## Conceptual Understanding of CLLMM Zooplankton Structure and Function

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### Propagule Sources and their Connectivity

The sources of the zooplankton in CLLMM samples include the egg bank established by previous generations of microinvertebrates, individuals that have been transported from littoral zones of the wetland (which support different species to those of 'open water' locations) and what has been referred to as the "inoculum" of the inflowing water to a sampling location. The influence that these sources have upon the recruitment to zooplankton populations is determined by the degree of connectivity between source and the location of the population in question.

Zooplankton propagules are resistant to degradation - having been demonstrated to survive passage through the gut of birds (reviewed by van Leeuwin *et al*. 2012) and fish (Battauz *et al.* 2014). That capacity may see the propagules subsequently hatching in locations at some distance from where they were ingested. Other (human-mediated) translocations include associations with bilge water in boats or with bulk fish stocking. Both of these modes are inadequately known/monitored in Australia.

Recruitment from the egg bank of saline-tolerant zooplankton in Lake Albert is likely to be cued by salinity increases during a drying phase, as water levels recede. Conversely, the occurrence of saline-tolerant zooplankton at Meningie in February 2012 following water level increases, is likely to have resulted from increased connectivity with their sources in localised saline 'backwaters' or littoral margins (Shiel and Tan 2013a). Primary among the inflows to the CLLMM site is the River Murray discharge into Lake Alexandrina. Other notable inflows are barrage releases, and flows from Lake Alexandrina into Lake Albert. A more seasonal inoculum is produced by localised catchment contributions to the Goolwa Channel.

### Presence of Current

The presence of water currents is a significant determinant of zooplankton composition. A typical riverine zooplankton assemblage has a large proportion of rotifers (as crustacean zooplankton actively avoid current, their strong presence in assemblages is indicative of standing water conditions, Shiel and Tan 2013a). Significant zones of current change will exist at the mouths of tributaries, and at the distal extent of barrage plumes during discharges (current reducing) and proximal to barrages when their opening generates plumes (current increasing). As a result, marked changes in the relative abundances of rotifers and crustaceans are expected under these circumstances.

### Physical Habitats

The structure and dynamics of physical habitats influence the composition of zooplankton assemblages. Some species have epiphytic/epibenthic habits, requiring the resources provided by macrophyte stands or sediments, which may include refuge from predators. These littoral species are thus uncommon in pelagic situations. Examples of these from CLLMM samples are *Difflugia* spp. and other testate Rhizopoda (Oliver *et al*. 2014). These taxa are not 'technically' planktonic, and are transported to sites by higher flows from Currency Creek and Finniss River. This is an example of lateral connectivity. Lateral connectivity in River Murray catchments has been shown to provide significant biomass for downstream foodwebs. Zooplankton derived from the Chowilla floodplain, were confirmed as inocula entering the Lower Murray channel during the 2010-11 flood (Furst *et al*. 2014).

At coarser scales, the movement and mixing that result from the hydrodynamics of the lakes, lagoons and Murray Mouth also shape physical conditions and influence zooplankton assemblages. Those hydrodynamics are expressed through wave action, seiching, tidal movement and barrage operations. A more challenging hydrodynamic environment likely accounts for some of the reduction of species diversity (Shiel and Tan 2013b) observed between the River Murray inflow site at Jockwar Road and mid-Lake Alexandrina.

**Trophic Roles**

The functions provided by the zooplankton include consumption of bacteria (exemplars being the ciliate protists), grazing of algae, and predation of rotifers and microcrustacea. Bacteriovorous species such as *Stenosemella lacustris, Difflugia globulosa* and *Filinia* spp. take advantage of senescent algae and their organic breakdown products, and show increased pulses of abundance at times of algal blooms (Shiel and Tan 2013a). Oliver *et al.* (2014) expressed concerns for managing protist taxa in the numerical analysis of CLLMM zooplankton counts, as although protists were much more numerous, they were also very much smaller than the other members of assemblages. Given those disparities, a comparison of counts between protists and other zooplankton taxa was considered to add little value and be prone to bias. Of further note, protists were not targeted for the CLLMM zooplankton monitoring; only those with a resistant test were collected consistently and enumerated from samples. These represent a minority of taxa within the protists - most of which are not preserved by ethanol, which was the fixative used. Consequently, the actual protist diversity/density at some sites, particularly in the presence of senescent algal blooms, could well have been several orders of magnitude higher than indicated in Oliver *et al.* (2014).

Integrating subgroups of the zooplankton that vary so greatly in size and abundance requires a change of approach from that of utilizing cell counts. The expression of zooplankton in terms of their nutritional value and availability to their consumers, or their biomass, may improve the basis for advancing our knowledge of ecosystem functions.

Whilst there is a range of zooplanktivorus animals, local literature examples (e.g. Bice 2010, Cheshire 2010) have emphasised the critical importance of zooplankton in providing food for the early development of fish larvae. More than half of the Lower Murray, Lower Lakes and Coorong fish species listed by Bice (2010) spawn in spring and summer, or in one of these two seasons. Larval predation of zooplankton is thus strongly seasonal, and larval growth rates are such that most species remain at the size that targets food of zooplankton dimensions briefly. The components that act as zooplankton predators with a baseline or core function are macroinvertebrates – as they spend longer periods of time with a gape size suited for zooplankton, occur in large numbers and produce multiple generations per year. Microcrustaceans form part of the adult diet for small bodied native fish at the site (e.g. sandy sprat, smallmouthed hardyhead, common galaxias, and Murray hardyhead). Shiel and Tan (2013b) have proposed that predation of the River Murray inoculum expressed at Jockwar Road may contribute to the depletion of diversity evident in mid-Lake Alexandrina samples. Planktivores were demonstrated to have had a significant impact on zooplankton populations in the channel habitats of Hindmarsh Island and Mundoo Island by Wedderburn *et al.* (2013).

**Physiological Tolerances**

Water quality, mediated through their physiological capability, can shape the assemblage composition of zooplankton of the wetland. Prominent in this regard are the effects of differing salinities over time and space. Temperature, light and particulate concentrations are also influential aspects of water quality.

With regards salinity, some species are known to occupy a relatively narrow range of salinities – in either the lower (freshwater) or higher (halophile) parts of the range present in the CLLMM site. In contrast, the halotolerant zooplankton are more adaptable, and their range of occurrence straddles freshwater and saline conditions. Examples of taxa with these tolerances are listed in Table 1. Studies of the Lower Murray at Mannum recorded the water quality ranges in which most of the CLLMM freshwater species are recorded (Shiel *et al.* 1982).

**Table 1. Examples of salinity tolerances among CLLMM zooplankton taxa.**

| HIGHER GROUP | FRESHWATER | HALOTOLERANT | HALOPHILE |
|---|---|---|---|
| Protist | *Stenosomella lacustris* | | |
| Rotifer | Most *Brachionus* spp.<br>Most *Keratella* spp.<br>Most *Filinia* spp.<br>*Hexarthra intermedia* | *Filinia pejleri*<br>*Hexarthra brandorffi*<br>*Keratella australis* | *Testudinella obscura*<br>*Synchaeta tremula*<br>*Synchaeta triophthalma* |
| Crustacean | *Moina micrura*<br>*Diaphanosoma* spp. | *Gladioferens spinosus*<br>*Boeckella triarticulata*<br>*Daphnia carinata s.l.* | *Acartia* spp.<br>*Diacypris* spp. |

A significant attribute of the CLLMM site is the transition, during barrage releases, of zooplankton along the increasing salinity gradient – with resultant transformations in population structure as taxa reach limits in their physiological capability. Barrage flows carry with them zooplankton that can osmoregulate at salinities up to concentrations of 4-5 ppt (Shiel and Tan 2013a); the advancing freshwater plumes will displace estuarine assemblages - through passive displacement, prompting active dispersal, or causing death ('physiological shock') of the halotolerant zooplankton species. Marine water intrusions ("reverse head" events) and reduction of barrage flows drive these species changes in the opposite fashion (Shiel and Tan 2013a). The stimulation of energy transfer through food webs by these 'fertilising' cycles of zooplankton mortality at freshwater/estuarine interfaces is an important ecological process in the site, benefitting particularly small-bodied fish and macroinvertebrates (Shiel and Tan 2013a).

**Subregional Characteristics, Resistance and Biodisparity**

Reflective of the same formative features by which they are recognised (i.e. geomorphology, hydrology and water quality), the subregions of the CLLMM site are associated with discrete zooplankton assemblages (Oliver *et al.* 2014). Many riverine zooplankton species entering Lake Alexandrina do not persist in their new environment, indicating a resistance of the lake zooplankton to connection with inocula. In Lake Albert, a heterogeneity of physical and chemical conditions contributes to a heterogeneity of cues for activation of its egg bank. Consequently, during changes in salinity regime, the eggs of freshwater species hatch when the lake is freshened, and halophile species' eggs hatch during periods of salinization (Shiel and Tan 2013b). This capacity to be readily responsive to changes in salinity is proposed to be the mechanism by which a "buffering" of species turnover takes place in Lake Albert, in turn explaining why 75% of zooplankton species were preserved there over consecutive years when the values in other subregions were around 50% (Shiel and Tan 2013b).

Seaward of the barrages, the influence of lake discharges and tidal influences can be such that consecutive sampling events reveal a freshwater assemblage replaced by an estuarine assemblage (Shiel and Tan 2013a). At other times, resistance prevails – and a more complex arrangement of distinct, vertically-separated, assemblages occurs. Freshwater releases through the barrages may overlie the denser, saline estuary water without appreciable mixing between the two bodies. Under such conditions, surface waters are populated by 'lacustrine' and freshwater plankton derived from Lake Alexandrina; the underlying saline layer supports an assemblage with estuarine or halophile chracteristics - typical of the Murray Mouth or North Lagoon. Despite their presence at the same "site" and same time, no species are shared between these assemblages.

The Coorong North Lagoon supports some halotolerant species that also occur in the South Lagoon, which is otherwise populated by obligate halophile species of zooplankton.

In conclusion, spatiotemporal variability across CLLMM in geomorphology, hydrology and water quality is expressed in the zooplankton similarly to that of other biotic components, that is, via biodisparity.

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