 g/ml (ppt) in the South Lagoon (Geddes & Butler 1984). Compared to the historical record, Geddes & Butler (1984) state that the system was in an extremely hypermarine phase given the long term salinity fluctuations of the Coorong. Many common estuarine macroinvertebrate species were absent and the low diversity of the Coorong was suggested to reflect the extreme salinity fluctuations in the lagoon. The salinity gradient from the North Lagoon into the South Lagoon was driving the species distribution in the system, with the infaunal community changing from an estuarine assemblage to one dominated by halophytic dipterans and salt-lake crustaceans once salinities increased above 70 g/ml (ppt) (Geddes & Butler 1984). In comparison with other estuaries, only three common species of amphipods occurred in the Coorong and their distributions were restricted to salinities less than 53 g/ml (ppt) (Kangas & Geddes 1984).

Following the reduced flows of the River Murray in 1982 (Geddes & Butler 1984), Geddes (1987) investigated the effects of above average flow in the River Murray in 1983-84 on the salinity and distribution of biota in the Coorong lagoons. By mid-1984, salinities were brackish (< 30 g/ml (ppt)) in the North Lagoon and moderately hypermarine in the South Lagoon (55-70 g/ml (ppt)). The distribution of the estuarine macrofaunal assemblage reached to the southern end of the North Lagoon, although species richness remained low and only two previously uncollected species were found. The South Lagoon, however, continued to be dominated by species tolerant to higher salinities, such as halophytic diptera, despite salinity being within the tolerance range of many estuarine species during winter-spring of 1984 (Geddes 1987). Following the closure of the barrages in 1984, salinities increased quickly to 36-70 g/ml (ppt) in the North Lagoon, and 80-140 g/ml (ppt) in the South Lagoon by March 1985, leading Geddes (1987) to suggest that high River Murray flows are needed to maintain an estuarine-marine system in the North Lagoon, and moderately hypermarine salinities in the South Lagoon.

Little further work was conducted on the macrobenthic fauna of the Coorong until an ecological survey at eleven sites from Ewe Island in the Murray Mouth to Salt Creek in the Coorong, following a period of extended closure of the barrages as a result of low flows of the River Murray (Geddes 2003). In the high salinities (80-90 g/ml (ppt)) of the South Lagoon, chironomid larvae were the only macroinvertebrates present albeit in low numbers, and estuarine-lagoonal macroinvertebrates were only collected in the Murray Mouth and northern part of the North Lagoon (Geddes 2003). Almost all
the macroinvertebrate species recorded by previous studies (Geddes & Butler 1984, Kangas & Geddes 1984, Geddes 1987) were found again by Geddes (2003), but their distributions and abundances were more restricted.

A managed barrage release in September-October 2003 aimed to flush and reduce salinities near Goolwa, provide freshwater flows to the Goolwa and Coorong channels, assist in flushing the Murray Mouth and provide mixing of freshwater southwards from Pelican Point into the Coorong Lagoons (Geddes 2005a). Prior to this release in September 2003, the barrages had been closed continuously since December 2001 - then the longest barrage closure since 1981. The outflow created estuarine salinities in the Murray Mouth and part of the North Lagoon, yet there was no substantial response in distribution and abundance of estuarine-lagoonal macroinvertebrates. Geddes (2005a) suggested that water releases of 280 GL can only produce limited spatial and temporal environmental benefits. Further small barrage releases in 2004 (40 GL) and 2005 (70 GL via Ewe Island Barrage and 52 GL via Boundary Creek gate), although improving freshwater, turbidity, phytoplankton and zooplankton in the system (Geddes 2005c), had little effect on the macrobenthic invertebrate communities close to the water releases (Dittmann et al. 2006b). With no further water release since 2005, macroinvertebrate abundances continuously decreased in the Murray Mouth (Baring et al. 2009).

The consistent period of no or low flow into the Coorong has essentially led to a constriction of the benthic invertebrate macrofauna towards the lower salinities in the Murray Mouth region, leading to a regime shift in the South Lagoon from a hypermarine lagoon to almost salt lake status. The brine shrimp, Parartemia zietziana, was collected at Salt Creek in the South Lagoon for the first time ever in the Coorong Lagoons in July 2004 (Geddes 2005a). In 2004, estuarine-lagoonal invertebrates were restricted to the Murray Mouth region and the northern part of the North Lagoon, despite salinities being within their tolerance ranges further south (Geddes 2005a, Dittmann et al. 2006c).

Condition monitoring of macrobenthic invertebrates of the Murray Mouth, Coorong and Lower Lakes commenced in 2004 (Dittmann et al. 2006c, Maunsell 2009) and quantitative surveys, mainly concentrated on the Murray Mouth and Coorong, have been performed on annually (Dittmann et al. 2006a, Dittmann & Nelson 2007, Dittmann et al. 2008a, Baring et al. 2009). In 2007, the survey still showed the previously consistent general pattern of benthic distribution and community composition throughout the Murray Mouth and Coorong, but changes emerged in the benthic fauna, such as loss of amphipods at several sites and an overall decline in species numbers, abundance and biomass, which could result from several years of no flow over the barrages (Dittmann et al. 2008a). Salinities in the Murray Mouth in 2007 were higher than in previous years, and in the South Lagoon salinities were significantly higher in 2006 and 2007 than previously measured (Dittmann et al. 2008a). Since the monitoring started in 2004, highest abundance and biomass was recorded in October/November 2005 shortly after the last water release (see above), leading Baring et al. (2009) to conclude that the ecological benefit of the last water release is now very apparent during the prolonged period of no flow.

In a recent pilot study of the trophic ecology at Pelican Point, Geddes & Francis (2008) found that both macrobenthic invertebrate diversity and abundance decreased sharply at depths below 1.5 m. Amphipods dominated the diet of small fish such as hardyheads and gobies, whilst juvenile mullet consumed mostly Capitella and Phyllodoce (polychaete worms). Adult mullet however had a broader diet, consuming crustaceans, polychaetes, bivalves and plant material. Consumers of macrophytes such as the amphipod Melita, the snail Hydrobia and the shrimp Macrobrachium, occurred in very low abundance in comparison to the 1980s, which may largely be due to the lack of macrophytes, with Ruppia megacarpa being almost absent in 2005 (Geddes & Francis 2008).
To assess short-term fluctuations, Rolston & Dittmann (2009) performed bimonthly surveys of adult and juvenile benthic macrofauna from October 2006 - March 2007 and October 2006 - October 2007 respectively. In December 2006, only insect larvae were present in the South Lagoon, and no other taxa were found in the South Lagoon in January and March 2007. Distinct adult and juvenile macrobenthic assemblages were identified for the Murray Mouth, North and South Lagoon, and these did not change significantly with time. The macrobenthic community in the Murray Mouth region was dominated by Polychaeta (particularly Capitella sp.), Amphipoda and the micro-bivalve Arthritica helmsi (Rolston & Dittmann 2009). The juvenile macrobenthic fauna was dominated by four species: the polychaete worms Capitella sp. and Simplisetia aequisetis, the micro-bivalve Arthritica helmsi and the Chironomid larva Tanytarsus barbitarsus. Juveniles of each of the four dominant species were present in the system throughout the year, whilst rarer species such as the polychaetes Boccardiella limnicola and Nephtys australiensis showed more seasonal abundances.

Adult and juvenile macrobenthic diversity and abundance were highest in the Murray Mouth region before decreasing in the North Lagoon, with highest abundance of both adult and juvenile macrobenthos occurring at Pelican Point, which was distinct from other sites by having sandier sediment (Rolston & Dittmann 2009). Salinity was the most important environmental variable of those measured in influencing macroinvertebrate distribution, followed by sediment organic content (Rolston & Dittmann 2009).

A complex sediment translocation experiment was undertaken to assess the effects of changes in salinity and mudflat exposure on macrobenthic invertebrates (Rolston & Dittmann 2009). Experimental translocations of macroinvertebrate fauna in sediment from areas of high salinity to low salinity, and from areas of high mudflat exposure to low exposure led to an increase in species diversity and abundance. The converse was true for the reciprocal translocations. Macrobenthic invertebrates were unable to survive in exposed sediment for one week without inundation (Rolston & Dittmann 2009).

Sediments around the Lower Lakes have been surveyed since 2004, although at irregular intervals and variations to sampling sites, as focal areas of interest regarding acid sulphate soils were added (Dittmann et al. 2006c, Dittmann et al. 2008b, Baring et al. 2009). Diversity, abundances and biomass were lower in the lakes, where insect larvae prevailed. Following seawater seepage into the Goolwa Channel, polychaetes colonised this area and abundances increased compared to the estuary (Baring et al. 2009). Estuarine benthos is now also present in sediments on the lake side of some other barrages (Baring et al. 2009).

Based on these macrobenthic investigations carried out in the CLLAMM region, a list of species present in the Coorong/Murray Mouth or Lower Lakes pre- and post- the 2006 drought was compiled (Table 1). The ecological character of the Ramsar site was described in 2006 (Phillips and Muller, 2006) and the table reveals how the system has changed since then. Many of the species now present in the Lower Lakes were first observed there in the summer of 2007/2008 (Dittmann et al. 2008b). Before 2006, only one individual of a polychaete worm, Capitella sp. had been found in both the Coorong and Lower Lakes, yet at only one site near Clayton in December 2004, and given the salinity at the time (0.7 ppt), misidentification cannot be ruled out (Dittmann et al. 2006c). While its presence in the Lower Lakes pre-2006 must be treated with caution, Baring et al. (2009) found several individuals of Capitella sp. in different core samples at the mouth of Currency Creek in December 2008, confirming its presence in the Lower Lakes post 2006. All annelid taxa present in the Murray Mouth and Coorong pre-2006 were present in the Lower Lakes, except for the polychaete worm Australonereis eihlersi. The spionid polychaete Boccardiella limnicola was rarely observed in the Coorong or Lower Lakes pre-2006, but is now common in both systems. Mysidacea and Isopoda were
found in the Coorong pre 2006 but have not been recorded since, although this may be a reflection of the sampling focus rather than their absence from this region. The freshwater snail *Physa acuta* was observed in the Lower Lakes pre-2006, but has not been found in sampling programmes since. No other molluscs have been recorded in the benthic samples around the shores of the Lower Lakes, yet shells of the large freshwater bivalve *Velesunio ambiguus* can be frequently seen on the now exposed lake floor. Chironomidae are the most abundant insect larvae in both the Lower Lakes and Coorong and the lack of larvae of Tabanidae from Lower Lake samples pre- and post-2006 and Ceratopogonidae post-2006 may reflect their low abundances, or the timing of sampling in relation to their life cycle, rather than their complete absence from the Lakes.

**Table 1:** Macrobenthic invertebrate species present in the Coorong and Lower Lakes regions pre- and post-2006. Green boxes with a tick indicate species presence. Red boxes indicate species absence. Many of the species now present in the Lower Lakes were first observed there in the summer of 2007/2008 (Dittmann et al. 2008b). Results of surveys in 2009 are not included.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Pre 2006 Coorong</th>
<th>Lower Lakes</th>
<th>Post 2006 Coorong</th>
<th>Lower Lakes</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ficopomatus enigmaticus</em></td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td><em>Australonereis ehlersi</em></td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td><em>Simplisetia aequisetis</em></td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td><em>Capitella sp.</em></td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td><em>Nephtys australiensis</em></td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td><em>Phyllochole novaehollandiae</em></td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td><em>Boccardiella limnicola</em></td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Oligochaeta</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Amphipoda</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Mysidacea</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Isopoda</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Ostracoda</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Decapoda</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td><em>Salinator fragilis</em></td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Glacidorbid sp.</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td><em>Physa acuta</em></td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td><em>Hydrobia sp.</em></td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td><em>Arthritica helmsi</em></td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Brachidontes sp.</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td><em>Notospisula trigonella</em></td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Soletellina alba</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td><em>Velesunio ambiguus</em></td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Chironomidae</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Dolichopodidae</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Ceratopogonidae</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
</tbody>
</table>

The general habitat requirements of a number of abundant and indicative species of the region are shown in Table 2. The majority of species inhabit soft sediments, which are the prevalent sedimentary habitat in the region. Only the tubeworm *Ficopomatus enigmaticus* requires hard substrate for settlement, and amphipods and decapode crabs frequently inhabit hard-substrate as well as soft-substrates. The period of water inundation is a significant driving force of macrobenthic invertebrate distribution in the nearshore areas, and determined by tides, wind, evaporation and freshwater inflow.
All of the species listed in Table 2 are able to withstand a short period exposure. *Ficopomatus enigmaticus* is an obligate filter feeder and therefore only able to survive short periods without inundation. The freshwater mussel, *Velesunio ambiguus*, however, is particularly adapted to withstand hypoxia and can close its valves in unfavourable conditions, surviving extreme hypoxia for nearly one year at air temperatures of 18-20 ºC, resulting in up to 37 % weight loss through desiccation (Walker 1981, Sheldon & Walker 1989).

The majority of the organisms listed in Table 2 are able to withstand a wide range of salinities and can therefore be classed as euryhaline species. Halinity is the extent to which water contains chloride and the Venice system divides brackish water bodies into zones describing this chloride content (Venice System 1959). Oligochaeta and Amphipoda encompass both marine and freshwater tolerant species, and identification of species is difficult and very time consuming, complicating the assessment of species specific salinity tolerances. The mussel *Velesunio ambiguus* and the spionid polychaete *Boccardiella limnicola* are the only truly freshwater and brackish water species respectively listed in Table 2 and are therefore indicative of these environments. Decapoda and the bivalves *Notospisula trigonella*, *Soletellina alba* and *Arthritica helmsi* are currently restricted in their distributions to the seaward side of the barrages where poly- to euhaline conditions prevail (Tables 1 and 2).

All species shown in Table 2 are mobile as adults, except for the tubeworm *Ficopomatus enigmaticus* and the freshwater mussel *Velesunio ambiguus*, and therefore have the potential to disperse to more favourable habitat if available. Yet, the adult mobility of errant polychaetes such as *Nephtys australiensis* is greater than, for example bivalves, allowing wider dispersal of adult polychaetes compared to bivalves. However, most benthic species, including *F. enigmaticus* and *V. ambiguus*, rely on the higher dispersal potential of their larval stages.

**Table 2**: General habitat requirements of abundant and indicative species of the CLLAMM region. Halinity is included in the table when known, and the key for halinity ranges is given below the table.
5. Species Interactions in the CLLAMM Region

Many of the key species listed in this review are significant food sources for both birds and fish (Table 3). As birds and fish are unlikely to discriminate between species of insect larvae, oligochaete worms and amphipods as prey, these have not been differentiated to species level in this review. Some of the macroinvertebrates that are prey organism of both birds and fish are also predators themselves. For example, polychaete worms of the family Nephtyidae, which are represented in the Murray Mouth and Coorong by Nephtys australiensis, play an important role in soft sediments as an infaunal predator of other polychaetes or small bivalves, but can be deposit-feeding when prey items are scarce (Faucalld & Jumars 1979, Wilson 2000).

In the Coorong and Murray Mouth, the number of wading birds declined over the past twenty years in response to environmental changes which resulted in a reduced availability of macrobenthic prey items (Geddes 2003, Dittmann et al. 2006c, Baring et al. 2009, Rogers & Paton 2009). The diversity of fish in the South Lagoon has also been reduced to one species tolerant to hypersalinity, the smallmouth hardyhead (Atherinosoma microstoma) (Brookes et al. 2009). With benthic macroinvertebrates contracted to the Murray Mouth region, where diversity of fish and bird predators is highest for the region, predatory interactions will be intensified, which may further affect benthic abundances.

The interaction of species with other organisms can change during their life cycle. For example, the glochidia larvae of the freshwater mussel, Velesunio ambiguus, act as obligate parasites, attaching to the gills of fish (Kat 1984) which subsequently disperse the organism throughout the lower Murray region. The mussel has a narrow range of host fish (Watters 1994) and the larvae are not capable of host selection – the reaction of the host to the parasite is the major factor determining specificity (Kat 1984). With mussel distributions closely correlated to those of their host fish species (Watters 1994, Haag & Warren 1998), environmental conditions that affect the host fishes will likely reduce the ability of V. ambiguus to disperse throughout the Lower Murray River and Lake Alexandrina.

Species interactions can also change when species are newly introduced to a system. An example is the colonisation of Lake Alexandrina by the tubeworm Ficopomatus enigmaticus. The tubeworm settles gregariously on almost any solid substrate in the Goolwa Channel, including shells of dead mussels (V. ambiguus), and freshwater tortoises (Dittmann et al. 2009). Dislodgement of overgrown dead mussel shells or movement of tortoises can enhance the dispersal of tubeworms in the Lower Lakes (Department for Environment and Heritage 2009, Dittmann et al. 2009). The encrustation of short- and long-necked tortoises by F. enigmaticus has caused severe mortality of tortoise populations throughout Lake Alexandrina, as the weight of the worm overgrowth interferes with their feeding and increases the vulnerability of the tortoises to predation (Department for Environment and Heritage 2009).
Yet, the tubeworms may have positive effects as well. Like all serpulid polychaete worms, *F. enigmaticus*, feeds on suspended detritus and phytoplankton, with rates of ingestion and particle clearance being among the highest known for serpulid and sabellid polychaetes (Dittmann et al. 2009). The high filtration rate of *F. enigmaticus* has been shown to significantly contribute to water clarity in lagoons around the world (Davies et al. 1989, Bruschetti et al. 2008), and the tubeworms may thus play a positive role on the ecology of the Lower Lakes by reducing phytoplankton blooms. Furthermore, the worms are extracting calcium carbonate from the water column for the formation of their tubes, and this may affect the alkalinity of the water in which they reside. As a result of the low water levels in the Lower Lakes, large areas of sulfidic sediments have been exposed and oxidated resulting in Acid Sulfate Soils. When re-wetted, metals can be precipitated into the water column along with sulfuric acid, leading to an acidification event which may have significant effects on the local ecology. The removal of calcium carbonate from the water column by *F. enigmaticus* has the potential to locally lower the alkalinity of Lake water, reducing its buffering potential thus increasing the risk of an acidification event.

Information regarding calcium carbonate uptake by *F. enigmaticus* within the literature is severely lacking and as such can be identified as a significant knowledge gap. There is also little information regarding calcium carbonate uptake rates for related polychaete species. Dixon (1980) notes that Mercierella enigmatica,(now Ficopomatus enigmaticus) directly precipitate crystals of calcium carbonate from the water, whilst Neff (1969) states that when removed from their tubes and placed in seawater, within a few hours many species of serpulid polychaetes begin to secrete concentrations of calcium carbonate from their calcium-secreting glands. For the polychaete Eupomatus dianthus (now Hydroides dianthus), up to 50 µg of calcium carbonate can be secreted per day (Neff, 1969). As Ficopomatus enigmaticus can exist in large aggregations of up to 180,000 worms m$^{-2}$ (Aliani et al., 1995), the potential for calcium carbonate removal from the water column is significant. Aliani et al (1995) found that one cubic metre of *F. enigmaticus* reef contained approximately 700Kg of calcium carbonate.

Given the potential for acidification events in the Lower Lakes to significantly negatively impact the ecology of the region, and the large abundance of *F. enigmaticus* in the Lower Lakes the gap in knowledge in relation to calcium carbonate uptake and the subsequent reduction in water alkalinity should be addressed as soon as possible in order to inform management decisions and mitigation actions.

Because of its ability to build reefs of substantial size that can influence water flow rates, sedimentation and subsequently the surrounding invertebrate community, *F. enigmaticus* is considered an ecosystem engineer (Thomas & Thorp 1994, Fornos et al. 1997, Schwindt & Iribarne 2000, Schwindt et al. 2001, Schwindt et al. 2004a, Schwindt et al. 2004b). The engineering processes include; reduced bedload flow around the reefs that facilitates silt accumulation and affects sediment transport, providing hard substrate in a soft substrate environment and thus increasing habitat availability for a greater number of species, providing shelter for predators (for example crabs) and thus altering distribution patterns and interactions among and between other species (see Dittmann et al. (2009) for a review).

The tubeworm is present in Lake Alexandrina (currently from Goolwa Channel up to Point Sturt (Dittmann et al. 2009) and pers. obs. January 2009) and is likely to remain present in the CLLAMM region unless significant freshwater flows are realised for a prolonged period (Dittmann et al. 2009).
Other ecosystem engineering macroinvertebrates in the Coorong and Murray Mouth mudflats are burrowing polychaetes (*Simplisetia aequisetis* and *Australonereis ehlersi*), who extend the oxygenated surface layer of the sediment into the depth of their burrow, and will have further effects on bioturbation.

**Table 3:** Species interactions of selected macrobenthic invertebrate species. Considered here are trophic interactions (feeding mode of organism, position in food web), and non-trophic interactions, based on available information.

<table>
<thead>
<tr>
<th>Phylum</th>
<th>Taxa</th>
<th>Trophic Interactions</th>
<th>non-Trophic Interactions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annelida</td>
<td><em>Ficopomatus enigmaticus</em></td>
<td>Filter-feeder; Fish food</td>
<td>Ecosystem Engineer, Effects Tortoises</td>
</tr>
<tr>
<td></td>
<td><em>Capitella</em> sp.</td>
<td>Deposit-feeder; Bird &amp; fish food</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Nephtys australiensis</em></td>
<td>Predator; Bird &amp; fish food</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Boccardiella limnicola</em></td>
<td>Filter-deposit-feeder; Bird &amp; fish food</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Australonereis ehlersi</em></td>
<td>Omnivore; Bird &amp; fish food</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Simplisetia aequisetis</em></td>
<td>Omnivore; Bird &amp; fish food</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Oligochaeta</td>
<td>Deposit-feeder; Bird &amp; fish food</td>
<td>Sediment stabilisation (if in patches)</td>
</tr>
<tr>
<td></td>
<td><em>Boccardiella limnicola</em></td>
<td>Deposit-feeder; Bird &amp; fish food</td>
<td>Bioturbation, ecosystem engineer</td>
</tr>
<tr>
<td></td>
<td><em>Australonereis ehlersi</em></td>
<td>Predator; Bird &amp; fish food</td>
<td>Bioturbation, ecosystem engineer</td>
</tr>
<tr>
<td>Arthropoda</td>
<td><em>Oligochaeta</em></td>
<td>Deposit-feeder; Bird &amp; fish food</td>
<td>Sediment destabilisation (if in patches)</td>
</tr>
<tr>
<td></td>
<td><em>Amphipoda</em></td>
<td>Predator; Bird &amp; fish food</td>
<td>Ecosystem Engineer</td>
</tr>
<tr>
<td></td>
<td><em>Grapsidae</em></td>
<td>Filter-feeder</td>
<td>Shells substrate for <em>F. enigmaticus</em></td>
</tr>
<tr>
<td></td>
<td><em>Insect Larvae</em></td>
<td>Filter-feeder; Bird &amp; fish food</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Velesunio ambiguus</em></td>
<td>Filter-feeder; Bird &amp; fish food</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Arthritica helmsi</em></td>
<td>Filter-feeder; Bird &amp; fish food</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Notospisula trigonella</em></td>
<td>Filter-feeder; Bird &amp; fish food</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Soletellina alba</em></td>
<td>Filter-feeder; Bird &amp; fish food</td>
<td></td>
</tr>
</tbody>
</table>
6. Critical Thresholds to Environmental Variables

The CLLAMM region is subject to numerous environmental stressors all occurring at the same time, making synergistic effects of salinity, oxygen, nutrients, pollutants and acidity possible (Rosenberg et al. 1992). Thrush et al. (2008) demonstrated that effects of multiple stressors are multiplicative, with different macroinvertebrate species responding differently to heavy metals subject to the sediment types, indicating feedback mechanisms between stressors and the organisms’ biology and habitat requirements. Yet, the tolerances of macroinvertebrates are usually studied in response to isolated factors and often in laboratory situations which may not reflect field-based sensitivities, limiting the full evaluation of effects (Thrush et al. 2008). Furthermore, extrapolating findings from related species to the species and populations occurring in the CLLAMM region is only possible with caution, as initial conditions and acclimatisation can affect the physiological response (Normant & Lamprecht 2006).

Ecologically, macroinvertebrate species may be placed into functional groupings such as feeding, locomotive and habitat guilds (Posey 1990, Pearson 2001). However, large variability in guild responses to changing environmental conditions is likely, making predictions based on functional groups for management purposes difficult (Piraino et al. 2002). We identified a number of key species in the CLLAMM region based on their distributions, abundances, habitat preferences and trophic linkages (chapter 4). These species and their suggested tolerance levels (also based on the literature) of salinity, pH, temperature, dissolved oxygen and heavy metals are shown in Table 4. It is important to note that specific information is not available for all of the macroinvertebrate species occurring in the CLLAMM region. As such, much of the information below is taken from the literature for closely related species (same genus or family).

The Lower Lakes have been shown to be an overall sink for phosphorous, nitrates-nitrites and silicon, but an overall source of organic forms of nitrogen (Cook et al. 2008). In times of flow over the barrages, water from the Lower Lakes will likely stimulate productivity in the Coorong as coastal waters are generally limited by nitrogen (Brookes et al. 2009). As no flow over the barrages has occurred over the past five years, the Coorong may be deprived of nutrients, exerting a bottom-up control over the macrobenthic infauna of the region. However, the previously estuarine area near the Murray Mouth can act as a net source of bioavailable nutrients probably due to the microbial breakdown of organic matter in the sediments which were deposited during times of high flow over the barrages (Aldridge et al. 2009). Macroalgal mats are still prevalent and can affect the benthos (Thiel et al. 1998, Raffaelli 1999, Jones & Pinn 2006).

The reduced water levels have exposed large areas of Acid Sulfate Soils (ASS) in the CLLAMM region, which may release contaminants when oxidised ASS are rewetted (Simpson et al. 2008, Fitzpatrick et al. 2009). The following evaluation therefore includes pH tolerances and bioaccumulation of heavy metals.

6.1 Salinity, temperature and oxygen

Based on condition monitoring carried out since 2004 and literature data, the macroinvertebrate species occurring in the CLLAMM region can be mostly classified as euryhaline, being marine species able to tolerate a wider salinity range. Many of the specific salinity, temperature and dissolved oxygen tolerance ranges shown in Table 4 are based on the species’ distributions elucidated by the surveys of Rolston & Dittmann (2009) and condition monitoring of macroinvertebrates (Dittmann et al. 2006a, Dittmann et al. 2006c, Dittmann & Nelson 2007, Dittmann et al. 2008a, Baring et al. 2009) and further literature records. Table 4 lists the extreme salinity values at which individuals of a particular species
were found, indicating wide tolerance ranges, yet abundances are only high in salinities below 50 ppt (Appendix 2), corresponding with the distribution pattern found in the Murray Mouth, North and South Lagoon of the Coorong (Baring et al. 2009). Several species appear to be stenohaline and are not found below 22 ppt, this includes the polychaetes *Australonereis ehlersi* and *Phyllodoce novaehollandiae*. Insect larvae of several species tolerate the widest range of salinities from freshwater to ultrahaline (Appendix 2). Apart from the freshwater snail *Physa acuta*, all other species occur in salinities above 18 ppt, and are thus not truly brackish. King et al. (2004) studied several macroinvertebrates common in Australian estuaries and found they were able to tolerate a range of salinities, yet hypersaline conditions were not tested. In the St. Lucia estuary in South Africa, chironomid larvae and ostracods were the only macroinvertebrates found when salinities increased above 55 ppt, and distribution ranges on benthic macrofaunal species went through cycles of range expansion and contraction subject to the prevailing salinities and colonisation potentials, with larval dispersal facilitated by wind seiching (Boltt 1975, Forbes & Cyrus 1993).

Oligochaeta and Amphipoda encompass both marine and freshwater tolerant species and as such their salinity tolerances are listed as variable in Table 4. Kangas & Geddes (1984) and Generich & Giere (1996) found a wide tolerance range of amphipods in the Coorong from 1 to 62 ppt. The life history of the euryhaline amphipod *Gammarus locusta*, occurring along the North Atlantic coast, was shown to be more affected by temperature than by salinity changes (Neuparth et al. 2002). A related euryhaline amphipod *Gammarus oceanicus* could adjust its physiology, as consumption decreased but absorption efficiency increased with higher salinities (Normant & Lamprecht 2006). Larvae of chironomids and ceratopogonids (Insecta) are able to tolerate a wide range of salinities from freshwater to hypersaline (Paterson & Walker 1974, Halse et al. 1998, Timms 1998). The freshwater mussel *Velesunio ambiguus* is only able to tolerate low salinity, whilst the other bivalve species listed are known to favour more brackish or marine environments. Yet, experimental reduction of salinity showed lethal and sublethal effects on *Soletellina alba*, which may explain mass mortalities observed after winter flooding in Victorian estuaries (Matthews & Fairweather 2004). Of the polychaete worms listed, *Capitella* sp., *Simplisetia aequisetis* and *Ficopomatus enigmaticus* have been shown to tolerate a wide range of salinities ranging from fresh/brackish through to hypersaline (Appendix 2) (Dittmann et al. 2006c, Dittmann et al. 2009, Rolston & Dittmann 2009).

The tubeworm *Ficopomatus enigmaticus* and the freshwater mussel *Velesunio ambiguus* are able to withstand low dissolved oxygen levels (Walker 1981, Kupriyanova et al. 2001). Yet the specific dissolved oxygen tolerances for many species are again largely unknown. Hypoxia (< 2 mg l⁻¹), which can affect estuarine organisms and increases the predation risk for macroinvertebrates (Diaz & Rosenberg 1995, Gray et al. 2002) was not detected during the macroinvertebrate monitoring from 2004 to 2008, and oxygen concentrations of 3 mg l⁻¹ in the water column were the lowest at which macroinvertebrates were recorded, with abundances being higher at normoxic concentration of 5-10 mg l⁻¹ (Appendix 2). However, sediments in estuaries are often hypoxic during low tide or prolonged exposure, and contain sulphide from the microbial breakdown of organic matter (Jørgensen & Fenchel 1974). Many polychaete and oligochaete species are physiologically adapted or have endosymbiotic bacteria to tolerate periods of hypoxia or anoxia (Schiedek et al. 1997, Stewart et al. 2005).

Temperature ranges are variable for all of the species listed in Table 4. Temperature in temperate South Australia is less likely to be limiting macroinvertebrate distributions in comparison to temperate regions in northern Europe, where severe winter affects abundances and distributions of benthic organisms (Beukema et al. 1988, Reise et al. 2001, Strasser et al. 2001). Yet, temperature may affect the tolerance towards other environmental factors, such as salinity, and impact on the larval development of macroinvertebrates (Bochert et al. 1996).
Table 4: Selected Key Species’ tolerance levels to a variety of environmental parameters, based on studies in the CLLAMM region and literature records (see text for detail). DO = Dissolved oxygen. Temperature is measured in degrees centigrade. ↑ = increase; ↓ = decrease.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Parameter</th>
<th>Salinity (ppt)</th>
<th>Temperature</th>
<th>DO (mg/L)</th>
<th>pH</th>
<th>Metals</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Annelida</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Ficopomatus enigmaticus</em></td>
<td></td>
<td>1.5 - 60</td>
<td>&gt; 10</td>
<td>10 to 33*</td>
<td>Unknown</td>
<td>Possible morphological abnormalities in embryo/larvae; bioaccumulator</td>
</tr>
<tr>
<td><em>Capitella sp.</em></td>
<td></td>
<td>1 - 138</td>
<td>13 to 30</td>
<td>&gt;3</td>
<td>7 to 10.1</td>
<td>Growth and ingestion rates affected by Cd, Pb and Ni</td>
</tr>
<tr>
<td><em>Nephtys australiensis</em></td>
<td></td>
<td>15 - 50</td>
<td>13 to 25</td>
<td>&gt;3</td>
<td>7.5 to 8.2</td>
<td>Fitness costs; Cu inhibits larval settlement; ↓ survival in sulfidic soils</td>
</tr>
<tr>
<td><em>Boccardiella limnicola</em></td>
<td></td>
<td>4 - 60</td>
<td>10 optimum</td>
<td>&gt;5</td>
<td>Unknown</td>
<td>Unknown, but likely bioaccumulator</td>
</tr>
<tr>
<td><em>Simplicia aequisetis</em></td>
<td></td>
<td>7 - 88</td>
<td>13 to 28</td>
<td>&gt;4</td>
<td>7 to 8.7</td>
<td>Fitness costs; Cu inhibits larval settlement; ↓ survival in sulfidic soils</td>
</tr>
<tr>
<td><em>Oligochaeta</em></td>
<td></td>
<td>0 - 93</td>
<td>Variable</td>
<td>&gt;3</td>
<td>Variable</td>
<td>Bioaccumulator from sediment†</td>
</tr>
<tr>
<td><em>Amphipoda</em></td>
<td></td>
<td>1 - 125</td>
<td>Variable</td>
<td>&gt;3</td>
<td>Unknown</td>
<td>Bioaccumulator and potential Biomonitor</td>
</tr>
<tr>
<td><em>Grapsidae</em></td>
<td></td>
<td>10 - 35</td>
<td>&gt; 12</td>
<td>Unknown</td>
<td>Unknown</td>
<td>Bioaccumulator; ↑ metals cause ↓ genetic variability; Cd inhibits molting</td>
</tr>
<tr>
<td><em>Chironomida (larvae)</em></td>
<td></td>
<td>1 - 138</td>
<td>0 to 35</td>
<td>&gt;3</td>
<td>6 to 10</td>
<td>Bioaccumulator from sediment†</td>
</tr>
<tr>
<td><em>Tabanidae (larvae)</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Ceratopogonidae</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>acid-tolerant</td>
</tr>
<tr>
<td><strong>Arthropoda</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Velesunio ambiguus</em></td>
<td></td>
<td>&lt; 4</td>
<td>0 to 35</td>
<td>Unknown*</td>
<td>Unknown</td>
<td>Uptake into gills and mantle</td>
</tr>
<tr>
<td><em>Arthritica helmsi</em></td>
<td></td>
<td>10 - 55</td>
<td>10 to 28</td>
<td>&gt;3</td>
<td>Unknown</td>
<td>Unknown, but likely bioaccumulator</td>
</tr>
<tr>
<td><em>Notospisula trigonella</em></td>
<td></td>
<td>Brackish/Marine</td>
<td>Unknown</td>
<td>Unknown</td>
<td>Unknown</td>
<td>Unknown, but likely bioaccumulator</td>
</tr>
<tr>
<td><em>Soletellina alba</em></td>
<td></td>
<td>Brackish/Marine</td>
<td>Unknown</td>
<td>Unknown</td>
<td>Unknown</td>
<td>Reduced survival in sulfidic soils and soils with high Cu</td>
</tr>
</tbody>
</table>

* Able to tolerate low dissolved oxygen environments
† Bioaccumulation not significantly influenced by Acid Volatile Sulfide soils
6.2 Acid Sulphate Soil (ASS) response: tolerance to pH, sulphide, hypoxia and heavy metals

Environmental parameters affect aquatic and benthic organisms not in isolation, but usually act at the same time. For example, the polychaetes *Nephtys australiensis* (Nephythidae) and *Notomastus torquatus* (Capitellidae) were sensitive to ASS runoff, and responded more to the combined influence of aluminium and pH than either factor alone (Corfield 2000). Factors like temperature or pH can also modify the response capabilities to other environmental factors (Bochert *et al.* 1996, Ringwood & Keppler 2002) or affect the toxicity of metals such as copper (Ho *et al.* 1999). As a combination of salinity and ASS is affecting many freshwater systems, Zalizniak *et al.* (2009) looked at the combined effects of pH and salinity on macroinvertebrates, but did not find a change in salinity tolerance with low pH (pH 5 or 6), yet strengthen that the acid tolerance of aquatic invertebrates is subject to the calcium concentration of the water.

Given the overall deterioration of water quality within waterways associated with ASS run off, pH and soluble heavy metal concentrations are of great concern (Corfield 2000, Powell & Martens 2005). Metal release into overlying water is greater at lower pH and dissolved oxygen concentrations, and further enhanced by physical disturbances and bioturbation, although the release of contaminants from sediments is far from fully understood (Eggleton & Thomas 2004, Atkinson *et al.* 2007). Low pH, low dissolved oxygen and the release of trace metals by rewetted ASS will likely impact all organisms that inhabit affected areas. How macrobenthic invertebrates are able to tolerate such conditions is important for any ecosystem assessment of the region.

Seawater (35 ppt) has a pH from 7.8 - 8.2, and because of the buffering capacity of seawater, effects of pH on estuarine and marine macroinvertebrates have received little scientific attention (Knutzen 1981). While marine organisms can be subjected to variation of pH of 0.2 units from equilibrium, any further decrease of 0.1 - 0.3 pH units can cause harm (Knutzen 1981). The lower recommended limit for estuaries is pH 6.5 (Perkins 1976 cit. in Knutzen (1981)). Field records and experiments in the reviewed literature rarely go below pH 6 for their lowest acidity level, well above some of the pH levels recorded in the Lower Lakes.

Acidification causes shell dissolution in gastropods (Hall-Spencer *et al.* 2008, Marshall *et al.* 2008) and reduction of growth rates and mortality occurs at pH levels of about pH 7 (Bamber 1990, Ringwood & Keppler 2002, Michaelidis *et al.* 2005). pH effects on growth rates of clams were more pronounced at lower salinities (Ringwood & Keppler 2002). The polychaetes *Capitella* sp., *Nephtys australiensis* and *Simiplisetia aequisetis* have been reported to have a low-alkaline tolerance range (Geddes & Butler 1984). Chironomid insect larvae have a wider pH range, being able to tolerate slightly acidic and alkaline environments (Oliver 1971, Kokkin 1986). Insects (Ceratopogonidae, Macrothricidae (Cladocera) and corixid beetles) were found to be acid-tolerant and increased in abundance in a drought affected lake in Western Australia subject to acidification, but were replaced by acid-sensitive aquatic invertebrates following artificial augmentation of the wetland (Sommer & Horwitz 2001, 2009). Tolerance levels and the effects of pH and heavy metals on key macroinvertebrates are shown in Table 4. Where information is available on species occurring in the CLLAMM region, macroinvertebrates have a low pH tolerance of about pH 7 or 6, and are negatively affected by heavy metals, which they accumulate and can thus pass on to higher trophic levels.

Hydrogen sulphide concentrations in estuarine sediments often co-occur with hypoxic conditions. Oligochaetes are physiologically well adapted to occur in hypoxic and sulphide rich sediments, with some gutless oligochaetes even having endosymbiotic bacteria which allows them to dwell in sulphide rich sediments (Giere *et al.* 1999, Dubilier *et al.* 2001). Some polychaetes can cope with anoxic
conditions by switching to anaerobic metabolism, but not if sulphide concentrations are high (Vismann 1990, Schiedek et al. 1997), and may thus rely on behavioural responses such as burrow irrigation or escape from the sediment. Burrow irrigation could explain the higher survival rate of *Australonereis ehlersi*, which occurs in the Murray Mouth, in sulfidic sediments compared to other tested species (King et al. 2004). If oxygen is still available in the worms tissue, sulphide can be detoxified by oxidation to thiosulphate (Vismann 1991). Salinity fluctuation put additional stress on worms, affecting their content of amino acids and thus their metabolic response to sulphide (Schiedek et al. 1997).

In a series of tolerance experiments, Gamenick et al. (1996) found reduced survival of macroinvertebrates for hypoxia plus sulphide compared to hypoxia alone, with thresholds of sulphide concentrations ranging from 0.9 to 1.8 mmol l\(^{-1}\) from the least to most resistant species respectively. The most resistant species was an ostracod who survived for three weeks, whereas the mudsnail (*Hydrobia ventrosa*), two oligochaete species, and the polychaete *Hediste diversicolor* (*Nereididae*) survived for several days only, with post-larval *H. diversicolor* surviving for 10-14 hours only. The amphipod *Corophium volutator* was the most sensitive species surviving for just a few hours and could tolerate only the lowest sulphide concentrations (Gamenick et al. 1996). Related species to those tested by Gamenick et al. (1996) occur in the mudflats of the Murray Mouth. Testing macroinvertebrates from Australian estuaries, King et al. (2004) found decreased survival after exposure to highly sulfidic sediment, with 100 % mortality in the polychaete *Nephtys australiensis*, which occurs in the Murray Mouth, and the bivalves *Tellina deltoidalis* and *Soletellina alba*.

Polychaete worms could be suitable bioindicators of trace metal contamination in soft sediments, because of their frequent dominance in terms of abundance and biomass, their ability to exist in a wide range of habitats (both contaminated and uncontaminated), their large number of obligate deposit feeding species and species of other feeding guilds who inadvertently ingest sediment whilst foraging (Waring et al. 2006). For example, the polychaete *Capitella* sp. is able to adjust feeding rates to maintain their growth in relation to ingested sediment under moderate pollution conditions (Horng et al. 2009).

The effects of heavy metals on macroinvertebrates is subject to their feeding and living habits, and the bioavailability of the metals (Morrisey et al. 1996, King et al. 2004). Feeding strategies and assimilation efficiencies determine metal accumulation rates, as the uptake of heavy metals from water and sediments occurs through permeable body surfaces as well as through the gut if feeding on contaminated sediment or food (Bat et al. 1998, Cardoso et al. 2009). Behavioural responses to metal concentrations in sediments include reduced burrowing activity and sediment avoidance (Bat et al. 1998). Contamination of sediments with heavy metals can also affect the colonisation, as sensitive macroinvertebrate species may not settle in these sediments (Olsgard 1999).

The literature on responses of benthic macroinvertebrates to heavy metals and acidity is revealing very complex mechanisms. Indications for effects of heavy metals on macroinvertebrates were documented by significant correlations between benthic assemblage patterns and heavy metals, in particular lead (Stark 1998). Polychaetes of the families Nereididae, Capitellidae and Spionidae were more abundance in the polluted bays, whereas nephtyid polychaetes, crustaceans and gastropods occurred in higher densities in unpolluted bays (Stark 1998). Elevated levels of copper can alter the abundances of benthic fauna, with amphipods and spionid polychaetes found to respond quicker than capitellid polychaetes (Morrisey et al. 2003). King et al. (2004) found no effect of zinc or copper spiked sediments on the survival of estuarine polychaete worms (*Nephtys australiensis* and *Australonereis ehlersi*), but showed the uptake and accumulation of copper in the worms' tissue, while zinc concentrations in the body could be regulated by the worms. The accumulation of metals in the tissues...
of benthic invertebrates can influence their physiology. Fitness costs associated with resistance to high metal concentrations in the polychaete worm *Nereis diversicolor* (the same family as *Simplisetia aequisetis*) include reduced growth, reduced lipid and carbohydrate storage and reduced fecundity (Pook et al. 2009).

The tolerance of some invertebrates to heavy metal pollution may fluctuate due to variations in environmental variables such as salinity, temperature and pH, as pH in particular may alter the availability and toxicity of heavy metals (Chapman et al. 1982). For example, the toxicity of cadmium to the estuarine crab *Paragrapus gaimardii* increases with low salinity and high temperature, possibly by affecting the osmoregulation of the crab, yet Sullivan (1977) also point out that the toxicity of heavy metals can vary with the stability of their complexed form in different salinities. The sensitivity to a particular metal also varies between different taxa (Chapman et al. 1982), and can further vary with season or size of the organism (Perez-Landa et al. 2008). The lack of consistent responses is further exemplified by studies of Ho et al. (1999) showing that at low pH the toxicity of copper to amphipods increased, whilst toxicity of lead, cadmium, nickel and zinc increased. There may be further interaction mechanisms between heavy metals, as Cd was less toxic for the amphipod *Corophium volutator* when applied in combination with Zn (Bat et al. 1998). LC50 values for *C. volutator* based on experiments by Bat et al. (1998) and literature therein range from 17 - 66 mg l\(^{-1}\) for copper, 1-16 mg l\(^{-1}\) for zinc, and 9-23 mg l\(^{-1}\) for cadmium. The amphipod *Melita plumulosa* occurring in temperate Australian estuaries can also take up Cd and Cu from metal contaminated algae (King et al. 2005). Amphipods of the genus *Melita* are epibenthic and have been shown to be sensitive to Cu and Zn contamination, in particular their juveniles (King et al. 2006a, King et al. 2006b).

Metal accumulation in chironomid insect larvae and in oligochaete worms is subject to the bioavailability and concentration of metals from sediment or water, the insects' feeding mode and physiological uptake of metals into the cells (Hare 1992, de Jonge et al. 2009). Chironomid larvae contain haemoglobin, which has been suggested to play a role in detoxification of metal accumulations (Hare 1992). Similarly, the accumulation of metals by grapsid crabs is strongly correlated with the levels of pollution in their environment, and consequences include less genetic variation in crab populations from polluted sites compared to unpolluted sites (Fratini et al. 2008). Bioaccumulation is also shown by amphipods, where metal accumulation correlates strongly with environmental contamination levels (Marsden & Rainbow 2004). Differences in trace metal accumulation in amphipods may vary with gender, breeding and developmental stage (Perez-Landa et al. 2008). Although an important food source for fish, biomagnification of metal accumulation from amphipods appears unlikely (Marsden & Rainbow 2004).

Bivalves are particularly susceptible to the uptake of heavy metals, largely due to their filter feeding ensuring contact with any soluble or suspended pollutant (Millington & Walker 1983, Loo & Rosenberg 1989). The freshwater mussels of the genus *Unio* and *Velesunio* accumulate iron, zinc, cadmium and manganese in their gills and mantel (Jones & Walker 1979), yet it does not accurately reflect environmental fluctuations of iron, zinc and manganese and has thus been deemed unsuitable as a biological indicator of heavy metal concentrations (Millington & Walker 1983, Ravera et al. 2003). Although no species-specific information is available, the bivalves *Notospisula trigonella* and *Arthritica helmsi*, like many bivalves, are likely bioaccumulators of metals (Lee et al. 2000). The bivalves *Soletellina alba* and *Tellina deltoidalis*, which occur in estuaries in South Australia, were sensitive to aqueous copper, with LC50 rates of 120 μg/l and 150 μg/l respectively, and also had reduced survival in copper-spiked sediments, but were less sensitive to zinc which was accumulated in their body tissue (King et al. 2004). Heavy metals can also have sub-lethal effects, such as affecting the burial rates of bivalves (Roper & Hickey 1994).
The bioaccumulation of heavy metals by macroinvertebrates can be rapid, thus posing health risks for their predators (Cardoso et al. 2009). Heavy metals can be transferred through food webs and in some cases, increased concentrations are observed at higher trophic levels (Gray 2002). Dietary exposure is seen as the most important route for metal accumulation in marine organisms (Wang 2002).

7. Knowledge Gaps for Marine/brackish Macroinvertebrates

While macroinvertebrates in the Coorong have been studied for some decades, many knowledge gaps still exist, in particular with regard to the current environmental challenges and habitat modifications experienced in the system. An example of these are:

1. Tolerance ranges
Specific environmental thresholds for species occurring in the CLLAMM region was scarce, and this review relied heavily on research conducted on related species. Given the threat of acid sulfate soils in the region, data available on pH tolerance were very limited. More specific tolerance ranges are needed to accurately predict future distributions and spread of species, in particular studies looking at combined effects of several environmental factors.

2. Recruitment
What are the environmental limitations for recruitment and the primary settlement cues of larval macroinvertebrates? Specific environmental tolerances/preferences of key species need to be investigated. Is the presence of adults an important cue? What are the salinity/pH/organic content/sediment grain size ranges limiting settlement? Answering these questions will enable more accurate predictions of macroinvertebrate distributions under different environmental and management scenarios, particularly with regard to changing ecological states.

3. Recolonisation
With falling water levels in both the Lower Lakes and Coorong Lagoons, large areas of sediment are becoming exposed. If significant flows become available in the future, with subsequent rising water levels throughout the region, how long will it take for macrobenthic invertebrates to recolonise available habitat? Which species colonise first? Rolston & Dittmann (2009) showed that sediment subjected to higher salinities can be colonised by a suite of macrobenthic invertebrate species within six weeks when subjected to significantly lower salinities. Yet macrobenthic invertebrates were unable to survive for one week in fully exposed sediment (Rolston & Dittmann 2009). With the pumping of water from Lake Alexandrina over the newly constructed Clayton regulator into the Goolwa Channel in spring 2009, the subsequent rise in water levels in the Goolwa Channel represents an opportunity to study the effects of changing salinities and water cover on benthic macroinvertebrates. Insight gained from changes following the flooding of the Goolwa Channel will enable predictions of how the Lower Lake benthic invertebrate community may recover if significant freshwater flows become available in the future.

4. Population connectivity
Although Rolston & Dittmann (2009) showed that juvenile Capitella sp., Simplisetia aequisetis, Arthritica helmsi and Chironomid larvae were present in the Murray Mouth and northern North Lagoon throughout the year, it is not known whether these or other macrobenthic invertebrate species in the region recruit from within the Coorong (i.e. mudflat to mudflat recruitment) or from outside the Coorong
larvae entering through the Murray Mouth). Molecular investigations possibly using microsatellite or AFLP markers would identify the population connectivity of macroinvertebrates. Due to costs, the number of species would have to be limited to about four key species. Adults would be sampled from a number of sites within the salinity gradient of the Coorong and also from a number of sites outside of the Coorong. Identifying the source populations of recruitment for key species of macrobenthic invertebrate species in the region would provide valuable information to the importance of an open Murray Mouth.

5. Subtidal macroinvertebrates
With much of the research on macroinvertebrates in recent years concentrated on providing assessments on the food availability for shorebirds, investigations had focussed on the nearshore sediments in the CLLAMM region. Very limited information exists on the subtidal macroinvertebrates in the deeper water of the Coorong and Murray Mouth, thus limiting our evaluation whether the permanently submerged sediments may function as refuge for macroinvertebrates.

8. Speculation About Effects of the Discussed Scenarios
The management options discussed to date can be summarised in four scenarios, ranging from no action("Do Nothing") to mitigation measures ("Remediate" and "Introduce seawater to neutralise acid") and long term perspectives ("Provide River Murray water"). Each of these different possible management strategies is likely to affect the environmental conditions of the CLLAMM region in a variety of ways. Table 5 represents a possible ecosystem component screening tool for undertaking risk assessments for given management or climate scenarios based upon species responsiveness (in terms of distribution and abundance) to ecosystem process.

The responses shown in Table 5 are based on the literature reviewed above, and the expert opinion of the authors and are therefore predictions based on the best available knowledge. The species represented in Table 5 have been chosen as a result of their distributions, interactions and indicative habitat requirements and as a result are termed key species. The micro-bivalve Arthritica helmsi is currently restricted in its distribution to the Murray Mouth and northern Coorong Lagoon but because potential management scenarios may lead to the incursion of this species into the Lower Lakes, it has been included in this speculative assessment.

Acidification of soils and water bodies would decimate or kill off the macroinvertebrate biota in the Lower Lakes, with preceding sublethal or lethal effects from hypoxia and heavy metal contamination in the sediments likely. Not mitigating this threat would appear careless. Yet mitigation can bring its own challenges and has to be evaluated. The ecological condition of the region will change subject to freshwater flows or incursions of seawater into the Lakes.

If salinities increase in the Lower Lakes, whether as a result of a ‘do nothing’ scenario (and presuming further restricted freshwater flows from the River Murray) or from the further incursion of seawater into the Lakes, the majority of annelids, and the micro-bivalve Arthritica helmsi are likely to show a significant positive response in terms of distribution and abundances (Table 5). Oligochaeta, Insecta and Amphipoda are represented in the CLLAMM region with both freshwater and more saline tolerant species and as such species specific responses will vary, with freshwater species likely to show negative responses, with the converse is likely for more saline tolerant species. The freshwater mussel, Velesunio ambiguous, will be negatively affected by increasing salinity.
Yet the macroinvertebrates will not only respond to changes in salinities and altered water regimes, but also to the overall connectivity between both habitats within and between the region, as well as between catchment and ocean, which is currently inhibited. The responses of the macroinvertebrate species listed in Table 5 are difficult to predict due to the levels of connectivity (between the Lakes and Coorong, between habitats within the Lakes or Coorong, between the Goolwa Channel and Lake Alexandrina) and where the organisms are occurring (Lakes, Coorong or both). Therefore, for table clarity, possible responses to increasing habitat and connectivity have been omitted.

Altering the water regime including flow patterns will have varying effects on key macroinvertebrate species. Decreased freshwater availability and subsequent reduced flow will have very similar effects as that of increasing salinity. Reduced flow strength and increasing salinities will provide ideal habitat for the tubeworm *Ficopomatus enigmaticus* and as a result this species will likely continue its spread into Lake Alexandrina. The converse scenario of increased freshwater availability and increased flow will likely have the opposite responses to that of increased salinity.

Increasing turbidity and sedimentation within the Lake system will negatively effect the suspension and filter feeders – i.e. the bivalves *Arthritica helmsi* and *Velesunio ambiguus*, and the tubeworm. Although *Ficopomatus enigmaticus* has been known to thrive in eutrophic lagoons (Keene 1980), increases in sedimentation rates may inhibit the formation of tubeworm reefs in the soft sediment environment. However, rapid tubeworm reef growth has also been show to increase sedimentation (Keene 1980). For the other annelids and arthropods, increased sedimentation and turbidity may be positive for detritus and deposit feeding species in the region (Table 5).

It is evident from this literature review that no simple solution for restoring the ecological state of the CLAMM region can be advised, and benefits and disadvantages of the various options have to be weighed up as to their ecological and socio-economic consequences. To assist this decision process, conceptual models on how these scenarios would affect the macroinvertebrates are presented in Appendix 3.
Table 6: Predicted responses of key macrobenthic invertebrate species to different ecosystem processes as a response to different management or climate scenarios. ↑ = Slight positive response; † = Significant positive response; ↓ = Slight negative response;  = Significant positive response.

<table>
<thead>
<tr>
<th>Phylum</th>
<th>Key Species</th>
<th>Increasing Salinity</th>
<th>Altered Water Regime Including Flow Patters</th>
<th>Increasing Turbidity and Sedimentation</th>
<th>Metal Toxicity</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Increased FW, Increased Flow</td>
<td>Decreased FW, Decreased Flow</td>
<td></td>
</tr>
<tr>
<td>Annelida</td>
<td>Ficopomatus enigmaticus</td>
<td>↑</td>
<td>↓</td>
<td>↑</td>
<td>↓</td>
</tr>
<tr>
<td></td>
<td>Capitella sp.</td>
<td>↑</td>
<td>↓</td>
<td>↑</td>
<td>↑</td>
</tr>
<tr>
<td></td>
<td>Nephtys australiensis</td>
<td>↑</td>
<td>↓</td>
<td>↑</td>
<td>↑</td>
</tr>
<tr>
<td></td>
<td>Simplisetia aequisetsis</td>
<td>↑</td>
<td>↓</td>
<td>↑</td>
<td>↑</td>
</tr>
<tr>
<td></td>
<td>Oligochaeta</td>
<td>↑↓</td>
<td>↑↓</td>
<td>↑↓</td>
<td>↑</td>
</tr>
<tr>
<td>Arthropoda</td>
<td>Amphipoda</td>
<td>↑↓</td>
<td>↑↓</td>
<td>↑↓</td>
<td>↑</td>
</tr>
<tr>
<td></td>
<td>Insect Larvae</td>
<td>↑↓</td>
<td>↑↓</td>
<td>↑↓</td>
<td>↑</td>
</tr>
<tr>
<td>Mollusca</td>
<td>Velesunio ambiguus</td>
<td>↓</td>
<td>↑</td>
<td>↓</td>
<td>↓</td>
</tr>
<tr>
<td></td>
<td>Arthritica helmsi</td>
<td>↑</td>
<td>↓</td>
<td>↑</td>
<td>↓</td>
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</tbody>
</table>
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