A synthesis of current knowledge of the food web and food resources for waterbird and fish populations in the Coorong

Qifeng Ye, George Giatas, Sabine Dittmann, Ryan Baring, Luciana Bucater, David Deane, Deborah Furst, Justin Brookes, Daniel Rogers and Simon Goldsworthy

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Enquires should be addressed to:
Goyder Institute for Water Research
209A Darling Building, North Terrace
The University of Adelaide,
Adelaide SA 5005
tel: (08) 8313 5020
e-mail: enquiries@goyderinstitute.org

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Respect and Reconciliation

Aboriginal people are the First Peoples and Nations of South Australia. The Coorong, connected waters and surrounding lands have sustained unique First Nations cultures since time immemorial.

The Goyder Institute for Water Research acknowledges the range of First Nations’ rights, interests and obligations for the Coorong and connected waterways and the cultural connections that exist between Ngarrindjeri Nations and First Nations of the South East peoples across the region and seeks to support their equitable engagement.

Aboriginal peoples’ spiritual, social, cultural and economic practices come from their lands and waters, and they continue to maintain their cultural heritage, economies, languages and laws which are of ongoing importance.

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Executive summary

The Coorong is a unique and important wetland that provides significant cultural, environmental and economic values at local, national and international scales. Freshwater inflow reduction, along with other anthropogenic impacts, have led to a long-term ecological decline in the Coorong, with conditions exacerbated during the Millennium Drought (2001–2010). Over the last decade, increased inflow supported the recovery of some elements of the Coorong ecosystem, although the South Lagoon remained in a deteriorated condition with the ongoing profound impacts of hypersalinity and eutrophication (nutrient enrichment) on invertebrates, fish, waterbirds, and the entire food web.

To restore and maintain the ecological condition of the Coorong, particularly for the South Lagoon, the Healthy Coorong Healthy Basin (HCHB) program has commenced, aiming to provide evidence-based solutions to both immediate threats and future conditions anticipated under a changing climate. The Phase One Trials and Investigations (T&I) Project (2020−2022) is part of the HCHB program and involves a series of research components that will collectively provide knowledge to inform the future management of the Coorong. Investigations for '*Restoring a functioning Coorong food web*' forms *Component 3* of the T&I Project.

This report is the output of Activity 3.1 "Knowledge review and synthesis" (Deliverable 3.1.1) of *Component 3* of the T&I Project, which aimed to: 1) Review and synthesise existing knowledge and information in relation to the Coorong food web, including the diets of fish and waterbird species, key food resources and environmental drivers, and food web conceptual models; and 2) Identify knowledge gaps and develop hypotheses of how the Coorong food web, particularly in the South Lagoon, may respond to key environmental drivers, including those potentially affected by management interventions. The main findings are summarised below:

Major food sources for key biota

- The diets of abundant fish species in the Coorong, in general, are well understood. Fishes in the Coorong demonstrate a variety of feeding modes. Most are zoobenthivores or omnivores and have benthic invertebrates as the main prey. The diet composition of several species (e.g. lagoon goby and bony herring) in the Coorong is unknown, and that of larval fish remains poor in this estuary, despite being an important nursery to many species.
- Current understanding of waterbird diets and their major food sources in the Coorong is predominantly based on unpublished feeding observations or limited, early recordings of the stomach contents. Literature on the feeding modes and diets of waterbirds in other geographical locations is available. With the exception of some waterfowl and shorebirds, there is poor understanding of the diet composition or the major food sources of key waterbirds in the Coorong.

Key biota – potential food resources and environmental drivers

- Ecological monitoring in the Coorong, particularly over the last two decades, has significantly advanced our foundational knowledge of the spatio-temporal dynamics of key biota (potential food resources) and their key environmental drivers.
- Freshwater inflow is the primary driver for physiochemical changes, ecological processes and biological responses in the Coorong.
- Zooplankton spatio-temporal dynamics in the Coorong reflect environmental conditions, which are affected by freshwater and marine inflows and the connectivity between and within systems. Barrage inflows not only homogenise Coorong zooplankton composition with upstream sources but affect the distribution of zooplankton in the Coorong.
- Flow, salinity, pH and water temperature are the abiotic factors with the strongest correlation with zooplankton abundance and composition. Nutrients and turbidity also likely contribute, via effects on phytoplankton density and composition. However, biotic factors may also be critical for zooplankton with bottom up and top down controls on composition and abundance, although these processes are poorly understood.

- Salinity, which is strongly influenced by barrage inflows, is the major factor influencing shifts in macroinvertebrate and fish assemblage structure in the Coorong.
- Macroinvertebrate species richness, abundance and biomass have improved in the North Lagoon post-drought under more regular barrage inflows. However, the South Lagoon has not changed as much and the assemblage remains dominated by insect larvae.
- Fish species richness and abundance have increased post-drought associated with increased freshwater inflows and connectivity. Nevertheless, species richness has remained low in the South Lagoon due to hypersalinity (>70 psu).
- Smallmouth hardyhead and sandy sprat are the most abundant prey fish species in the Coorong, with smallmouth hardyhead dominating the South Lagoon and North Lagoon, with sandy sprat being more abundant in the Murray Estuary.
- From the food web perspective, further research is needed to investigate the changes in biomass of key biota across space and time to inform quantitative modelling.
- Furthermore, investigations into the energetic and nutritional values of key biota will improve our understanding of the quality of different food resources for waterbirds and fish and help quantify bioenergetic trophic links in the food web.

Current Coorong food web conceptual models

- Our conceptual understanding of the Coorong food web, keystone species, and how it operates spatially and temporally has improved considerably over the last two decades. At least four distinct food webs have been described for the Coorong along its salinity gradient, with a general decline in the diversity of feeding guilds and food chain length with increasing salinity. Freshwater inflow, being the key driver, is fundamental in: reducing salinities and increasing the distribution of biota; transporting nutrients and food resources to increase productivity; and maintaining connectivity between environments for movement.
- Food web models that have been developed in the past for the Coorong are semi-quantitative or qualitative, and thus have limited capacity to predict responses to environmental change, including management options/interventions. Integrated, quantitative food web models can assess food web responses to various environmental changes and will be useful tools to help guide the management for food web restoration in the Coorong.

Knowledge gaps and hypotheses for the Coorong food web

The prolonged hypersaline and hypereutrophic conditions in the southern Coorong are currently constraining the reinstatement of key ecological attributes of a desired ‘healthy’ state. To restore a healthy ecological state, including a more complex and resilient food web in the South Lagoon, we hypothesise that lower salinity, reduced nutrient load and water level management are key to reinstate suitable conditions and improve ecological functions and services. This report provides a knowledge synthesis for the Coorong food web and identifies key knowledge gaps for further study. The food web investigations through T&I Project *Component 3*, building on existing knowledge and data, will provide critical information and an integrated quantitative food web model to support the assessment of the ecological response under different environmental conditions to potential management scenarios/options. The model will provide a decision support tool to help identify and optimise management options that will maximise the ecological outcomes in the Coorong, particularly concerning the ecological restoration in the South Lagoon.

Acknowledgments

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1 Introduction

1.1 Background

The Coorong is widely regarded as the most important waterbird wetland in the Murray-Darling Basin (MDB) (Kingsford et al. 2011). It is a unique and important wetland that provides significant cultural, environmental and economic values at local, national and international scales. Along with Lake Alexandrina, Lake Albert and the Murray Mouth and Estuary, the Coorong is a listed Ramsar wetland of International Importance (Phillips and Muller 2006).

Located at the end of the MDB, the Coorong has been profoundly impacted by altered flow regimes due to river regulation and water extraction for consumptive use (e.g. irrigation). There has been a substantial decrease in mean annual inflow to ~39% (4,723 GL) of the natural inflow (12,233 GL) for the period of 1895−2006, whilst periods of cease-to-flow occur 40% of the time compared with 1% under natural unregulated conditions (CSIRO 2008). Furthermore, five barrages (total length of 7.6 km) create an extensive ecological barrier, largely separating the freshwater Lower Lakes (Alexandrina and Albert) from the Coorong estuary (Figure 1).

The reduction of inflows, along with other anthropogenic impacts, have led to a long-term decline in the Coorong ecosystem with ecological condition, which was exacerbated during 2001−2010 due to the Millennium Drought (Brookes et al. 2009b, 2018). Whilst there has been a recovery of some elements of the Coorong ecosystem associated with increased inflows over the last decade, the South Lagoon has not recovered to the levels expected. In this region, there has been a switch of the ecosystem from being dominated by aquatic plants (in particular *Ruppia tuberosa*) to algae associated with eutrophication (nutrient enrichment), with subsequent impacts on invertebrates, fish, waterbirds, and thus the entire food web (Collier et al. 2017, Brookes et al. 2018, Ye et al. 2019c). These ecosystem changes and the lack of recovery in the South Lagoon is likely caused by a number of complex interacting factors, many of which are not well understood (Mosley et al. 2020). This is limiting the capacity to forecast the ecological response to future management scenarios and therefore the capacity of water managers to identify management interventions required to improve the health of the Coorong.

The Phase One Trials and Investigations (T&I) Project (2020−2022) of the Healthy Coorong Healthy Basin (HCHB) program consists of a series of integrated components that will collectively provide knowledge to inform the future management of the Coorong. *Component 3 – Restoring a functioning Coorong food web* (hereafter, '*Food web*') forms part of the T&I Project (Table 1).

Table 1. Activities within *Component 3 Restoring a functioning Coorong food web* of the Trials and Investigations Project.

ACTIVITY	OBJECTIVES
3.1	Review, synthesis and conceptual food web models - to review the literature and data to develop conceptual food web models for the Coorong.
3.2	Diet and food consumption of key species - to investigate the major food sources and their relative contribution to the diet for key waterbird and fish species.
3.3	Bioenergetics and key drivers for food resource availability - to investigate food resource abundance, productivity, biomass, energy content and availability, and the influence of key environmental factors.
3.4	Quantitative food web model - to develop an integrated quantitative food web model for the Coorong ecosystem.

Maintaining a productive and resilient food web is critical to preserving the ecological character of the Coorong. Under suitable environmental conditions, the trophic productivity supports a diversity of biota across multiple trophic levels, including fish and waterbirds (Deegan et al. 2010, Dittmann et al. 2018, Giatas et al. 2018). A more complex food web with multiple trophic levels, as present in the Murray Estuary and North Lagoon is considered to be more resilient and can support higher biodiversity than a simple food web with a few species in low numbers, occurring under extremely hypersaline conditions in the South Lagoon (Brookes et al. 2015, Giatas and Ye 2016, Breaux et al. 2019). To inform the development of strategies to restore a functioning South Lagoon food web, T&I *Component 3 Food web* focuses on investigating the food resources and conditions required to increase food resource availability and energy supply for key biota (waterbirds and fish) in the Coorong. Findings will support the development of an integrated quantitative food web model that can be used to assess food web responses to various conditions (e.g. through management actions and interventions). The specific aims of *Component 3 Food web* research are to:

- Identify key food resources (e.g. invertebrates, small-bodied fishes) for waterbirds and fish.
- Determine food resource habitat requirements and key environmental effects on their spatial and temporal trends (i.e. abundance, biomass, distribution).
- Quantify the trophic links, also including food resource availability and accessibility, and bioenergetic quality.

To achieve these aims, an empirical approach (including field, laboratory and modelling work) has been adopted over the period of 2020−2022. This data and literature review (Activity 3.1, Table 1) was conducted to synthesise existing knowledge and information to support further investigation on the Coorong food web and food resources via *Component 3 Food web*.

1.2 Aims

The specific aims of this report (Activity 3.1 "Review, synthesis and conceptual food web models") are to:

- Review and synthesise existing knowledge and information related to the Coorong food web, including the diets of fish and waterbird species, key food resources and environmental drivers, and food web conceptual models.
- Identify knowledge gaps and develop hypotheses of how the Coorong food web, particularly in the South Lagoon, may respond to key environmental drivers, including those potentially affected by management interventions.

The review considers information from Coorong studies in all geomorphic regions (the Murray Estuary, North Lagoon and South Lagoon) (Figure 1), as habitat heterogeneity and environmental conditions can affect prey availability and foraging patterns (Rosa et al. 2007, VanDusen et al. 2012) and the functioning of estuarine food webs (Breaux et al. 2019).

Section 2 of the report provides a summary of major food sources for key biota, including fish and waterbirds; Section 3 presents the contemporary ecological understanding of potential food biota (zooplankton, macroinvertebrates and fish) and key environmental drivers in the Coorong; Section 4 describes current conceptual food web models for the Coorong; and Section 5 summarises the knowledge gaps and provides hypotheses to guide future research.

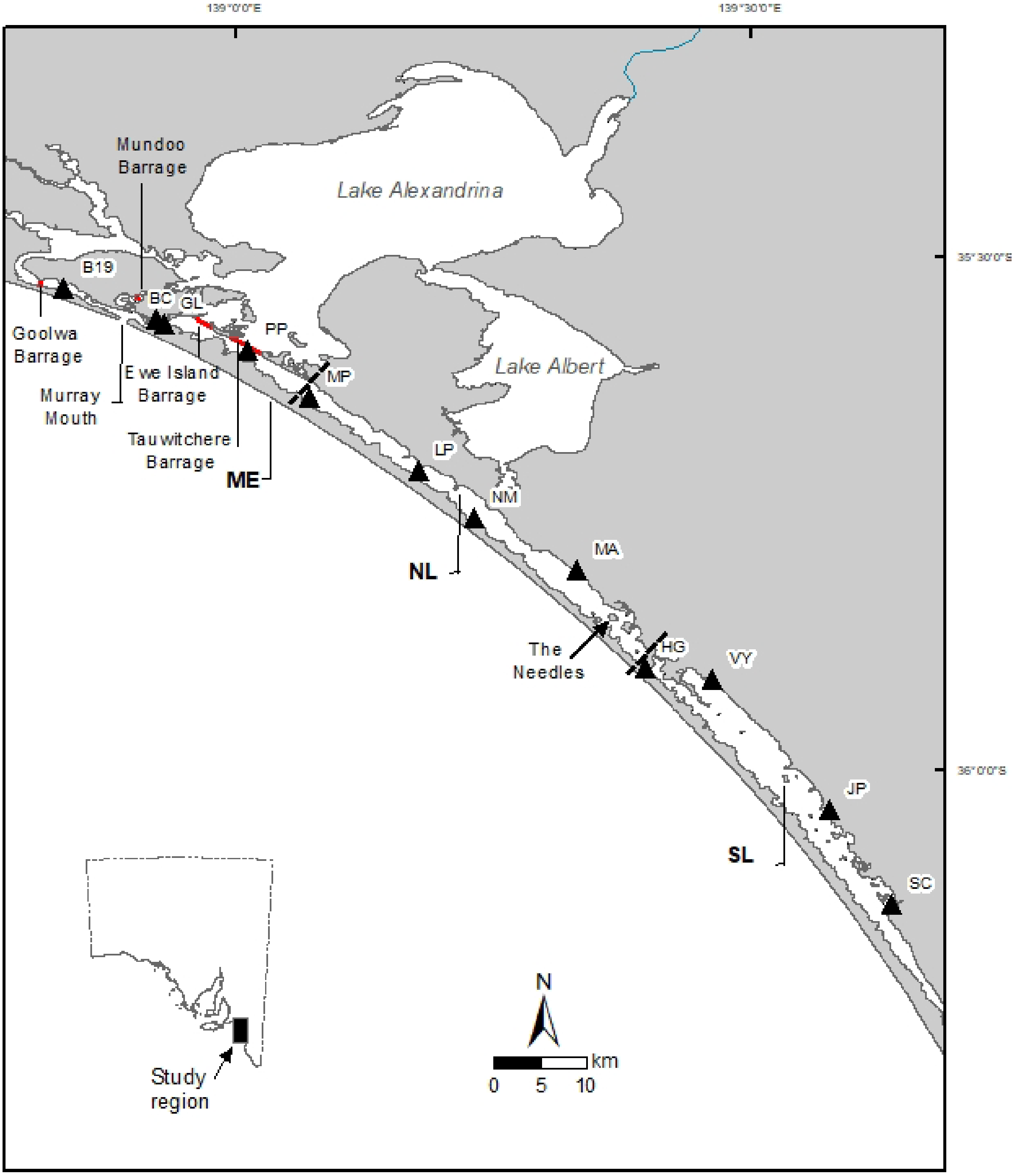


Figure 1. A map of the Coorong regions showing the Murray Estuary (ME), North Lagoon (NL) and South Lagoon (SL), barrages and key sites. B19 = Beacon 19, BC = Boundary Creek, GL = Godfrey's Landing, PP = Pelican Point, MP = Mark Point, LP = Long Point, NM = Noonameena, MA = Mt Anderson, HG = Hells Gate, VY = Villa de Yumpa, JP = Jack Point and SC = Salt Creek.

1.3 Flow, salinity and water levels

Freshwater inflow from the Murray River is a key driver of ecological processes and biological responses in the Coorong. Over the last two decades, which cover the main temporal scope of the research and monitoring projects synthesised in this review, there has been significant hydrological variability, incorporating a protracted drought from 2001–2010 (the Millennium Drought), followed by high flows in 2011–2013, and a subsequent decrease in discharge until 2020 apart from high flows in 2016-17 (Figure 2). From July 2001 to June 2020, the southern end of the South Lagoon also received small volumes of fresh/brackish water (mean = 16.4 GL y^{-1} from a network of drains (the Upper South East Drainage Scheme) through Salt Creek (Figure 2).

In the Coorong, salinities are largely influenced by discharge from the barrages and interplay with tides, driven by oceanic water-level fluctuations, and winds (Gibbs et al. 2018). The hydrology and geomorphology of the Coorong, however, also produces a salinity gradient, with salinity increasing from the Murray Estuary southeast to the South Lagoon, irrespective of freshwater inflow (Gibbs et al. 2018, also see Figure 3). During the drought, the lack of freshwater inflows led to a general increase in salinity throughout the Coorong and the contraction, and ultimately loss, of a salinity gradient from brackish to marine. During the drought years, the mean salinity was 38 psu (seawater = 36 psu) in the Murray Estuary, 70 psu in the North Lagoon and 146 psu (~4 x seawater) in the South Lagoon (Figure 3). Connectivity between estuarine and freshwater habitats was substantially reduced or lost due to barrage closure (e.g. 2007–early 2010) and dredging at the Murray Mouth was required for eight years (2002–2010) to maintain estuarine–marine connectivity (DEWNR 2015).

With increased flows post-2010, salinity was substantially reduced throughout the system with the salinity gradient (freshwater–brackish–marine) restored in the Murray Estuary and northern part of the North Lagoon and salinity reduced to <100 psu in the South Lagoon (Figure 3). Importantly, connectivity was re-established between freshwater, estuarine and marine environments and has persisted since late-2010. Due to reduced inflows after 2013, dredging of the Murray Mouth recommenced in January 2015 (DEWNR 2015).

Inflow through the barrages also has a strong influence on water levels in the Coorong (Figure 4). Annual mean water level was around 0.2 m (Australian Height Datum (AHD)) during the drought years, whereas it increased to near 0.4 m (AHD) in high flow years (Figure 4).

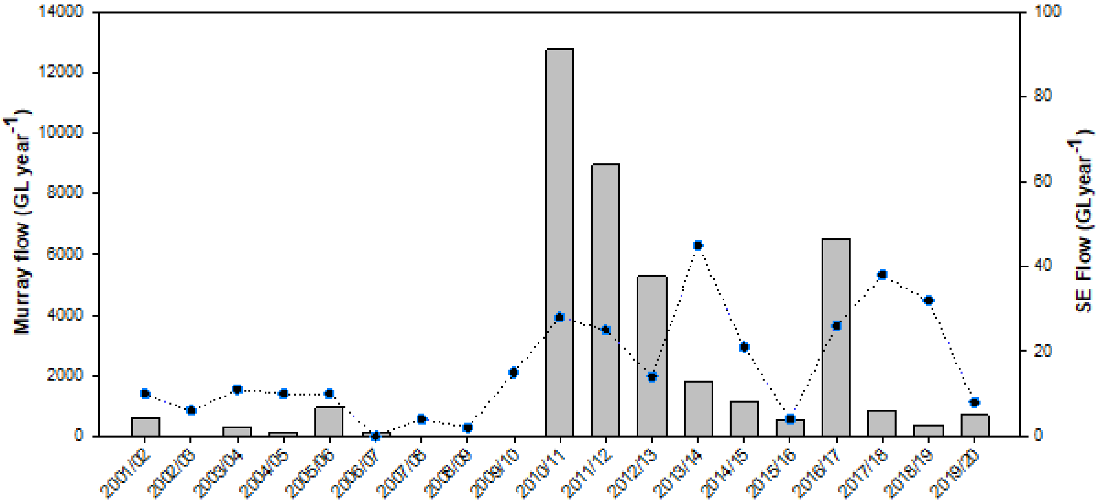


Figure 2. Annual flow discharge over the Murray barrages (grey bars) and South East (SE) flow discharge (blue dotted line). Note the different axis scaling. Data sources: Dashboard data for Murray flow and WaterConnect website for SE flow.

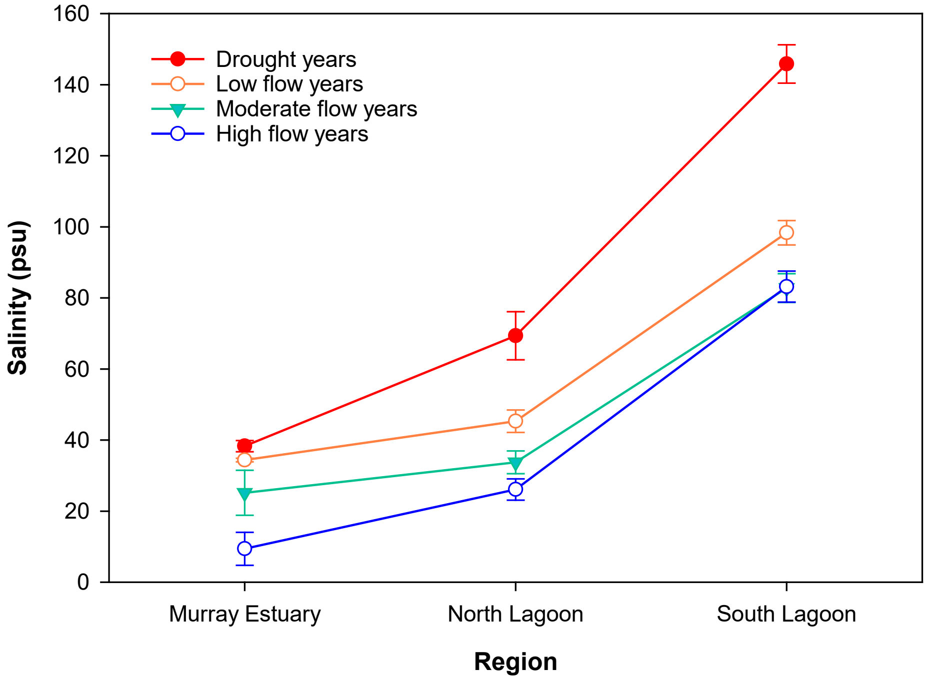


Figure 3. Annual mean salinity (sites pooled) ± SE in different regions along the Coorong during years of drought (2006-07 to 2009-10), low (2015-16, 2018-19, 2019-20), moderate (2013-14, 2014-15, 2017-18) and high (2010-11–2012-13 and 2016-17) flows. Data sources: Noell et al. 2009, Ye et al. 2020.

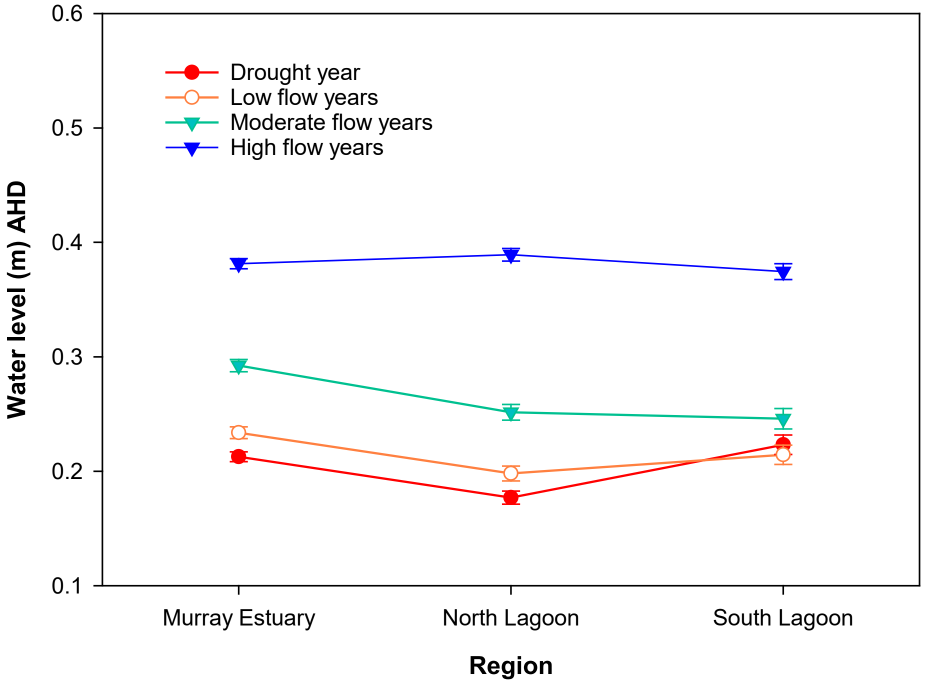


Figure 4. Annual mean water levels (sites pooled) ± SE in different regions along the Coorong during years of drought (2006-07 to 2009-10), low (2015-16, 2018-19, 2019-20), moderate (2013-14, 2014-15, 2017-18) and high (2010-11–2012-13 and 2016-17) flows. Data sources: Surface WaterConnect Data.

2 Major food sources for key biota

Identifying the major food sources of key biota such as fish and waterbirds is fundamental in understanding trophic interactions of food webs. Understanding how food webs operate and may respond to environmental change is critical knowledge for the effective management of ecosystems. In an attempt to restore the ecological condition of the South Lagoon, a key objective of the HCHB project is to promote or provide food resources for key biota (i.e. abundant waterbird and fish species and/or those of a significant conservation value). In order to do this, good knowledge of the diets of key biota in the system is required. Further, the relationship between the distribution and abundance of these food species and the hydro-ecology of the system is required (See Section 3). The objective of this section is to summarise the current knowledge of the diets and feeding modes of fish (Section 2.1), waterbirds (2.2) and macroinvertebrates (2.3) in the Coorong, and identify knowledge gaps (Section 2.4) to guide future research (Activity 3.2, Table 1).

2.1 Fish diet

Diets of many key fish species in the Coorong have been assessed, primarily through the identification and quantification of gut contents (e.g. Geddes and Francis 2008, Deegan et al. 2010, Giatas and Ye 2015, Hossain et al. 2017) and stable isotope approaches (e.g. Lamontagne et al. 2016), although the latter has generally been used to understand trophic positions (Table 3) and groupings (‘trophic guilds’). Our understanding of the diet composition of abundant estuarine and marine species (e.g. smallmouth hardyhead *Atherinosoma microstoma*, sandy sprat *Hyperlophus vittatus* and yelloweye mullet *Aldrichetta forsteri*) is based on work carried out predominantly over the last two decades during variable hydrology (Section 1.3). The knowledge of the diets of common freshwater species (e.g. bony herring *Nematalosa erebi* and common carp *Cyprinus carpio*), whose abundances are temporally variable in the Coorong, is based on data (e.g. Hall 1981, Atkins 1984, Wedderburn et al. 2014) from the freshwater habitats of the lower MDB (i.e. Lower Lakes and Lower Murray River).

There is no dietary information available from the Coorong, Lower Lakes and Murray Mouth (CLLMM) region for other, less-abundant species, such as estuarine river garfish (*Hyporhamphus regularis*), lagoon goby (*Tasmanogobius lasti*), bluespot goby (*Pseudogobius olorum*), bridled goby (*Arenigobius bifrenatus*) and longsnout flounder (*Ammotretis rostratus*); marine Australian herring (*Arripis georgianus*); and freshwater flathead gudgeon (*Philypnodon grandiceps*) and Australian smelt (*Retropinna semoni*). Our understanding of the diets of most of these species is based on external literature in locations where the availability of food items is likely to differ from that in the CLLMM.

2.1.1 Feeding modes and major food sources for fish

While fishes in the Coorong collectively demonstrate a variety of feeding modes (Table 2), many show broad diets (e.g. yelloweye mullet) and feed on a variety of food sources (Table 4). This is common in estuaries and an adaptation to variable environmental conditions such as food availability. Most fishes in the Coorong are zoobenthivores or omnivores (Table 2), and have large proportions of their diets made up by benthic invertebrates (Table 4, Figure 5).

Table 2. Feeding modes of abundant fish species in the Coorong. Feeding modes are adapted from Giatas et al. (2018).

FEEDING MODE	DESCRIPTION	SPECIES
Piscivore	Predominantly feed on fish, but their diet can include other food items such as large invertebrates.	Mulloway, Australian salmon, golden perch*, redfin perch*
Zoobenthivore	Predominantly feed on benthic macro-invertebrates, but diet may include other food items such as fish or pelagic invertebrates	Smallmouth hardyhead, Tamar goby, congolli, greenback flounder, Australian herring, longsnout flounder, flathead gudgeon*
Zooplanktivore	Predominantly feed on zooplankton, but diet may include other animal items.	Sandy sprat
Herbivore	Exclusively feed on macroalgae, macrophytes and/or microalgae.	N/A
Detritivore	Exclusively feed on detritus.	Sea mullet
Omnivore	Omnivores feed on macroalgae, macrophytes, microalgae and/or detritus, along with animal items.	Yelloweye mullet, black bream, lagoon goby, bridled goby, river garfish, goldspot mullet, smooth toadfish, common carp*, bony herring*
Insectivore	Predominantly feed on insects.	Australian smelt*, common galaxias*

*freshwater species

The feeding modes and diets of fishes in the Coorong have been presented previously in Giatas et al. (2018) and are summarised in Tables 2 and 4, respectively, with Figure 5 showing dietary overlap among species. While each species has been classified into one of several feeding modes based on available data, individuals of certain species can change feeding modes because of shifts in diet related to their life cycle (‘ontogenetic shifts’; Werner and Gilliam 1984, Elliot et al. 2002). For example, most fishes have a zooplanktivorous larval stage (also see ‘pelagic microcrustaceans and rotifers’ section below), but several transition to piscivory in the adult life stage. Mulloway (*Argyrosomus japonicus*) demonstrate a pronounced ontogenetic shift in diet typical of many large-bodied fishes, with trophic level generally increasing through ontogeny (Table 3) as small crustacean prey are replaced by larger decapods and fish (Giatas and Ye 2015). Yelloweye mullet exhibit a more atypical ontogenetic dietary shift, with the proportion of animal prey items in the diet declining with fish size, while the proportion of filamentous algae and detritus increases (Giatas 2012).

Major prey items for fish species of different feeding modes, based on dietary data from the Coorong and Lower Lakes, have been summarised in Table 4. These prey are based on composition data, not selectivity indices, and so reflect the major prey contributing to diet, but may not reflect the preferred prey. ‘Major’ prey/food items were classified as those that contributed towards ≥20% of the diet composition by weight or volume, or occurred in ≥50% of stomachs, or were the most frequently occurring/contributing prey item, of a particular study. It is important to note that the number of prey items recorded in Table 4 may not reflect how broad the diet of that species is, as there may be sampling effort biases towards some fish species or hydrological periods.

Table 3. Mean estimated trophic positions of fish species across size ranges, sites and/or regions in the Coorong. Trophic levels: 1 = primary producers, 2 = primary consumers (herbivores/detritivores), 3 = secondary consumers (carnivores that feed on primary consumers), 4+ = higher-order consumers (carnivores that feed on secondary consumers or higher) (see Figure 40).

SPECIES	MEAN TROPHIC POSITION
Bony herring*	2.5[4]
Sandy sprat	3.3[1], 2.9[4], 2.9[5]
Congolli	3.3[1], 3.0[4]
Gobies (incl. Tamar)	3.2[1], 3.1[4]
Smallmouth hardyhead	3.3[1], 3.2[4]
Yelloweye mullet	3.4[1],3.4[2],3.2[4]
Greenback flounder	3.2[1], 3.4[3], 3.4[4]
Common galaxias	3.5[1]
Australian salmon	3.5[4]
Black bream	3.6[1]
Mulloway	4.2[1], 3.6[4]
Mulloway >700 mm	4.0[4]

*Omnivorous species, based on their trophic position (i.e. TP>2<3)

[1.] Deegan et al. 2010, [2.] Giatas 2012, [3.] Earl 2014, [4.] Giatas and Ye 2015, [5.] Bice et al. 2016a.

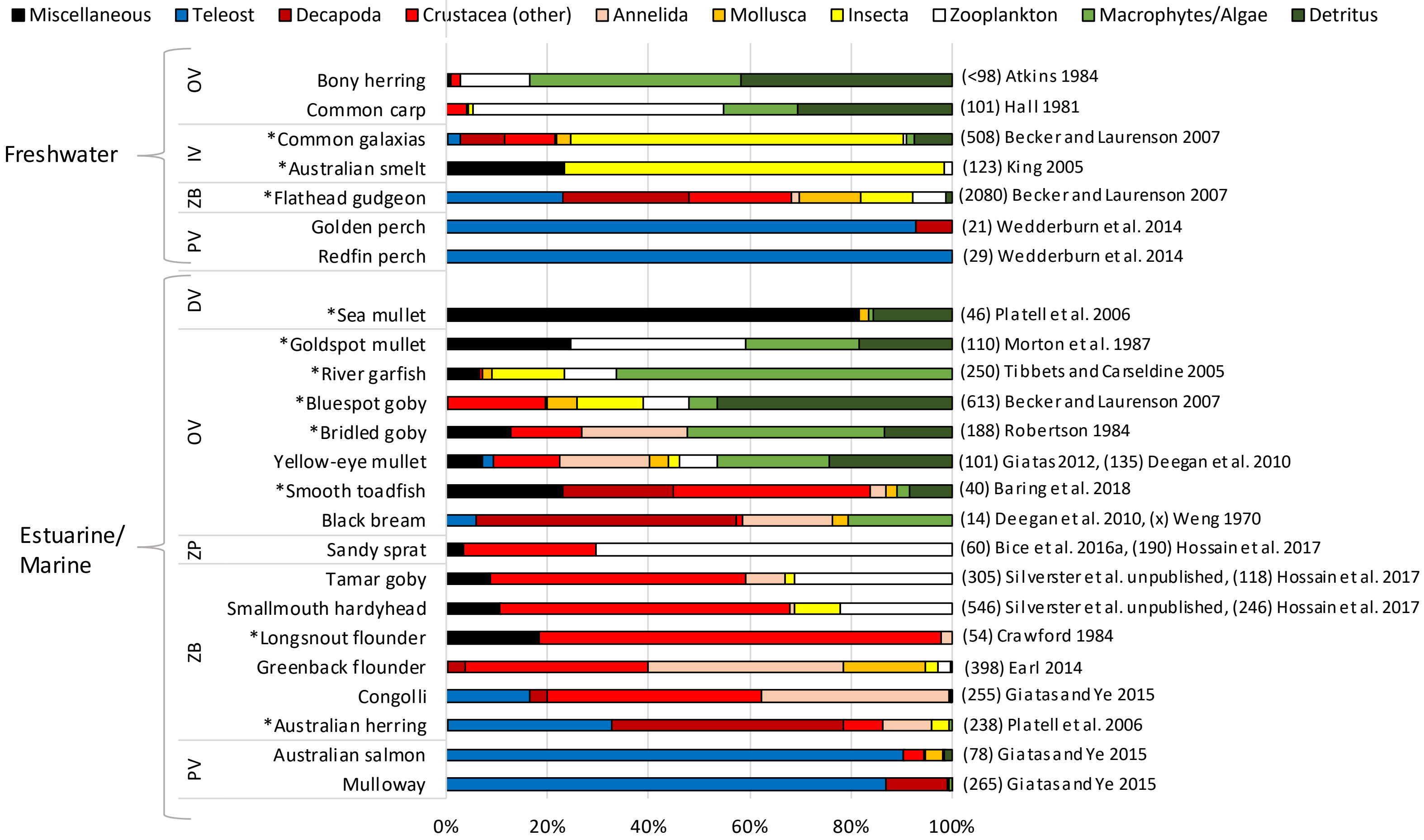


Figure 5. Boxplots showing the proportional abundance of major dietary components and dietary overlap of common fish species in the Coorong. Diet composition is calculated using data from the indicated studies and sample numbers. Feeding modes are: PV = piscivore, ZB = zoobenthivore, ZP = zooplanktivore, OV = omnivore, DV = detritivore, IV = insectivore, HB = herbivore (Table 2). x = unknown sample size. * = Data not from the CLLMM region. Miscellaneous category includes sand/shell fragments, unidentified matter and animals not belonging to any of the other categories.

Table 4. Food items for fishes in the Coorong, based on Coorong data. Major prey for species are indicated by dark blue shading, while other prey consumed are in lighter shading. Literature from which the information is obtained is shown. Size categories (in millimetres) are presented for some species (e.g. mulloway) in parenthesis.

FOOD ITEMS	MULLOWAY	AUSTRALIAN SALMON	CONGOLLI	GREENBACK FLOUNDER	SMALLMOUTH HARDYHEAD	TAMAR GOBY	SANDY SPRAT	BLACK BREAM	YELLOWEYE MULLET	REDFIN PERCH	GOLDEN PERCH	COMMON CARP	BONY HERRING
Small-bodied fish	**1 (<500)**	**2**	2							3,4	3,4		
Atherinids (incl. smallmouth hardyhead)													
Sandy sprat	**2 (<500)**	**2**											
Gobies (incl. Tamar, lagoon, bridled and bluespot)	2,6	2	**2,6**					5,6					
*Flathead gudgeon				7						**3,4**	3		
*Australian smelt	2										3,4		
*Gambusia			2										
Large-bodied fish	**2,8**	2											
Mugilids (incl. yelloweye mullet)													
Bony herring	1,2	2								**3**	**3**		
*Common carp										**3**	3		
*Redfin perch	2									**3**	**3**		
Congolli	2,8												
Mulloway	2 (>500)												
Australian salmon	2,6												
Pleuronectidae (incl. greenback and longsnout flounder)	2												
*Common galaxias		2											
Decapods	**2,6**	2	**6**	6,7				**5,6**	6,8				
Crabs (incl. *Paragrapsus gaimardii*)													
Penaeid shrimp (*Melicertus latisulcatus*)				7									
Ghost shrimp (*Biffarius* spp.)				7									
*Carid shrimp (*Macrobrachium* spp. and *Paratya australiensis*)	2,6	2	2								3		
*Freshwater yabby (*Cherax destructor*)			2										
Other crustaceans	2,6 (<500)	2	**2**	**7,8**	**6,8,9,10**	**8,9,10**	**10**		**11 (<150)**			12	
Amphipods													
Mysids	**2 (<400)**	2	6,11	7	8,10	10	10		6,11				
Ostracods		2		7	**10**	10	10,13		6,8,11				
Cumaceans			2	7									
**Isopods			2										
Annelids			2	6,7	6,8	8		6	**8**				
Capitellids (*Capitella* spp.)													
Nereids (*Simplisetia aequisetis* and *Australonereis ehlersi*)	2	2	**2**	6,7	9	9,10		6	6,8,11				
Phyllodociids (*Phyllodoce*)				6,7					6,8				
Nephtyiids (*Aglaophamus*)	2,6			**7**				6	6,11				
Spionids					8	8			8,11				
Ficopomatus enigmaticus				7									
Oligochaetes			2	7	9	9							
Arenicolids (*Arenicola* spp.)									8				
Molluscs			2	6,7				6	6,8,11				
Arthritica													
Tellina				7					6				
Notospisula				7									
Donax deltoides		2											
Salinator fragilis				6									
Hydrobiids		2	2						6				
Insect larvae/pupae		2		7	9,10	9			11			12	14
Chironomidae													
Other dipterans (Ephydridae, Dolichopodidae, Ceratopogonidae)				7	9				11				14
*Hemipterans (e.g. Corixids and Notonectids)		2	2		9	9			11				
*Nymphs and larvae (damselfly, dragonfly, caddisfly)			2		9								
Other insects (e.g. moth), thrips stratiomyidae, coleoptera	2		2		9				11				
Copepods					9	**9**						12	
Calanoid			2	6			10,13		6				14 (<80)
Harpacticoid				6	**9**	10	**10,13**		6				
Cyclopoid		2	2				13						
Cladocerans									11				
Daphniids (*Daphnia* and *Ceriodaphnia*)			2	7	9	9						**12**	14
Bosminids (*Bosmina*)						10	**13**					12	14
Moinids													14
Chydorids (e.g. *Illocryptus, Leydigia, Biapertura, Macrothrix*)												12	
Other zooplankton							10,13		6,11				
Macroinvertebrate pelagic larvae (e.g. crab zoea and megalopa)													
Rotifers (e.g. *Keratella australis*, *Filinia* spp., *Brachionus* sp., *Lecane* sp.)						10	13						14
Detritus									**11**			**12**	**14**
Algae								6					
Filamentous (e.g. *Cladophora*, *Ulva*)									**11**			12	**14**
Diatoms									6,11				14
Macrophytes													
Ruppia tuberosa													

1. Hall 1986, 2. Giatas and Ye 2015, 3. Wedderburn et al. 2014, 4. Wedderburn and Barnes 2016, 5. Weng 1970, 6. Deegan et al. 2010, 7. Earl 2014, 8. Geddes and Francis 2008, 9. Silvester et al., 10. Hossain et al. 2017, 11. Giatas 2012, 12. Hall 1981, 13. Bice et al. 2016a., 14. Atkins 1984. *freshwater or catadromous species considered to occur in low abundance in the Coorong. Golden perch is a piscivore based on data from the Lower Lakes (Wedderburn et al. 2014) but is considered to be a zoobenthivore based on other literature (e.g. Baumgartner 2007). **isopods may not be a prey item, but a parasite. Species with detritus and algae present in their stomachs that are not considered to be omnivorous or detritivorous have been excluded from this table and it is assumed this material has been incidentally ingested with animal items.

Fish

The most abundant piscivorous fishes in the Coorong are mulloway and Australian salmon (*Arripis trutta*) (Table 2, Figure 5). During times of high freshwater inflow to the Coorong and low salinities, freshwater piscivores such as redfin perch (*Perca fluviatilis*) and golden perch (*Macquaria ambigua*) may enter the Coorong (Section 3.4, Bice et al. 2018). A summary of the major fish prey for different fish species is provided in Table 4.

'Prey' or 'forage' fishes (e.g. fish <100 mm) are important in the diets of Australian salmon and small mulloway (<500 mm). Examples of these in the Coorong are smallmouth hardyhead and sandy sprat, which are abundant, schooling species (Section 3.4, Bice et al. 2018). In 2013-14, these species collectively contributed, by weight, to 33 and 50% the diet composition of small mulloway (<400 mm) and Australian salmon, respectively (Giatas and Ye 2015). Sandy sprat is a major food source for Australian salmon (Hoedt and Dimmlich 1994, Edgar and Shaw 1995, Stewart et al. 2011) and mulloway (Taylor et al. 2006) in other estuaries. While sandy sprat has not been recorded as prey for mulloway in other Coorong studies, smallmouth hardyhead were reported as the most frequently occurring prey item for mulloway (150–460 mm) in the North Lagoon in 1984 (Hall 1986).

Gobies are a key prey species for Australian salmon in the Coorong. In 2013-14, gobies contributed to 19% (by weight) of this species diet in the Coorong, with Tamar goby making up 12% (Giatas and Ye 2015). Gobies are the only fish prey item recorded for black bream (*Acanthopagrus butcheri*) in the Coorong, although they occurred in relatively low frequency (5–7%) in stomachs (Weng 1970, Deegan et al. 2010). While gobies are also the key fish prey group for black bream in Western Australian estuaries, atherinids (*Atherinosoma* sp.) have also been reported (Chuwen et al. 2007, Linke 2011) and are likely consumed by black bream in the Coorong.

Mugilids (e.g. yelloweye mullet) are the dominant prey item for large mulloway in the Coorong. In the Coorong during 2013-14, yelloweye mullet contributed, by weight, to 95% of the diet composition of mulloway >700 mm (Giatas and Ye 2015). Other medium- and large-bodied fish species (e.g. bony herring and congolli *Pseudaphritis urvillii*) are also consumed by mulloway in the Coorong (Table 4).

Benthic invertebrates

Zoobenthivorous fishes in the Coorong include greenback flounder (*Rhombosolea tapirina*), smallmouth hardyhead, Tamar goby (*Afurcagobius tamarensis*), congolli, longsnout flounder, flathead gudgeon and Australian herring (Table 2, Figure 5). During times of high freshwater inflow to the Coorong, freshwater zoobenthivores such as flathead gudgeon may be abundant (Ye et al. 2019c). Benthic invertebrates also form considerable proportions of the diets of some omnivores, which include yelloweye mullet, black bream and some gobies (e.g. bridled and bluespot) (Table 2, Figure 5). A summary of the major benthic invertebrate prey for different fish species is provided in Table 4.

Decapods

In the Coorong, crabs are the main prey item for black bream, mulloway and congolli (Table 4). During 2006-07, crabs were the most frequently occurring prey item in the stomachs of black bream (86% of stomachs), mulloway (<550 mm, 54%) and congolli (155–205 mm, 35%) (Deegan et al. 2010). In 2013-14, the shorecrab *Paragrapsus gaimardii* contributed, by weight, to 28% of the diet composition of mulloway 400–700 mm (Giatas and Ye 2015). While other species (e.g. *Amarinus lacustris*) are present in the Coorong and consumed by these species (Giatas and Ye 2015), *P. gaimardii* is likely to make up the majority of the decapod biomass (e.g. Ye et al. 2019c) and be the main decapod prey to consumers.

Carid (e.g. *Macrobrachium* spp.) and penaeid (Western king prawn *Melicertus latisulcatus*) shrimp, and freshwater (*Cherax destructor*) and saltwater (ghost shrimp) yabbies, are other decapods that are not abundant in the Coorong, but may occur (Deegan et al. 2010). They may be consumed by a number of carnivorous fish such as congolli, mulloway and greenback flounder (Table 4). In 2006-07, *Macrobrachium* sp. occurred in 33% of mulloway (<550 mm) stomachs in the Murray Estuary (Deegan et al. 2010). In freshwater habitats (e.g. Lower Lakes) where they are more abundant, carid shrimp are a major prey item for congolli. In 2013-14, *Macrobrachium* sp. contributed, by volume, to 64% of the diet composition of congolli in the Lower Lakes in 2013-14 (Giatas and Ye 2015). In other estuaries where shrimp/prawns are abundant, they form a large proportion of the diet of zoobenthivores and piscivores (e.g. Hortle and White 1980, Taylor et al. 2006).

Other crustaceans

In the Coorong, amphipods are one of the major prey items for small-bodied Tamar goby and smallmouth hardyhead. In previous investigations, amphipods occurred in 90–95% and 53–76% of Tamar goby and smallmouth hardyhead diets, respectively (Deegan et al. 2010, Hossain et al. 2017). While sandy sprat are considered pelagic feeders (zooplanktivores, see 'pelagic microcrustaceans' section), amphipods may also be a major prey item for this species (59% frequency; Hossain et al. 2017). They are also a major prey item for congolli (Giatas and Ye 2015), greenback flounder (Earl 2014) and small (<150 mm) yelloweye mullet (Giatas 2012), and have made up, by volume, 37, 33 and 18% of the diet composition of these species, respectively (Table 4). Based on studies outside of the Coorong, amphipods are likely to be major food items for other zoobenthivores such as longsnout flounder (Crawford 1984).

While mysid shrimp are consumed by many fish species in the Coorong, they are only considered to be a major prey item for small mulloway. In the Coorong during 2013-14, mysids occurred in 49% of stomachs of mulloway <400 mm (Giatas and Ye 2015). The importance of mysids in the diet of juvenile mulloway has also been documented in South African (Marais 1984, Griffiths 1997) and eastern Australian estuaries (Taylor et al. 2006).

Ostracods are known to occur in high frequency in stomachs of smallmouth hardyhead (58%) and sandy sprat (37%) (Hossain et al. 2017). In the South Lagoon where ostracods are more present (Dittmann et al. 2018), they form a considerable proportion of the diet composition of smallmouth hardyhead (Section 2.1.2, Hossain et al. 2017).

Annelids

In the Coorong, polychaetes are major prey items for greenback flounder, congolli and yelloweye mullet (Table 4). By volume, *Aglaophamus australiensis* made up 31% of the diet of greenback flounder during 2009–2011 (Earl 2014), while nereid polychaetes (i.e. *Simplisetia aequisetis* and *Australonereis ehlersi*) made up 34% of the diet of congolli in 2013-14 (Giatas and Ye 2015). At Pelican Point in 2004-05, *Capitella* sp. occurred in the stomachs of 85% of small (30–80 mm) and 80% of large (230–300 mm) yelloweye mullet (Geddes and Francis 2008). This prey species has a high tolerance for poor environmental conditions (e.g. salinity of 0–90 psu and dissolved oxygen of 3–11 mg/L) (Dittmann et al. 2018). Highest abundances are often found to be at salinities ~40 psu in the Coorong (Figure 27, Section 3.3.3), with it considered to be an important prey item for zoobenthivores at these salinites. In other estuaries, polychaetes are major food items for omnivorous gobies, such as bridled goby (Robertson 1984).

Other annelids (e.g. *Phyllodoce* spp., oligochaetes, spionids and arenicolids) are consumed by benthic-feeding species (Table 4). Castings of the tubeworm *Ficopomatus enigmaticus* have been recorded in low quantities in the stomachs of greenback flounder (Earl 2014) and another tubiculous tubeworm (*Galeolaria*, likely misidentified for *Ficopomatus*) has been observed in the diet of black bream in South Australia (Weng 1970). Based on current knowledge, *F. enigmaticus* is not considered to be a major prey species for any fish species.

Molluscs

Bivalves and gastropods are not considered to be major food items for any fish species in the Coorong. Nevertheless, they are consumed by zoobenthivores such as greenback flounder and omnivores such as yelloweye mullet (Table 4). In 2009–2011, siphons of the bivalve *Tellina* spp. contributed, by volume, towards 15% of greenback flounder diet (Earl 2014). In other estuaries, bivalves and gastropods form major proportions of the diet composition for black bream (Sarre et al. 2010, Linke 2011).

Insects

In the Coorong, insects are not considered to be major food items for any fish species. This may be reflective of the low relative abundance and biomass in the Coorong, relative to other macroinvertebrate prey (Ye et al. 2019c). Chironomid larvae and pupae (e.g. *Tanytarsus* spp.) are the most abundant insect in the Coorong; they are salt tolerant and occur in salinities from 0–140 psu (Dittmann et al. 2018). Chironomids, as well as other benthic dipteran larvae/pupae, are consumed by a number of zoobenthivores and may play an important role in the diet of fishes (e.g. smallmouth hardyhead) in the South Lagoon, where biomass and variety of other prey are low (Ye et al. 2019c, Section 3.3.2). In the Coorong during 2013-14, chironomid larvae occurred in 32% of stomachs of smallmouth hardyhead (Hossain et al. 2017).

Based on studies done outside of the Coorong in terrestrial riverine systems, common galaxias (*Galaxius maculatus;* Becker and Laurenson 2007) and Australian smelt (King 2005) are considered to be insectivores (Figure 5). Their diets in the Coorong may be composed of greater proportions of benthic crustaceans and pelagic crustaceans, respectively.

Pelagic microcrustaceans and rotifers

Sandy sprat is a zooplanktivore (Table 2, Figure 5), although it is also capable of feeding on epi-benthic prey such as amphipods and ostracods. In the Coorong, pelagic microcrustaceans form considerable proportions of the diets of some zoobenthivores, such as Tamar goby and smallmouth hardyhead (Figure 5). Based on studies outside of the Coorong, pelagic microcrustaceans are also considered to be important in the diet of some omnivores, including bony herring (Atkins 1984), common carp (Hall 1981), goldspot mullet (*Liza argentea*) (Morton et al. 1987) and river garfish (Tibbets and Carseldine 2005). It is well understood that pelagic microcrustaceans are the primary prey source for the larvae of many key large-bodied fish species that occur in the Coorong, such as greenback flounder (Jenkins 1987, Shaw and Jenkins 1992) and black bream (Newton 1996, Willis et al. 1999), before undergoing an ontogenetic shift and transitioning into the typical juvenile/adult diet/feeding mode, although no studies have specifically assessed this in the Coorong. A summary of the major pelagic microcrustacean prey for different fish species is provided in Table 4. It is important to note that, on most occasions, taxonomic resolution in identification of zooplankton is coarse (e.g. to a level of Order) due to difficulties in identifying damaged or degraded specimens or a lack of expertise. For this reason, copepods, cladocerans and macroinvertebrate larvae have been considered as ‘pelagic microcrustaceans’, although some species within these groups (e.g. harpacticoid copepods) may be benthic in habitat.

Copepods

In the Coorong, copepods are a major prey item for sandy sprat, smallmouth hardyhead and Tamar goby (Table 4). Harpacticoids, which are generally considered benthic, are the major prey in the diets of these three species, while calanoid and cyclopoids have been recorded as prey for sandy sprat and other large-bodied species. In the Coorong during 2013-14, harpacticoid copepods occurred in the stomachs of 73% of sandy sprat (Hossain et al. 2017) and, in 2015-16, numerically dominated (56%) the diet composition of sandy sprat (Bice et al. 2016a).

Microcrustaceans are the major prey for bony herring <80 mm, before this species undergoes an ontogenetic shift in diet, and detritus and algae become the major food sources for larger individuals (Atkins 1984). At Point Sturt in Lake Alexandrina during 1984-85, microcrustaceans occurred in ~60-70% of bony herring stomachs (30–80 mm), and calanoids were the most abundant prey (Atkins 1984).

Cladocerans

Cladocerans are considered to be a major food source for common carp, based on literature from the Lower Lakes, and for sandy sprat. The freshwater cladoceran *Bosmina* sp. contributed numerically to 19% of the diet of sandy sprat in 2015-16 (Bice et al. 2016a). Being an omnivore, it is expected that the diet of common carp and bony herring will be composed of greater proportions of non-animal material (i.e. detritus and plants/algae) in the Coorong, where cladocerans and copepods are generally less abundant compared to the Lower Lakes (Leterme et al. 2018).

Other

Macroinvertebrate larvae and rotifers are not considered to be a major food source for any species in the Coorong, but are consumed by sandy sprat. In 2014-15, the freshwater rotifer *Keratella australis* contributed to 9% of the diet of sandy sprat (Bice et al. 2016a).

Macrophytes, algae and detritus

There are no herbivorous fishes in the Coorong (Table 2), although detritivores, such as sea mullet (*Mugil cephalus;* Platell et al. 2006), may occur at times in low abundance (Section 3.4, Bice et al. 2018). Omnivorous fishes in the Coorong include yelloweye mullet, black bream, bony herring, common carp, river garfish, goldspot mullet, bluespot goby and bridled goby. A summary of the major vegetation (including detritus) items for these different fish species is provided in Table 4.

Filamentous algae and detritus

In the Coorong during 2011-12, filamentous algae (24%) and detritus (42%) dominated the diet of yelloweye mullet (Giatas 2012). In South Australian estuaries, including the Coorong, algae (e.g. filamentous green) has formed a large proportion (≥30%) of the diet composition of black bream (Weng 1970, Harbison 1974). In other Australian estuaries, large volumes of algae (e.g. *Cladophora* spp.) and macrophytes (e.g. *Ruppia megacarpa*) have been observed in the diet of this species (Sarre et al. 2000, Chuwen et al. 2007).

While yelloweye mullet and black bream diets in the Coorong have included vegetation, these species generally have a larger proportion of animal prey in their diet (Geddes and Francis 2008, Deegan et al. 2010), particularly as juveniles. Estimated trophic positions (≥3) established through stable isotope analyses (Table 3) have supported this. It is unknown how efficiently these species can digest and utilise non-animal items. Nevertheless, the digestive system (‘gizzard-like’ pyloric stomach) of yelloweye mullet and feeding modes of other mugilids (Al-Hussaini 1947, Odum 1970) suggest that these species can assimilate vegetation to some degree.

Based on studies from outside of the Coorong, detritus and vegetation (e.g. filamentous algae) is considered to be a major food item in the diet of some other omnivores, including bony herring (Atkins 1984), common carp (Hall 1981), river garfish (Tibbets and Carseldine 2005), goldspot mullet (Morton et al. 1987), bluespot goby (Becker and Laurenson 2007) and bridled goby (Robertson 1984) (Figure 5).

Macrophytes

Seagrass is a major prey item for hemiramphids (garfish), with diurnal feeding patterns evident (e.g. Robertson and Klumpp 1983, Earl 2011). In Stradbroke Island, Queensland, seagrass occurred in most (99%) of the stomachs of river garfish (>100 mm) captured during the day (Tibbets and Carseldine 2005). A higher proportion of benthic animal prey (e.g. amphipods) were in the diet of garfish captured at night. *R. tuberosa*, the main submerged macrophyte in the Coorong, is distributed in salinities where river garfish are unlikely to occur (Bice et al. 2018), although the diet of this species in the Coorong is unknown. Macrophytes (e.g. *R. tuberosa*) are thus unlikely to be a direct major food source for any fishes in the Coorong, although they may be consumed by black bream (Harbison 1974, Sarre et al. 2000, Chuwen et al. 2007).

2.1.2 South Lagoon

Fish diet studies undertaken in the Coorong have generally focussed on the Murray Estuary and North Lagoon regions, as the distribution of most species is mostly confined to these areas due to salinity tolerances. Smallmouth hardyhead is the only fish species that has been assessed for diet in the South Lagoon of the Coorong (Hossain et al. 2017), although yelloweye mullet diet was reported (Giatas 2012) for two individuals at Hells Gate, at the northern end of the South Lagoon. Both of these fish (121–151 mm) consumed chironomid larvae, while diatoms, algae and detritus were present in one individual.

From November 2013 to March 2014, the diet of smallmouth hardyhead was investigated at two sites (Jack Point and Salt Creek) in the South Lagoon (Hossain et al. 2017). In this region, ostracods were the most numerically abundant (61%) prey consumed, followed by harpacticoid copepods (17%) and chironomid larvae and pupae (13%). The results from this study are reflective of prey items of this species in 2013-14 under environmental conditions following several high flow years (2010–2013). A number of other fish species (e.g. congolli, yelloweye mullet, black bream) occur in the South Lagoon (Section 3.4, Bice et al. 2018), particularly seasonally during lower salinities. The diets of these species in this region are unknown, but may be predicted based on known diets from other regions of the Coorong.

2.2 Waterbird diet

Knowledge of the diet of waterbirds can be derived from direct observations of food uptake, stomach content analyses from stomach-flushing, droppings, regurgitated pellets or discarded remains of prey, such as hard shells (Dann 1987). Observations or video recordings can provide additional insight to foraging strategies and the uptake of different prey taxa (Lourenço et al. 2016). Some of the earliest records of birds from the Coorong and their diet are found amongst records from field trips and stomach content recordings published in the 1910s and 1930s (White 1918, Sutton 1930a, Lea and Gray 1935). In the 1970s and 1980s, several studies into the Coorong were undertaken, including observations on the diet of waterfowl (Delroy 1974) and shorebirds (Paton 1982), while Keuning (2011) investigated the feeding behaviour of shorebirds in the Murray Estuary. Foraging activity and correlations between waterbirds and their prey were studied in the Coorong by Rogers and Paton (2009).

The review here considers information on diet and foraging behaviour from the literature (e.g. Lea and Gray 1935, Vestjens 1977, Marchant and Higgins 1990b, 1990a, 1993, Higgins and Davies 1996) and, where possible, knowledge from the Coorong. A literature review on the diets of waterbirds from the Coorong has been previously conducted by Brookes et al. (2009a).

2.2.1 Feeding modes and major food sources for birds

Based on the food items recorded in the literature, waterbirds from the Coorong have been grouped into feeding modes and these are listed in Table 5. Piscivores are represented by the Australian pelican (*Pelecanus conspicillatus*), grebes, cormorants, egrets, heron, ibises, terns and gulls. Shorebirds are generally considered to be zoobenthivores and feed predominantly on invertebrates, although *Ruppia* seeds and tubers are also eaten (Paton 1982), while waterfowl (e.g. ducks and swans) may be classified as herbivores or omnivores. Over half of the protected species are zoobenthivores, six species are piscivores, four are omnivores and one species is a herbivore (Table 5). The relative abundance of each species in each region, based on total counts from January 2018 (Paton et al. 2018a), is shown in Table 5.

Major food items for waterbirds of different feeding modes and functional groups are summarised in Tables 6–8, based on data from the Coorong. Foraging behaviour that has previously been captured in Paton (2010) is also discussed below. Unlike fish, waterbirds have the capability to forage in alternative habitats, for example, other wetlands or adjacent terrestrial, marine or freshwater habitats. This makes the assessment of their diet in a particular area/habitat complex and caution has to be taken during interpretation. Diet data specific to the Coorong are not available for most species, and prey availability is likely to differ considerably between the Coorong and other geographical areas (e.g. other Australian estuaries), where quantitative data are available. Therefore, food items recorded in other locations are not discussed in detail below. The food items recorded in the diets of 80 species of waterbirds from the Coorong is presented in Appendix 3 of Brookes et al. (2009a).

Table 5. Feeding modes of abundant waterbirds in the Coorong. Abundance (total count) is based on the annual monitoring from January 2018 by Paton et al. (2018a). The abundance of waterbird species in each region was ranked and the rank number given with 1= highest count for the region. Not all waterbird species were recorded from each region. Refer to Brookes et al. (2009a) for a summary of the diet items of these species.

SPECIES	FEEDING MODE	TOTAL COUNT	CONSERVATION STATUS*			RANK ORDER OF ABUNDANCE		
		JANUARY 2018	SA	EPBC	IUCN	SOUTH LAGOON	NORTH LAGOON	MURRAY ESTUARY
Whiskered tern	Piscivore	9064				3	6	10
Hoary-headed grebe	Piscivore	5118				4	36	32
Australian pelican	Piscivore	4684				9	9	9
Crested tern	Piscivore	3851				7	14	11
Little black cormorant	Piscivore	3562				12	8	14
Great cormorant	Piscivore	1185				36	15	13
Pied cormorant	Piscivore	695				22	16	41
Caspian tern	Piscivore	680				24	18	21
Little pied cormorant	Piscivore	581					19	20
Australian white ibis	Piscivore	491					29	19
Great crested grebe	Piscivore	360	RA			18	24	36
Fairy tern	Piscivore	357	END	VUL	VUL	16	32	30
White-faced heron	Piscivore	251				21	26	31
Black-faced cormorant	Piscivore	236				20	38	28
Great egret	Piscivore	58				30	35	37
Royal spoonbill	Piscivore	48				34	41	33
Little egret	Piscivore	32	RA			37	37	47
Gull-billed tern	Piscivore	22				31	44	38
Straw-necked ibis	Piscivore	6					43	48
Little tern	Piscivore	5	END			32		49
Common tern	Piscivore	5	RA			33	47	
Pacific gull	Piscivore	5					48	45
White-bellied sea-eagle	Piscivore	2	END				45	
Red-necked stint	Zoobenthivore	11696		MIG	NT	5	4	2
Sharp-tailed sandpiper	Zoobenthivore	7910		MIG		13	5	3
Red-necked avocet	Zoobenthivore	3291				11	11	12
Red-capped plover	Zoobenthivore	1261				14	21	22
Curlew sandpiper	Zoobenthivore	968		MIG, CR	NT	23	17	16
Banded stilt	Zoobenthivore	820	VUL			15	34	25
Masked lapwing	Zoobenthivore	517				17	22	26
Black-winged stilt	Zoobenthivore	368				27	28	24
Common greenshank	Zoobenthivore	238		MIG		25	25	27
Pied oystercatcher	Zoobenthivore	111	RA			26	31	34
Red-kneed dotterel	Zoobenthivore	70					39	29
Black-tailed godwit	Zoobenthivore	42	RA	MIG	NT		33	
Bar-tailed godwit	Zoobenthivore	14	RA	MIG, CR	NT		42	39
Pacific golden plover	Zoobenthivore	11		MIG				40

SPECIES	FEEDING MODE	TOTAL COUNT	CONSERVATION STATUS*			RANK ORDER OF ABUNDANCE		
		JANUARY 2018	SA	EPBC	IUCN	SOUTH LAGOON	NORTH LAGOON	MURRAY ESTUARY
Far eastern curlew	Zoobenthivore	6	VUL	MIG, CR	END			43
Hooded plover	Zoobenthivore	4	VUL	VUL	VUL	35	49	
Great knot	Zoobenthivore	4	RA	MIG, CR	END		40	
Sanderling	Zoobenthivore	4	RA	MIG				46
Sooty oystercatcher	Zoobenthivore	1	RA					51
Black-fronted dotterel	Zoobenthivore	1						52
Red knot	Zoobenthivore	1		MIG, CR	NT	41		
Grey teal	Omnivorous	83602				1	1	1
Australian shelduck	Omnivorous	17916				2	2	18
Chestnut teal	Omnivorous	7362				10	3	17
Silver gull	Omnivorous	6648				6	7	6
Eurasian coot	Omnivorous	3145				39	12	4
Australasian shoveler	Omnivorous	1842	RA			40	13	8
Hardhead	Omnivorous	1173					46	7
Pacific black duck	Omnivorous	630				29	27	15
Pink-eared duck	Omnivorous	205					20	
Blue-billed duck	Omnivorous	138	RA		NT	19		
Musk duck	Omnivorous	110	RA			28	30	35
Freckled duck	Omnivorous	6	VUL					42
Black-tailed native hen	Omnivorous	6				38		44
Purple swamphen	Omnivorous	1						50
Black swan	Herbivore	5741				8	10	5
Cape Barren goose	Herbivore	408	RA	VU			23	23

* The conservation status is given as per Paton et al. (2018a) for species listed in SA (National Parks and Wildlife Act), the EPBC (Environment Protection and Biodiversity Conservation Act) Act, and the IUCN (International Union for Conservation of Nature) red list. RA = Rare, VUL = Vulnerable, END = Endangered, CR = Critically endangered, NT = Near Threatened, MIG = Migratory.

Piscivorous bird diet and foraging (fish)

Piscivorous birds in the Coorong include the Australian pelican, cormorants (e.g. great cormorant *Phalacrocorax carbo* and little pied cormorant *Microcarbo melanoleucos*), terns (e.g. whiskered tern *Chlidonias hybrida* and fairy tern *Sternula nereis*), grebes (e.g. hoary-headed grebe *Poliocephalus poliocephalus*), egrets, herons and ibises, and the pacific gull (*Larus pacificus*) (Table 5). While many of these birds (e.g. pelicans, cormorants and terns) are predominantly piscivorous, and their abundance positively correlated to fish density (Rogers and Paton 2009), invertebrates may form a large portion of the diet composition of grebes, herons, ibises and the pacific gull (e.g. Lea and Gray 1935, Fjeldså 1988, Marchant and Higgins 1990a, 1990b, Higgins and Davies 1996). Silver gull (*Chroicocephalus novaehollandiae*) is an opportunistic scavenger and so its diet composition may reflect food availability in the area. While this species preys on fish, it is considered omnivorous as vegetation is also consumed (Higgins and Davies 1996, Auman et al. 2011). Shorebirds, such as the red-necked avocet (*Recurvirostra novaehollandiae*), banded stilt (*Cladorhynchus leucocephalus*) and, in particular common greenshank (*Tringa nebularia*), may also feed on fish (Paton 1982, Marchant and Higgins 1993 and Higgins and Davies 1996).

Foraging techniques vary extensively for piscivorous birds (Paton 2010). The Australian pelican uses its large bill and pouch to scoop fish out of the water, often working together in groups to concentrate schools of fish, and is generally limited to capturing fish in water depth <1 m. Terns take fish from the surface of the water by diving, and so, for small terns (e.g. fairy and whiskered terns), >30 cm of water depth is considered adequately for feeding. Cormorants and grebes, on the other hand, catch fish by swimming underwater, and herons, egrets and ibises forage by wading in shallow water.

Many piscivorous birds (e.g. Australian pelican and crested tern *Thalasseus bergii*) may forage extensively outside of the Coorong, whereas foraging of fairy tern is restricted to the Coorong (Paton et al. 2018b). For pelicans that nest in the Coorong, the adults are considered to feed in freshwater environments after the breeding season, and bring food to chicks (Paton 2010), and there is supporting evidence from other locations (Hitchcock 2007). White (1918) noted cyprinids ('golden carp') were the dominant prey identified in regurgitates from pelican chicks, while congolli were also present. It is not clear where these prey were captured as this time period preceded the construction of the barrages, but likely from water of fresh or brackish salinity.

It is difficult to quantify the diet composition or major prey species of piscivores in the Coorong as there is limited Coorong data available, or information is based on limited observations. Quantitative data are available on the diets of some of these species elsewhere in Australia (e.g. Vestjens 1977, Blaber and Wassenberg 1989, Humphries et al. 1992, references within Marchant and Higgins 1990a and 1990b), which is based on the analysis of stomach contents and/or regurgitated pellets. Based on the available diet literature, foraging behaviour of piscivorous birds, and fish prey size/habitat, fish prey (grouped by size and habitat type) expected to form a major part of the diet of certain predator groups are provided below (Table 6). Smallmouth hardyhead have been documented as a major food source for fairy tern (Paton 2010) which may forage in the South or North lagoons, but sandy sprat may also be an important food source depending on Coorong inflows and the location of foraging. Observations of piscivorous birds (e.g. cormorants and pelicans) congregating below the barrages and foraging in front of fishways and barrage gates during inflows to the Coorong suggests that freshwater species (e.g. bony herring) displaced or actively entering the Coorong may be important in their diets.

Table 6. Fish species expected to be major prey for piscivorous bird groups in the Coorong, based on Coorong observations and studies from outside of the Coorong (e.g. Marchant and Higgins 1990a, 1990b, Higgins and Davies 1996).

MAJOR PREY SPECIES	PREDATOR GROUPINGS/SPECIES	COMMENTS*
Small-bodied pelagic/bentho-pelagic (e.g. smallmouth hardyhead, sandy sprat)	Gulls and terns, grebes, cormorants and darters, egrets, heron and ibises, Australian pelican	
Small-bodied benthic (e.g. gobies and congolli)	Grebes, cormorants and darters, egrets, heron and ibises	Benthic species unlikely to be major prey for terns due to foraging behaviour
Medium pelagic/bentho-pelagic (e.g. yelloweye mullet, bony herring and river garfish)	Australian pelican, cormorants and darters, gulls and large terns	
Medium benthic (e.g. greenback and longsnout flounder)		Unlikely to be major prey for any species due to wide prey size, lower relative abundance in the Coorong, and prey habitat
Large-bodied fish (i.e. mulloway and common carp)	Australian pelican	Mulloway unlikely to be prey for any other species due to prey size

*Juveniles of medium-/large-bodied prey (e.g. yelloweye mullet) may also be consumed by smaller piscivores (e.g. terns and grebes).

Shorebird diet and foraging (benthic invertebrates)

Zoobenthivorous birds in the Coorong are represented by shorebirds, feeding predominantly on macroinvertebrates, although plant seeds (e.g. *Ruppia* spp.) may be frequent in their diet (e.g. Thomas and Dartnall 1971, Poore et al. 1979, Paton 1982, Lane 1987) and thus this group of birds may be considered omnivorous. Quantitative data are available on the diets of shorebird species elsewhere in Australia (e.g. Thomas and Dartnall 1971, Vestjens 1977, Poore et al. 1979, Tulp and de Goeij 1994, Dann 1999, other references within Marchant and Higgins 1993 and Higgins and Davies 1996), which is based on the analysis of stomach or gizzard contents, feeding observations and/or scat analysis. The foraging behaviour and recorded prey items of shorebirds in the Coorong (Table 7) are discussed below. Understanding of the relative contribution of food items to overall diet composition for shorebirds is mostly limited to Paton (1982) for banded stilt, red-necked avocet, curlew sandpiper (*Calidris ferruginea*), red-capped plover (*Charadrius ruficapillus*) and red-necked stint (*Calidris ruficollis*) (*n* = 1–6). The diet composition of shorebirds may vary over time and between locations, and most shorebirds can be opportunistic in their prey selection. Their habitat choice and food intake rate have been shown to be related to prey density (Goss-Custard et al. 2006, Finn et al. 2008).

Shorebirds can forage during the day and night, and feed mostly on exposed mudflats. In the South Lagoon, foraging shorebirds have been noted to aggregate near freshwater soaks at the end of summer (Paton 1982). They are visual or tactile feeders, detecting prey by sight or touch respectively (Dann 1987, Esser et al. 2008). Feeding specialisation in shorebirds is mostly related to bill morphology (Durell 2000). Shorebirds feed by pecking prey items from the sediment surface, probing (inserting the bill into the sediment for nearly the full length), or jabbing (inserting the bill for half its length), sweeping their bill through the water (e.g. avocets), or searching through flotsam (e.g. ruddy turnstone *Arenaria interpres*) (Dann 1987). The prey accessible to shorebirds varies with their bill lengths, and long bills, as in the far eastern curlew (*Numenius madagascariensis*), are an adaptation to access prey at greater depth in sediments (Dann 1987, 2005). Not all prey is harvestable, only the fraction which is accessible, ingestible and profitable for the birds (Piersma et al. 1993, Zwarts and Wanink 1993, Backwell et al. 1998).

In the Coorong, the shorebird species occurring in highest abundance (e.g. red-necked stint, sharp-tailed sandpiper *Calidris acuminata*) have short to medium bill lengths and access prey in the top 2 cm of sediment (Keuning 2011). Most of the macroinvertebrates occurred in the top sediment horizon to 5 cm depth and were thus harvestable prey, with some larger worms occurring to greater depths. During the study by Keuning (2011), which occurred during the Millennium Drought in the Murray Estuary, prey availability over depth varied between sites and sampling events. The polychaete *Simplisetia aequisetis* was a main prey item for shorebirds in the mudflats of the Murray Estuary (Keuning 2011), similar to related polychaete species being the main prey for shorebirds along other flyways (Kalejta 1993a, Lourenço et al. 2016).

Table 7. Shorebird categories in the Coorong and their prey items. Developed based on Keuning (2011), Lea and Gray (1935), Paton (1982), Lane (1987), Paton (2010), Paton et al. (2018a). Bill lengths/feeding depths are 0–2.5 cm for short-billed, 2.5–6 cm for medium-billed, and 6–19 cm for long-billed shorebirds.

CATEGORY	SHOREBIRD SPECIES	PREY ITEMS
Local shorebird, short-billed	Banded lapwing Black-fronted dotterel Hooded plover Masked lapwing Red-capped plover Red-kneed dotterel Red-necked avocet*	Worms, amphipods, brine shrimp, bivalves (e.g. *Arthritica*), gastropods (e.g. *Coxiella*), insect (Chironomidae) larvae, beetles, ants, spider Fish (e.g. smallmouth hardyhead) Seeds (e.g. *Ruppia*)
Local shorebird, medium to long-billed	Black-winged stilt Banded stilt Pied oystercatcher Sooty oystercatcher	Worms, bivalves, gastropods (e.g. *Coxiella*), brine shrimp, amphipods, isopods (e.g. *Haloniscus*), ostracods, crabs, insect (Ephydridae, Chironomidae) larvae, beetles Fish (e.g. smallmouth hardyhead) Seeds and root stock (e.g. *Ruppia*)
Migratory, short-billed	Grey plover Lesser sand plover Pacific golden plover Red-necked stint Ruddy turnstone Sharp-tailed sandpiper	Small gastropods (e.g. *Salinator*), crabs, small crustacea (e.g. amphipods), worms, insect (Chironomidae) larvae, ants Seeds and root stock (grasses, *Ruppia*)
Migratory, medium-billed	Common greenshank Curlew sandpiper Great knot Oriental plover Red knot Sanderling	Insect larvae and pupae, beetle larvae, grasshopper, caterpillars, spider, beetles (e.g. *Aphodius*), ants, worms (e.g. *Simplisetia, Aglaophamus*), amphipods, gastropods, bivalves Seeds (e.g. *Ruppia*)
Migratory, long-billed	Bar-tailed godwit Black-tailed godwit Far eastern curlew Little curlew Terek sandpiper	Worms, crabs (e.g. *Macrophthalmus, Paragrapsus,* ghost shrimp), gastropods, bivalves, grasshopper, beetles Seeds

*Avocets have a long, upturned bill, but mostly forage in shallow water

Smaller shorebirds spend more time feeding than larger shorebirds, reflecting energy demands, prey availability and feeding success (Dann 1987, Paton et al. 2018a). Time-budgeting also includes decisions to cease foraging when disturbances arise (Butler et al. 2020). Shorebirds can forage singly but are more often seen feeding in mixed species flocks, which can effect foraging efficiency and response to interference (Dann 1999, Folmer et al. 2010, Butler et al. 2020). When several species target the same prey species, such as polychaete worms, competition can be reduced by each shorebird species feeding on a different size of worm (Dann 1999).

Most shorebirds forage in wet sand and mud near the water edge, but some also feed in shallow water (e.g. curlew sandpiper, great knot *Calidris tenuirostris*) (Dann 1987, Rogers and Paton 2009). Tides, overall water level in an estuary and lagoon, and wind affect mudflat exposure and thus foraging activity. Penetrability of the sediment can affect foraging success and choice of foraging habitat (Mouritsen and Jensen 1992, Finn et al. 2008). In times of drought, low water levels in the Coorong can reduce penetrability and foraging by shorebirds. Almost all of the shorebirds seen in the Coorong are foraging, which is indicative of the effort needed to search for food (Paton et al. 2015). Keuning (2011) recorded an increased effort (increase in number of steps per minute, and decreased number of jabs and probes) for red-necked stint and sharp-tailed sandpiper between two years of increasing drought (2006/07–2007/08).

Migratory shorebirds have high energy expenditure for flights between their breeding grounds in the northern hemisphere and overwintering ground in the southern hemisphere. Investigations on captive birds indicated an energy demand of 45.66 kJ for 1 g increase in body weight for pre-migratory fattening, with 88% efficiency in energy deposition (Kersten and Piersma 1987). For post-breeding flights, smaller shorebirds in particular follow an 'energy-minimisation' strategy, taking more time to return to their overwintering grounds (Zhao et al. 2017). For pre-breeding migration, most species follow a 'time-minimisation' strategy, which is energetically expensive (Kersten and Piersma 1987, Zhao et al. 2017). During their overwintering time in the Coorong, migratory shorebirds thus need to obtain enough food to meet the energy demand for their pre-breeding return flight. If this energy demand is not met, the birds may not embark on the return flight to the breeding ground. An indication of such an effect was apparent during the Millennium Drought, when the normal phenology (migratory shorebirds arrive in spring and depart in autumn) was no longer apparent as birds remained in the Coorong and Lower Lakes (Figure 6, Figure 7). Abundance and biomass of benthic prey items decreased during the Millennium Drought, and took several years to recover (Dittmann et al. 2015).

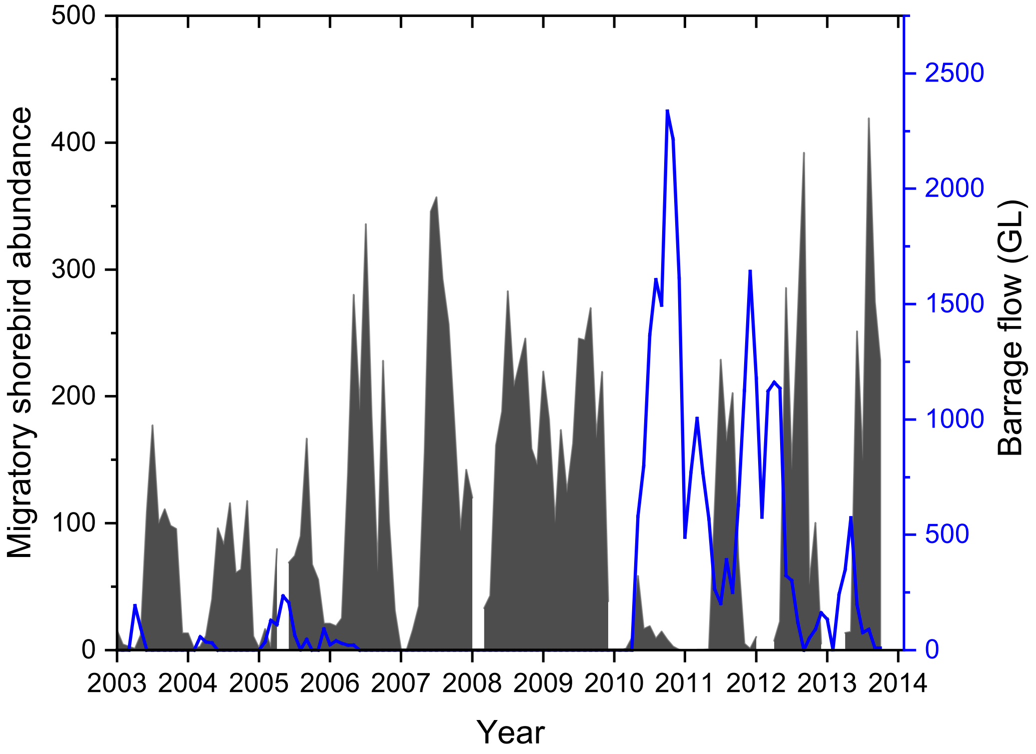


Figure 6. Phenology of migratory shorebirds in the Coorong, Lower Lakes and Murray Estuary. Based on monthly surveys by David and Margaret Dadd (see also O'Connor and Rogers 2013). Average abundance of all migratory shorebirds per month is plotted against the flow over the barrages over the same timeframe. Shorebird abundance as shown here is no indication of population size.

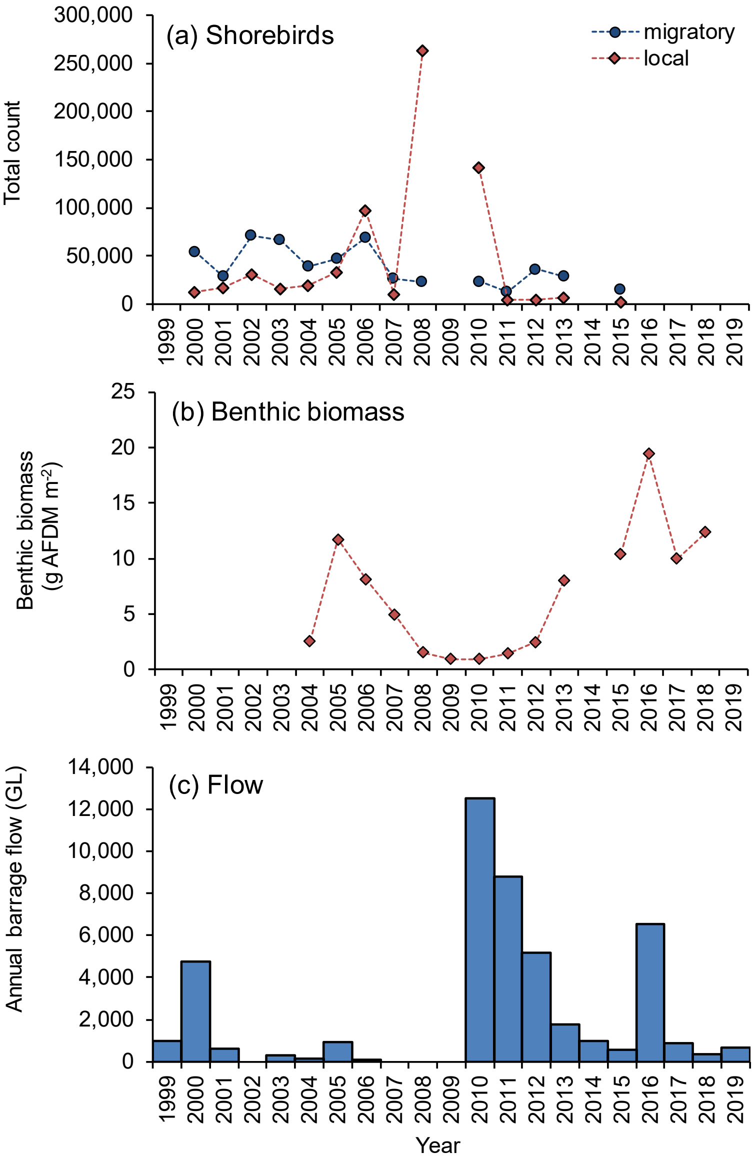


Figure 7. (a) Annual count of shorebirds in the Coorong based on data from the Australian Wader Study Group (BirdLife Australia), compared to (b) biomass of macroinvertebrate prey (from The Living Murray monitoring, Dittmann et al. 2020), and (c) annual flow over the barrages.

Waterfowl diet and foraging (vegetation)

The black swan (*Cygnus atratus*) and Cape Barren goose (*Cereopsis novaehollandiae*) are considered to be the only obligate herbivores in the Coorong (Table 5). Other species of waterfowl are omnivorous, with the degree to which animal prey items contribute to diet varying across species. For example, musk ducks (*Biziura lobata*) are considered to have invertebrates comprise a larger component of their diet than other species (Gamble 1966, Frith et al. 1969, Marchant and Higgins 1990a).

Waterfowl forage by 'dabbling' in shallow water, and so their access to food is limited by water depth (Paton 2010). Black swan can use their longer neck to reach vegetation on the benthos in deeper water than some other species (Paton 2010). The abundance of black swan in the Coorong was positively correlated with the percent cover of *R. tuberosa* (Rogers and Paton 2009). Foraging of waterfowl is likely to occur beyond the Coorong lagoons, including feeding on pasture in adjacent terrestrial habitats.

Quantitative data are available on the diets of waterfowl species in the Coorong (Delroy 1974), and elsewhere in Australia (e.g. Lavery 1967, 1971, Frith et al. 1969, Gamble 1966, Vestjens 1977, Norman and Mumford 1982, Norman 1983, Briggs et al. 1985, references within Marchant and Higgins 1990b), and are mostly based on the analysis of stomach or gizzard contents. From March 1965 to January 1966, the diets of grey teal (*Anas gracilis*), chestnut teal (*Anas castanea*) and Australian shelduck (*Tadorna tadornoides*) from the South Lagoon were quantitatively assessed through gut-content analysis (Delroy 1974). Wigeongrass (*Ruppia spiralis*, potentially mistaken for *R. tuberosa*), muskgrass tubers (*Lamprothamnium papulosum*) and seed contributed to most (>90%) of the diet of each species (Table 8). Terrestrial vegetation (e.g. *Chenopodium* sp.) (Lea and Gray 1935) and brine shrimp (Paton 2010) have also been reported in the diet of waterfowl (e.g. grey teal) in the Coorong. Based on studies outside of the Coorong, these duck species are considered to be omnivorous (Norman 1983, Briggs et al. 1985, Marchant and Higgins 1990), and thus their diets are expected to also include animal items such as invertebrates in the Coorong, contrary to findings by Delroy (1974). Being the main aquatic macrophyte in the Coorong, *R. tuberosa* is considered the major food item for herbivorous and omnivorous waterfowl in the Coorong, and thus the occurrence of various waterfowl is influenced by the distribution and abundance of *R. tuberosa* (O'Connor and Rogers 2013). The contribution of other aquatic vegetation (e.g. filamentous algae) to the diets of waterfowl in the Coorong is unknown. Algae (e.g. Chlorophyta and Charophyceae) has been reported in the diets of waterfowl, such as black swan, in other locations (Frith et al. 1969, Lavery 1967, 1971a).

Table 8. Food items of waterfowl in the Coorong (Lea and Gray 1935, Delroy 1974, Paton 2010).

SPECIES	DIET
Grey teal	*Lamprothanium papulosum* and *Ruppia spiralis* tubers and seeds, *Althenia cylindrocarpa* seed, *Chenopodium* sp. seeds and material. Other: brine shrimp (observations)
Chestnut teal	
Australian shelduck	

2.2.2 Waterbird abundance and prey availability

Analysing links between shorebirds and their prey should be considered in a broader environmental context. Shorebirds, and other waterbirds, are not only affected by prey availability, but accessible foraging habitat and roost sites (Lisson et al. 2017), which can also vary with changing environmental conditions (Nebel et al. 2008). Numbers of several waterbird species in the Coorong have decreased since the time of listing as Ramsar site in 1985 (Nebel et al. 2008, Paton et al. 2009, O'Connor 2015). Some of the major environmental events that have affected waterbirds include the Millennium Drought, and the flood event associated with the La Niña in 2010 (O'Connor and Rogers 2013). In the Coorong, flow over the barrages affects water levels, salinity and prey abundance, with consequences for accessibility of foraging habitat and food availability for waterbirds (O'Connor and Rogers 2013, O'Connor 2015).

Records since the early 2000s indicate different effects of drought and floods on birds of different feeding modes. Increasing hypersalinity during the drought favoured brine shrimp and chironomid larvae in the South Lagoon over other macroinvertebrates, supporting the breeding of banded stilt and red-necked avocets (Figure 7) (Gosbell and Christie 2006, O'Connor et al. 2013). Following the Millennium Drought, the return of flow in 2010 had positive effects for the recovery of the population size of the Australian pelican, chestnut teal, red-necked avocet and banded stilt (O'Connor and Rogers 2013). Banded stilt abundance has, however, decreased substantially in recent years (O'Connor 2015, Paton et al. 2018a). Shorebird (red-necked stint, sharp-tailed sandpiper and red-capped plover) abundance has also been recovering since flows resumed in 2010, however curlew sandpiper and common greenshank have shown little sign of recovery since flows resumed (O'Connor and Rogers 2013).

For the piscivorous fairy tern, a decline in abundance occurred despite an increase in abundance of their main fish prey species (smallmouth hardyhead) (O'Connor et al. 2013). Abundances of waterbird species have also been documented to vary differently in different regions of the system (O'Connor et al. 2013). Other long-term patterns in abundance are not easily linked to the provision of food, such as the increase in herbivorous black swan numbers in relation to *Ruppia* (depleted) and aquatic macrophytes (recovering) (O'Connor and Rogers 2013). There was no coherent response in the temporal and spatial pattern of different waterbird species to the effects of drought and floods, but more continuous flow since 2010 was beneficial for the populations of most waterbird species (O'Connor et al. 2013).

2.3 Macroinvertebrate diet

Benthic macroinvertebrates in the Coorong have mainly been allocated to trophic positions using stable isotope approaches in the past (Lamontagne et al. 2007, Deegan et al. 2010, Giatas 2012, Earl 2014, Johnson 2014, Giatas and Ye 2015) (Table 9). Feeding modes are quite well known for many species and families of macroinvertebrates found in the Coorong (e.g. Jumars et al. 2015). However, more detailed information of diet descriptions for various macroinvertebrate taxa vary, with species-specific information available for the annelid worms (e.g. oligochaetes and polychaetes) and information for bivalves, crustaceans and some gastropods based on broader feeding modes (Table 10).

Annelid worms in the Coorong are mainly restricted to the Murray Estuary and North Lagoon (Section 3.3) and are largely deposit feeders where they move along sediments or within the benthos and consume fine organic matter (Table 10). Four annelid species also prey on other mobile invertebrates (*A. australiensis*, *A. ehlersi*, *P. novaehollandiae*, *S. aequisetis*), but none of those species are solely predators and will switch to deposit feeding if prey are scarce. Only one annelid species (*S. aequisetis*) uses scavenging as a feeding strategy and will consume dead or decaying animal and plant matter. The sessile tubeworm *Ficopomatus enigmaticus* is a suspension feeder that will capture fine particles of food from the water column.

Molluscs are divided into the bivalves that are mainly suspension feeders, and gastropods that are deposit feeders or grazers (Table 10). There are also two species of bivalves that deposit feed (*Arthritica semen* and *Hiatula alba*), mainly feeding on fine organic matter and detritus. The gastropod *Nassarius pauperatus* is the only scavenging mollusc (i.e. feeding upon carrion) found within the Coorong and is restricted to the Murray Estuary region. The only molluscs present in the South Lagoon of the Coorong are the micro-bivalve *A. semen* and micro-gastropods (Hydrobiidae), relying on fine particulates.

Crustaceans in the Coorong are mainly found within the Murray Estuary and North Lagoon where they have some of the broadest feeding strategies including deposit, predatory or scavenging (Table 10). The sessile barnacle *Amphibalanus variegatus,* is found in the Murray Estuary region and filter feeds to capture fine organic matter from the water column. One grazing species of isopod (*Halonisucs searlei*) is found in the North and South lagoons only and most likely feeds upon algae and detritus.

Throughout all regions of the Coorong, insect larvae (Hexapoda) are found, with those larval stages having broad feeding strategies and mostly omnivorous diets, with the exception of the predatory Dolichopodidae (e.g. long-legged flies) (Table 10).

Table 9. Mean estimated trophic positions of macroinvertebrate species in the Coorong. Trophic levels: 1 = primary producers, 2 = primary consumers (herbivores/detritivores), 3 = secondary consumers (carnivores that feed on primary consumers), 4+ = higher-order consumers (carnivores that feed on secondary consumers or higher) (see Figure 40). Means have not been calculated across sites for Deegan et al. (2010) data, instead the range of site mean is presented. * = indicates some degree of carnivory (i.e. predatory or scavenger mode), based on trophic position (i.e. 2.5>3).

SPECIES	MEAN TROPHIC POSITIONS
Polychaeta	
*Aglaophamus australiensis**	2.63–2.81[1], 3.2[2], 2.76[3]
*Australonereis ehlersi**	2.00–2.27[2], 1.91[3]
Capitellidae	2.28[2], 2.07[3]
Ficopomatus enigmaticus	1.90–2.34[2], 1.99[3]
*Phyllodoce novaehollandiae**	2.88–2.89[1], 2.37[3]
*Simplisetia aequisetis**	2.98–3.01[2], 2.22-2.74[3]
Bivalvia	
Soletellina (Hiatula) alba	1.78[3]
Notospisula (*Spisula*)	1.87[2]
Gastropoda	
Salinator fragilis	1.44[2], 2.32[3]
Crustacea	
Amphipoda	1.84–1.86[2], 1.91–2.18[3]
*Helograpsus haswellianus**	3.32[2]
Mysidae	2.33[2]
Macrobrachium (Palaemonidae)*	2.54–2.81[1]
*Paragrapsus gaimardii**	3.32–3.58[2], 2.81–2.94[3]
Crab (juvenile)	1.96–2.27[1]
Crab (adult)*	2.36–2.87[1]
Hexapoda	
Chironomidae larvae	1.94–2.15[2]

[1]. Deegan et al. 2010, [2]. Giatas 2012, [3]. Giatas and Ye 2015.

Table 10. Feeding modes and diet description of macroinvertebrate taxa found throughout the three Coorong regions. ME = Murray Estuary, NL = North Lagoon, SL = South Lagoon. D = Deposit, G = Grazer, P = Predator, S = Suspension, SC = Scavenger.

TAXA	FEEDING MODE	DESCRIPTION OF DIET	COORONG REGION FOUND	REFERENCE
Oligochaeta	D	detritus, bacteria, dissolved organic matter	ME, NL, SL	Giere (2006)
Polychaeta				
Aglaophamus australiensis	D, P	molluscs, crustaceans, other polychaetes	ME, NL	Beesley et al. (2000)
Australonereis ehlersi	D, P	fine organic matter	ME, NL	
Boccardiella limnicola	D, S	organic matter	ME, NL	
Capitellidae	D	organic matter, algae	ME, NL, SL	
Ficopomatus enigmaticus	S	fine organic matter	ME, NL	
Phyllodoce novaehollandiae	P, S	forage for invertebrate prey	ME, NL	
Simplisetia aequisetis	D, P, SC	broad, organic matter, carrion, omnivorous	ME, NL, SL	
Bivalvia				Lamprell and Whitehead (1992), Matthews and Fairweather (2003), Murawski and Serchuk (1982), Wells and Threlfall (1982)
Arthritica semen	S, D	fine organic matter	ME, NL, SL	
Hiatula alba	S, D	detritus, algae	ME, NL	
Limnoperna sp.	S	algae	ME	
Spisula trigonella	S	algae	ME, NL	
Gastropoda				
Coxiella striatula	G	algae	SL	McKillup and Butler (1983), Ponder et al. (1991), Roach and Lim (2000)
Hydrobiidae spp.	D, G	algae, fine organic matter	ME, NL, SL	
Nassarius pauperatus	SC	omnivorous, carrion	ME	
Salinator fragilis	D, G	algae, fine organic matter	ME, NL	
Crustacea				
Amphibalanus variegatus	S	fine organic matter	ME	Burden et. al. (2014), Fenton (1986), Ellis and Williams (1969), Poore (2004)
Biffarius limosus	D	algae, detritus	ME, NL	
Halicarcinus ovatus	P, SC	invertebrates, carrion	ME	
Haloniscus searlei	G	algae, detritus	NL, SL	
Helograpsus haswellianus	G, P, SC	omnivorous, carrion	ME	
Mysidae	D, S	algae, detritus	ME, NL	
Palaemonidae	D, P, SC	omnivorous, carrion	NL	
Paragrapsus gaimardii	SC	carrion	ME, NL	
Pilumnopeus serratifrons	D, G, P, SC	omnivorous, carrion	ME	
Tanaidacea	P, S	invertebrates, fine organic matter	ME	
Tasmanoplax latifrons	P, SC	invertebrates, carrion	ME	
Hexapoda				
Ceratopogonidae larvae	D, G, P	omnivorous, detritus	ME, NL, SL	Gooderham and Tsyrlin (2003), LaSalle and Bishop (1990), Mullen and Hriber (1988)
Chironomidae larvae	SC	omnivorous, detritus	ME, NL, SL	
Dolichopodidae larvae	P	invertebrates	ME, NL, SL	

2.4 Conclusions and knowledge gaps

Identifying the major food sources of key biota, such as fish and waterbirds, is fundamental in understanding trophic interactions of food webs. To restore the ecological condition of the South Lagoon, and more broadly the Coorong, a key objective of the HCHB program is to promote or provide food resources for key biota. In order to do this, knowledge of the diets of key biota in the system is required. This is a critical input into quantitative food web models, that can be used to assess responses to environmental change to underpin management decisions.

Fish

Our knowledge of the diets of abundant fish species, which likely play major roles in the food webs as prey and consumers in the Coorong, has improved considerably over the last two decades. For these species, quantitative diet composition data from the Coorong is available for quantitative food web modelling input. For lesser abundant species (e.g. river garfish and bridled goby), our understanding relies on diets of these species from other geographical locations, where prey presence and availability is different to the Coorong. No data exists for lagoon goby.

While the diets of freshwater species (e.g. bony herring, common carp) have been assessed in nearby freshwater habitats in the Lower Lakes (e.g. Hall 1981, Atkins 1984), their diet composition in the Coorong is unknown. Prey occurrence and abundance are considerably different in these two different habitats (e.g. Walker et al. 2008, Dittmann et al. 2018, Bice et al. 2018), and thus diets are likely to be different. Bony herring has a greater tolerance to high salinities (e.g. 70 psu, SARDI unpublished data) and can be abundant in the Coorong, especially during periods of freshwater inflow (Section 3.4, Bice et al. 2018).

The Coorong supports a number of estuarine fish species that depend on the system for their entire life cycle (e.g. smallmouth hardyhead and black bream), and is an important nursery area for many marine species (e.g. mulloway, yelloweye mullet and greenback flounder) (Phillips and Muller 2006). In the Coorong, the diets of early life stages of fish (e.g. larval) are poorly understood for most species. Seasonality in fish diet is not well understood in the Coorong for most species, particularly diet during winter (excluding greenback flounder). Therefore, the influence of seasonal variation in species assemblages and environmental conditions (e.g. inflow) on trophic interactions of food webs is poorly understood.

Waterbirds

Our understanding of waterbird diets in the Coorong is predominantly based on unpublished feeding observations or limited stomach content observations from the 1910s–1930s. With the exception of data collected for some waterfowl in the 1970s (Delroy 1974) and shorebirds in the 1980s (Paton 1982), there is limited understanding of the relative composition of diet items or the major food sources of key waterbirds. While current work (FRDC Project 2018-036) is aiming to characterise the diets of key piscivorous birds (i.e. Australian pelican and cormorants) through scat-DNA metabarcoding, our understanding of the diet of other key waterbirds (e.g. sharp-tailed sandpiper) in the Coorong is limited. In particular, the importance of *R. tuberosa* seeds and turions in the diet of shorebirds in the Coorong has been documented during a period of extensive distribution and cover (Paton 1982), but is unquantified during current conditions. Furthermore, the contribution of filamentous algae to the diet of herbivorous waterfowl in the South Lagoon of the Coorong is unknown. The effects of filamentous algal mats on prey availability for waterbirds also requires further investigations.

In the past, quantitative bird diet data has relied on invasive or destructive methods, such as stomach flushing and stomach or gizzard content analysis (Marchant and Higgins 1990b, 1990a, 1993, Higgins and Davies 1996), although non-invasive diet assessment is also achievable through analysis of faeces/scats. While the identification of waterbird prey through hard-part analysis of faeces has commonly occurred (e.g. Dekinga and Piersma 1993, Tulp and deGoeij 1994, Zhang et al. 2011, Faria et al. 2018), DNA meta-barcoding has recently become an increasingly popular technique (e.g. Gerwing et al. 2016, Goldsworthy et al. 2019, McClenaghan et al. 2019, SARDI unpublished).

Macroinvertebrates

The feeding modes are well known for key species and families of macroinvertebrates, based on literature (Jumars et al. 2015, Lam-Gordillo et al. 2020) and trophic positions of biota in the Coorong. The specific food items or basal food sources supporting these biota are, however, poorly understood. For example, the proportional origin (e.g. plant, algal or animal) of detritus that supports many deposit-feeding macroinvertebrates (e.g. polychaetes), and how this changes with flow, in relatively unknown. What is better understood in the system, is how the relative contributions of organic matter from terrestrial, marine and (local) estuarine habitat contribute towards productivity under different hydrological periods (see Section 4.2.2).

Investigations into the energetic and nutritional values of key food sources (e.g. macroinvertebrates and fish) will improve our understanding of the food quality of different prey species and provide data to quantify bioenergetic trophic links. Methods were successfully trialled for assessing the energy content in a recent pilot study (Ye et al. 2019c) and are currently being refined for the food web investigations through T&I Project *Component 3*.

3 Key biota, potential food resources and environmental drivers

3.1 Introduction

This section presents the contemporary ecological understanding of key biota (potential food), including zooplankton, macroinvertebrates and fish, and key environmental drivers influencing their population and assemblage dynamics in the Coorong. Based on the published information and available data, additional analyses were conducted to understand spatio-temporal patterns of abundance, distribution, diversity and assemblage structure of key biota. This knowledge synthesis does not include biotic groups of primary producers and waterbirds, for which T&I *Component 2 Algae and aquatic plants* and *Component 4 Maintaining viable waterbird populations* are undertaking comprehensive research and will generate complementary data and knowledge to support *Component 3 Food web* investigations.

3.2 Zooplankton

3.2.1 Review of Coorong zooplankton studies

Although published zooplankton studies from the Coorong and surrounding waterbodies extend back to much earlier (e.g. Dedeckker and Geddes 1980), zooplankton have been routinely studied in the Coorong since 2003 (Leterme et al. 2018), with most intensive data collection over the period 2010–2014 (Table 11). This timing imposes caveats on our understanding of Coorong zooplankton dynamics; by 2003 the river was already two years into the most severe drought on record. Drought conditions persisted over much of the sampling period until a near-record high flow period began in 2010–2011, which was among the largest sustained high-volume barrage flows on record. Thus, existing zooplankton sampling data reflect a Coorong system during, and immediately following, extremes in flow variation, which differ markedly from mean historical flow patterns (Section 3.2.4). The importance of this extreme antecedent flow on observed zooplankton dynamics is unknown, as we have no baseline for comparison (Oliver et al. 2013, Oliver et al. 2014). Moreover, zooplankton data have been collected using different sampling methods (e.g. mesh sizes, nets versus traps) and with unbalanced spatial designs, making the drawing of reliable general inference challenging (Oliver et al. 2013, Oliver et al. 2014).

Most studies have occurred over a timeframe of 12 months or less but because of high inter-annual (year-year) variability, the most useful information comes from multi-year studies. There are two such data series, both largely descriptive in nature, mainly aiming to characterise zooplankton composition and abundance. The first data series were collected approximately monthly over three spring–summer periods from 2003/04–2007/08 from sites in the Murray Estuary and North Lagoon (see Geddes et al. 2016). This series of sampling was initiated following a small flow release in 2003 during the Millennium Drought. Sampling continued over subsequent years to monitor changes in composition and abundance as zero-flow conditions returned and persisted. The second data series were collected over the period 2010–2014 (Shiel and Aldridge 2011, Shiel and Tan 2013a, 2013b). This monitoring was also initiated to opportunistically track changes in zooplankton composition following the large flood-related barrage releases in 2010, and continued annually until 2014 following reduced volumes of barrage releases. These data were later collated with water quality and flow data to analyse spatio-temporal patterns in abundance and composition (Oliver et al. 2013, Oliver et al. 2014). Data from the latter sampling series are more detailed, as they relate to samples collected using finer mesh nets, and are also analysed within this sub-section. However, both data series are spatially and temporally unbalanced (e.g. the sampling sites differed from year-year, few sites were sampled every year allowing direct comparisons), and any conclusions on zooplankton population dynamics using these data should be interpreted cautiously.

Table 11. Summary of zooplankton studies in the Coorong, 2003–2019. ME = Murray Estuary, NL = North Lagoon, SL = South Lagoon.

SOURCE	DATES/REPS/EFFORT	REGIONS /SITES	TOTAL ABUNDANCE (IND L^{-1})	TAXONOMIC RICHNESS	SALINITY (PSU)
Geddes (2005)* Reported in Geddes et al. (2016)	3 samples: Sep – Dec 2003 59 µm mesh 20 cm diameter net 10 m oblique tows	ME, NL (5 sites)	6.5–1599	2–12	9–94
Geddes and Tanner (2007) Reported in Geddes et al. (2016)	4 samples: Oct 2004 – Apr 2005 Methods as above	ME, NL (6 sites)	3.4–430	2–11	16–88
Geddes et al. (2016)	3 samples: Jan 2007 – Jan 2008 158 µm mesh 20 cm diameter net 75–150 m oblique tows	ME, NL (8 sites)	0.05–3.9	1–12	35–130
Shiel and Aldridge (2011)	6 samples: Nov 2010 – Apr 2011 35 µm mesh 23 cm diameter net 3 x 5 m oblique hauls 3 x 4 L Haney traps (quantify abundance)	ME, NL (10 sites)	8–4992	1–28	16.6
Shiel and Tan (2013a)	7 samples: Oct 2011 – Apr 2012 Methods per Shiel and Aldridge (2011)	ME, NL (4 sites)	9–2817	4–36	0.2–38.4
Shiel and Tan (2013b)	4 samples: Sep 2012 – Mar 2013 Methods per Shiel and Aldridge (2011)	ME, NL, SL (5 sites)	1–2035	1–17	NA
Unreported sampling	5 samples: Sep 2013 – Jan 2014 Methods per Shiel and Aldridge (2011)	ME, NL, SL (6 sites)	1–1728	1–34	NA
Bice et al. (2016a)	3 samples: Nov – Dec 2014 3 x 4 L Haney traps at surface, mid-water and bottom with 35 µm mesh	ME (5 sites)	4–292	1–15	~17.3–35
Hemraj et al. (2017b)	12 samples (monthly): Nov 2013 – Oct 2014 35 L Schindler-Patalas trap filtered through 50 µm mesh	ME, NL, SL (7 sites)	NA	NA	NA
Furst et al. (2019)	7 samples: Oct 2018 – Feb 2019 3 x 4.5 L Haney traps, at surface and bottom with 30 µm mesh filter	ME, NL (6 sites)	0–1600	1–9	~18–25

The other main data sources are from investigations over the period 2013‒2019 (Table 11), aimed at understanding the role of zooplankton within Coorong food webs or as possible indicators of ecological condition. These studies sampled across trophic levels, including zooplankton as primary consumers, at multiple points in time and space (Bice et al. 2016a, Hemraj et al. 2017a, Hemraj et al. 2017b, Hossain et al. 2017, Furst et al. 2019, Ye et al. 2019b). Notably, some earlier Coorong food web studies found little contribution of zooplankton, as these were not present in sufficient abundance to comprise a large part of food webs (Lamontagne et al. 2007, Deegan et al. 2010) or were present only in immature forms (Geddes and Francis 2008). This is unsurprising, given the studies were characterising food webs during the height of the Millennium Drought, with the system under considerable salinity stress with almost no freshwater input.

To support the T&I Project *Component 3 – Restoring a functioning Coorong food web* research, the findings of the existing zooplankton monitoring and targeted research studies are synthesised in this sub-section, supported by some additional analyses. However, as there exist no pre-drought taxonomic or food web studies for comparison (see Section 4), the possibility that the zooplankton community is still recovering from the Millennium Drought should be considered when interpreting the data (Oliver et al. 2014) (discussed in Section 3.2.4).

3.2.2 Spatio-temporal patterns in zooplankton composition and abundance

Spatial and temporal variation in zooplankton assemblages reflects differential connectivity and relative contributions of external water sources (both freshwater and marine) within and across the three regions of the Coorong (i.e. Murray Estuary, North Lagoon and South Lagoon). Th different connectivity and sources results in longitudinal patterns of water quality (particularly salinity) along the Coorong estuary-lagoon system that are reflected in zooplankton species composition and abundance (Oliver et al. 2013, Oliver et al. 2014, Geddes et al. 2016, Hemraj et al. 2017a, Hemraj et al. 2017b, Hossain et al. 2017). However, as these patterns shift according to tidal, seasonal and inter-annual cycles, teasing apart the effects and interactions of each on zooplankton assemblages is challenging.

Moreover, in addition to the temporal limitations on sampling discussed above, Coorong zooplankton sampling effort has been spatially unbalanced among the three regions (Oliver et al. 2013, Oliver et al. 2014). In both targeted research and monitoring, effort has been heavily concentrated in the Murray Estuary and areas of the North Lagoon nearest to the Murray Mouth (Figure 8). Sampling effort in the South Lagoon has been particularly sparse in space and time. The distribution in sampling effort likely reflects interest in quantifying the ecological responses to barrage flow releases, which have the greatest impact in the heavily sampled regions due to their proximity to the barrages. The strongest gradients in water quality appear along the North Lagoon (Hemraj et al. 2017a), so it is potentially the region most suited to investigating zooplankton tolerances to variations along these gradients. Despite the limited spatial and temporal coverage of the sampling (Section 3.2.1) and the uncertainty of how representative the ecology of the Coorong system has been over the period that zooplankton have been studied (Oliver et al. 2014) (see Section 3.2.4), some consistent patterns in composition and abundance have emerged.

Over the sampling period, Coorong zooplankton has been dominated by protists, rotifers, and immature copepods, particularly calanoid nauplii (Oliver et al. 2013, Oliver et al. 2014, Geddes et al. 2016). For the Murray Estuary and North Lagoon during 2003–2007, Geddes et al. (2016) noted a community dominated by rotifers, particularly from the genus *Synchaeta*, but lacking many calanoid copepod species common to other estuaries of southern Australia. Adult copepods and juveniles (nauplii and copepodites) typically become more abundant during periods of barrage flow (Leterme et al. 2018), with calanoid copepodites absent at salinities above 60 psu (Geddes et al. 2016).

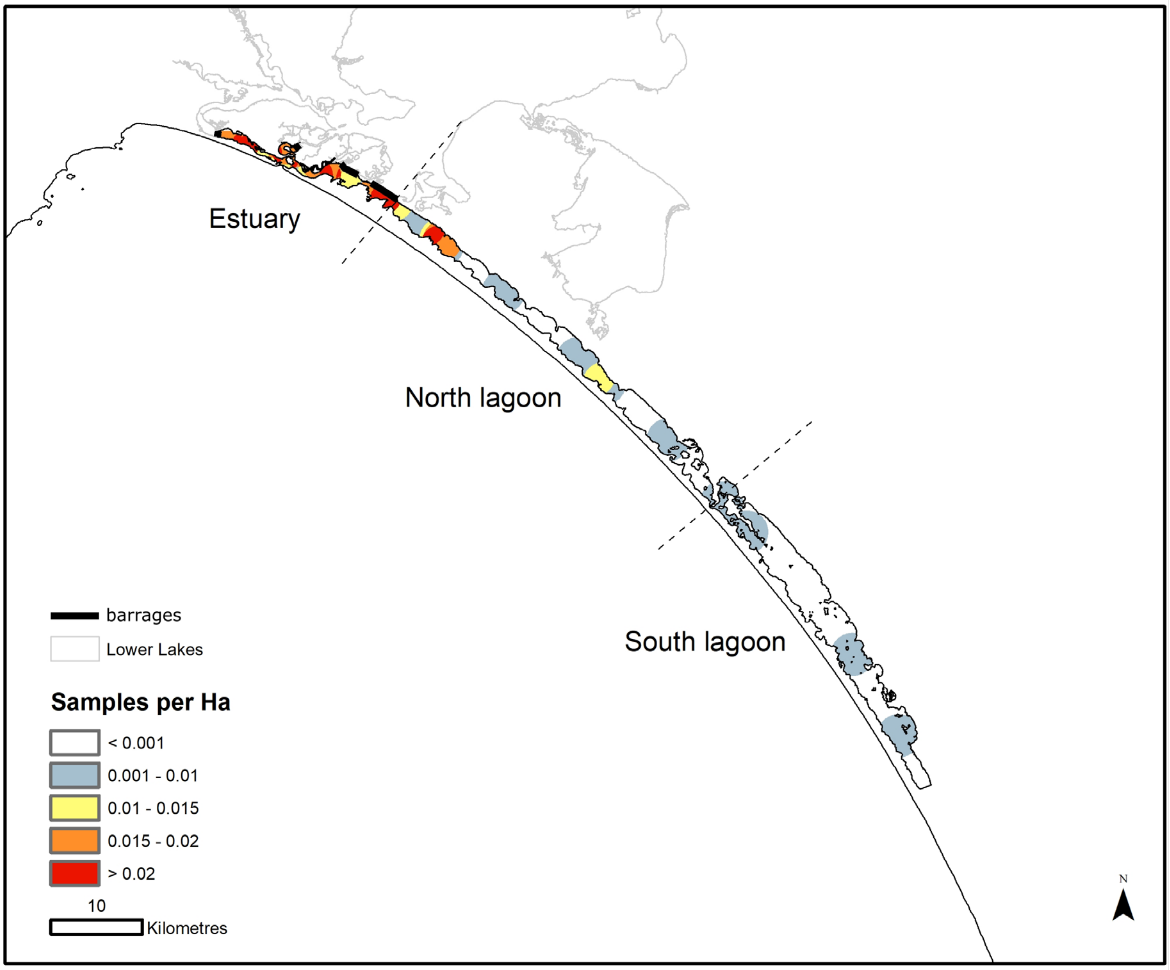


Figure 8. Sampling density for zooplankton in the Coorong 2003–2019. Colour indicates the density of sampling effort. Note the majority of sampling effort has been concentrated in the Murray Estuary and northern areas of the North Lagoon. Samples include all studies discussed in this section with the density surface calculated using ArcMap.

Antecedent barrage flow history can result in different zooplankton assemblages in the Coorong. During a small flow event early in the Millennium Drought, Geddes et al. (2016) found the highest zooplankton diversity and abundance immediately downstream of Tauwitchere Barrage as freshwater copepods and rotifers were added to the assemblage. However, Bice et al. (2016a), sampling similar sites during a comparable range in barrage flows (~11 000−14 000 ML d^{-1}) and with a similar density of individuals, found few freshwater copepods but abundant rotifers (discussed in Section 3.2.3).

During zero-flow periods, zooplankton assemblages become poorer in species diversity and of more predictable composition, with estuarine or marine species in the Murray Estuary and taxa being increasingly constrained to halophilic (salt tolerant) species with distance along the North Lagoon and particularly in the South Lagoon (Geddes et al. 2016). During late Millennium Drought with no barrage flows, Geddes et al. (2016) reported Murray Estuary and North Lagoon samples were dominated by *Synchaeta* sp., cyclopoid copepods from the genus *Halicyclops*, and the harpacticoid *Mesochra* cf. *pygmaea*. High densities of calanoid, cyclopoid and harpacticoid nauplii and copepodites along with meroplankton, including crab, polychaete and gastropod larvae, were also present in greater abundance during zero flow periods. Furst et al. (2019), monitoring the Murray Estuary during a period of comparably low barrage flow similar to that of Geddes et al. (2016), found few pelagic estuarine copepods, despite the presence of salt wedge conditions previously found to favour such species (e.g. *Gladioferens* sp.). In contrast, benthic harpacticoid copepods were abundant during this period and were assumed to be benefiting from organic material delivered via barrage flows (Furst et al. 2019).

To analyse zooplankton taxonomic composition and the factors driving it , Oliver et al. (2014) collated data from monitoring over the period 2010–2014. They found the most common taxa (accounting for >90% of abundance) within the Murray Estuary were calanoid copepod nauplii, protists (notably *Stenosemella lacustris* and *Difflugia* sp.) and estuarine and freshwater rotifers (notably *Filinia pejleri*, *Synchaeta* sp., *Trichocerca pusilla*, and *Keratella tropica*). Essentially these same taxa were also the most common in North Lagoon sites, along with the halophilic rotifer *Proalides tentaculatus* and ciliate *Cothurnia* sp. Abundant taxa in the South Lagoon over the period were sub-adult calanoids (nauplii and copepodites), estuarine and halophilic rotifers (notably *Testudinella obscura* and genera *Acartia* and *Synchaeta*). Hemraj et al. (2017b) suggest that the presence of *Acartia* cf. *fancetti* is indicative of good ecological condition in salinities ranging from 40–60 psu. Several authors have recorded zooplankton taxa from the Coorong that are also found in salt lakes in the South East of South Australia, including the ostracod *Diacypris* (Oliver et al. 2014) and the harpacticoid copepod, *Quinquelaphonte wellsi* (Geddes et al. 2016). It is possible that these taxa were imported to the South Lagoon via the Upper South East drainage scheme outlet at Salt Creek (see also 3.2.3), but other vectors are also possible (e.g. birds). Morella Basin, appears not to have been directly investigated as a potential source for zooplankton.

Taxonomic richness

Data from monitoring (Shiel and Aldridge 2011, Shiel and Tan 2013a, 2013b) illustrate the general pattern in taxonomic richness (the number of different types of zooplankton organisms) across Coorong regions, where the most diverse (number of taxa) sites are found within the Murray Estuary, with the North Lagoon supporting fewer taxa and the South Lagoon zooplankton depauperate by comparison (Figure 9). This spatial pattern is directly related to flow along the system, via the constraints it imposes on the taxa that can persist, particularly salinity (Shiel and Tan 2013b, Hemraj et al. 2017b) and decreasing presence of freshwater taxa (Geddes et al. 2016, Hemraj et al. 2017b). Generally, freshwater zooplankton require adequate flows to maintain salinity below ~4–5 psu to persist in the Coorong (Shiel and Tan 2013b).

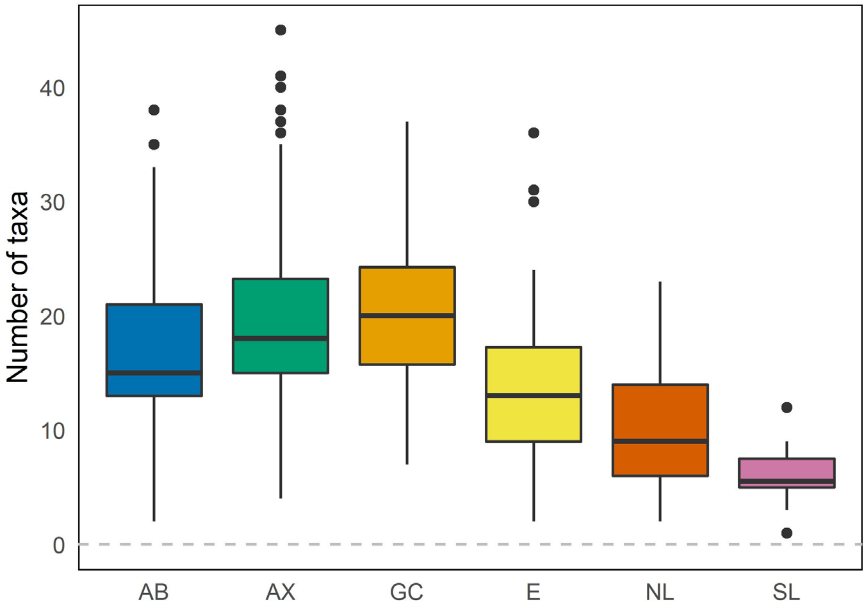


Figure 9. Distribution of taxonomic richness, collated for samples from different regions of the Coorong and Lower Lakes, 2010–2014. AB = Lake Albert, AX = Lake Alexandrina, GC = Goolwa channel (upstream the barrage), E = Murray Estuary, NL = North Lagoon, SL = South Lagoon. Filled boxes indicate the 25th and 75th quartiles, with horizontal lines showing the median value. Vertical lines and points show range in data. Note data are based on different numbers of samples from each region over time and are illustrative only of general patterns. Data sources: Shiel and Aldridge 2011, Shiel and Tan 2013a, 2013b.

In the South Lagoon the zooplankton composition was restricted to obligate halophiles (i.e. species that will only be found in high salinity conditions) in the period 2012-13 (Shiel and Tan 2013b, Oliver et al. 2014). In early stages of the Millennium Drought, this reached extremes, where hypersaline conditions in the South Lagoon led to the brine shrimp, *Parartemia zeitziana*, reaching high abundance after colonising the South Lagoon in 2004 (Geddes et al. 2016). However, brine shrimp were not detected in the later period of sampling in this region (2012-13), presumably because of a return to lower salinity after drought ended in 2010, allowing the return of fish predators to the South Lagoon. Taxonomic richness of the Murray Estuary over the period since the drought ended was highest, but still below all the upstream freshwater regions, including Lake Albert (Figure 9). The higher diversity in the Goolwa channel region was attributed to additional zooplankton taxa transported from the Finniss River and Currency Creek (Shiel and Tan 2013a).

Analysis of published data (Shiel and Aldridge 2011, Geddes et al. 2016), suggests zooplankton richness declines non-linearly with increasing salinity according to a power function (showing a rapid initial decline) (Figure 10). However, salinity had a greater explanatory effect on North Lagoon taxa, accounting for over 75% of variation in taxonomic richness in samples (Figure 10b). This seems plausible, as the influence of barrage flows decrease with distance along the North Lagoon and the greater salinity exerts increasing pressure on taxonomic richness.

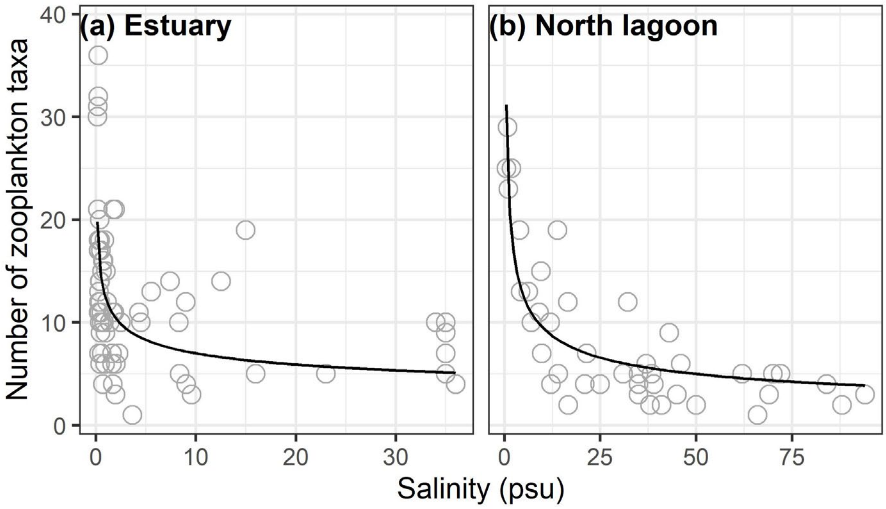


Figure 10. Zooplankton taxonomic richness from (a) the Murray Estuary and (b) the North Lagoon. Lines show power function fitted to the data using non-linear least squares. Equations are: Estuary: No. taxa = 12.4 x Salinity$^{-0.25}$; pseudo-R^2 = 0.28; North Lagoon: No. Taxa = 24.0 x Salinity$^{-0.40}$; pseudo-R^2 = 0.77. Overlap in 95% parameter confidence intervals suggest no difference in the scaling pattern. Data sources: Geddes et al. (2016), Shiel and Aldridge (2011).

Taxonomic composition

As with taxonomic richness, distinctive spatial patterns of species composition (i.e. the particular organisms found in a sample) tend to occur in the three regions in the Coorong and upstream areas in the Goolwa channel and Lower Lakes (Oliver et al. 2013, Oliver et al. 2014, Bice et al. 2016a, Hemraj et al. 2017b, Furst et al. 2019). However, species composition is highly variable over time at all locations, and – depending largely on the homogenising effects of barrage flow releases on species composition – there is considerable overlap between Lake Alexandrina and the Coorong (Oliver et al. 2013) and between sites within regions of the Coorong (Oliver et al. 2014). Although there can be some overlap in species composition (mean similarity >20%) between all three Coorong regions, due to their increased connectivity, the Murray Estuary and North Lagoon are more similar to one another than either is to the South Lagoon (Oliver et al. 2014, Hemraj et al. 2017b).

Due to the high inter-annual variability of flow and its strong influence on composition, it is difficult to characterise zooplankton assemblages among the regions of the Coorong and Lower Lakes. This is particularly true based on a single year's sampling, as seasonal variations are nested within inter-annual climatic cycles. Notwithstanding issues related to spatio-temporal sampling patterns, as the longest available comparable period of monitoring over the period 2010–2014, it is worth inquiring of these data to determine what multi-year patterns can be inferred, as shown by Oliver et al. (2013) and Oliver et al. (2014).

Despite lacking matching water quality data, it was possible to use these data to group samples according to their similarity and ask what factors determine this similarity, using statistical techniques known as clustering and categorisation. This analysis yielded five compositional groups (based on a Hellinger dissimilarity of at least 8), with each group characterised by particular suite of taxa (known as indicator species or taxa) (Table 12). Classifying samples according to (i) the region within the Coorong, Lower Lakes or Goolwa channel in which it was collected, (ii) year and month of sampling, (iii) 30 day mean barrage flow (gl30) and (iv) days with zero barrage flow in the last 90 days (zq90), suggest seasonal variations dominate variations in composition (Figure 11). Outside of the period September to February, samples in the CLLMM region were most likely to be from compositional Group 4 (purple symbols in Figure 11), which had a single indicator species: the ciliate *Stenosemella lacutris* (Table 12). Unsurprisingly (given they analysed largely the same dataset), Oliver et al. (2014) also found the same species dominated compositional differences among samples.

Table 12. Indicator species (Dufrene and Legendre 1997) for five taxonomically defined zooplankton assemblages from the Coorong, Lower Lakes and Goolwa channel over the period 2010–2014. The indicator value combines the relative abundance and relative frequency to identify species with a statistically significant (p <0.01) affinity for one of the groups (for Group 5, only taxa with an indicator score >0.3 are shown).

GROUP	TAXON	INDICATOR VALUE
1	Calanoid nauplii	0.5719
	Harpacticoid copepodites	0.2543
	Acartia sp.	0.2433
2	*Ceriodaphnia* sp.	0.4567
	Bosmina meridionalis	0.3728
	Boeckella triarticulata	0.3593
	Daphnia carinata	0.3226
3	*Difflugia* sp.c	0.9098
	Alona sp.	0.1818
	Difflugia sp.b	0.1437
4	*Stenosemella lacustris*	0.6673
5	*Filinia pejleri*	0.7169
	Polyarthra dolichoptera	0.6545
	Trichocerca pusilla	0.4489
	Proalides tentaculatus	0.4373
	Keratella tropica	0.4059
	Asplanchna priodonta	0.3511
	Hexarthra intermedia	0.3449
	Brachionus calyciflorus.amphiceros	0.3266
	Brachionus angularis	0.3002

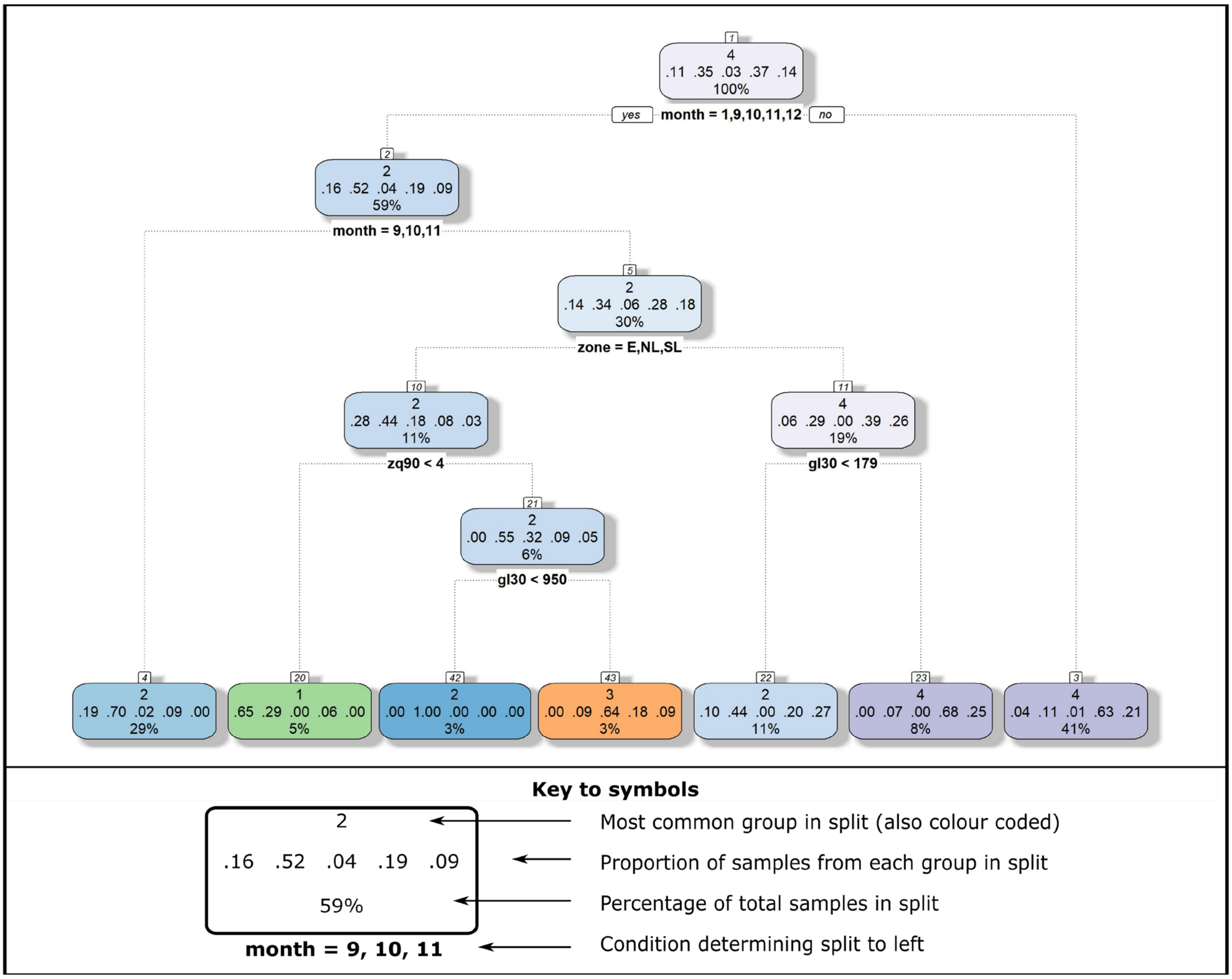


Figure 11. Classification tree (Therneau et al. 2019) dividing zooplankton samples collected over the period 2010–2014 among five taxonomically-defined categories as a function of CLLMM region. E = Murray Estuary, NL = North lagoon, SL = South lagoon. Other zones were Goolwa channel, Lake Alexandrina, Lake Albert, sampling month, gl30 = 30 day mean barrage flow, zq90 = days zero barrage flow in the last 90 days. Key shows information in each panel (see Table 12 for indicator species). Each split in the tree represents a condition, which if true, determines the classifications to the left. Note none of the factors used in classification resulted in a dominance of Group 5.

Samples collected during spring (again irrespective of CLLMM region), were most likely to fall into Group 2 (blue symbols in Figure 11), characterised by the cladocerans *Ceriodaphnia* sp. and *Bosmina meridionalis*, the calanoid copepod *Boeckella triarticulata*, and freshwater rotifer *Keratella australis* (Table 12). Notably, these taxa include some important prey species for fish (see Section 2.1). Lack of any influence of Coorong region in this level of classification is likely a spurious result due to the unbalanced sampling, as the South Lagoon is typically far too saline to support freshwater zooplankton. However, it is notable that Hemraj et al. (2017b) sampled a similar assemblage at Salt Creek (a site in the southern part of the South Lagoon) on one occasion during high flow from the Upper South East Drainage Scheme – an intriguing result that remains unexplained.

Within the Coorong summer–autumn samples, Groups 1, 2 and 3 were separated according to mean barrage flow and the length of time barrages had been closed during the preceding three months. The most probable assemblage in the Coorong outside of spring was Group 1 (characterised by calanoid nauplii, harpacticoid copepodites and *Acartia* sp.), but Group 2 assemblages were more likely to persist outside spring at mean 30-day flow volumes below 950 ML d^{-1}, following a period of barrage closure exceeding 4 days in the last 3 months. In contrast, Group 3, characterised by rhizopoda from genus *Difflugia* and the freshwater cladoceran *Alona* sp. (Table 12), was favoured during high summer flow (orange symbols in Figure 11).

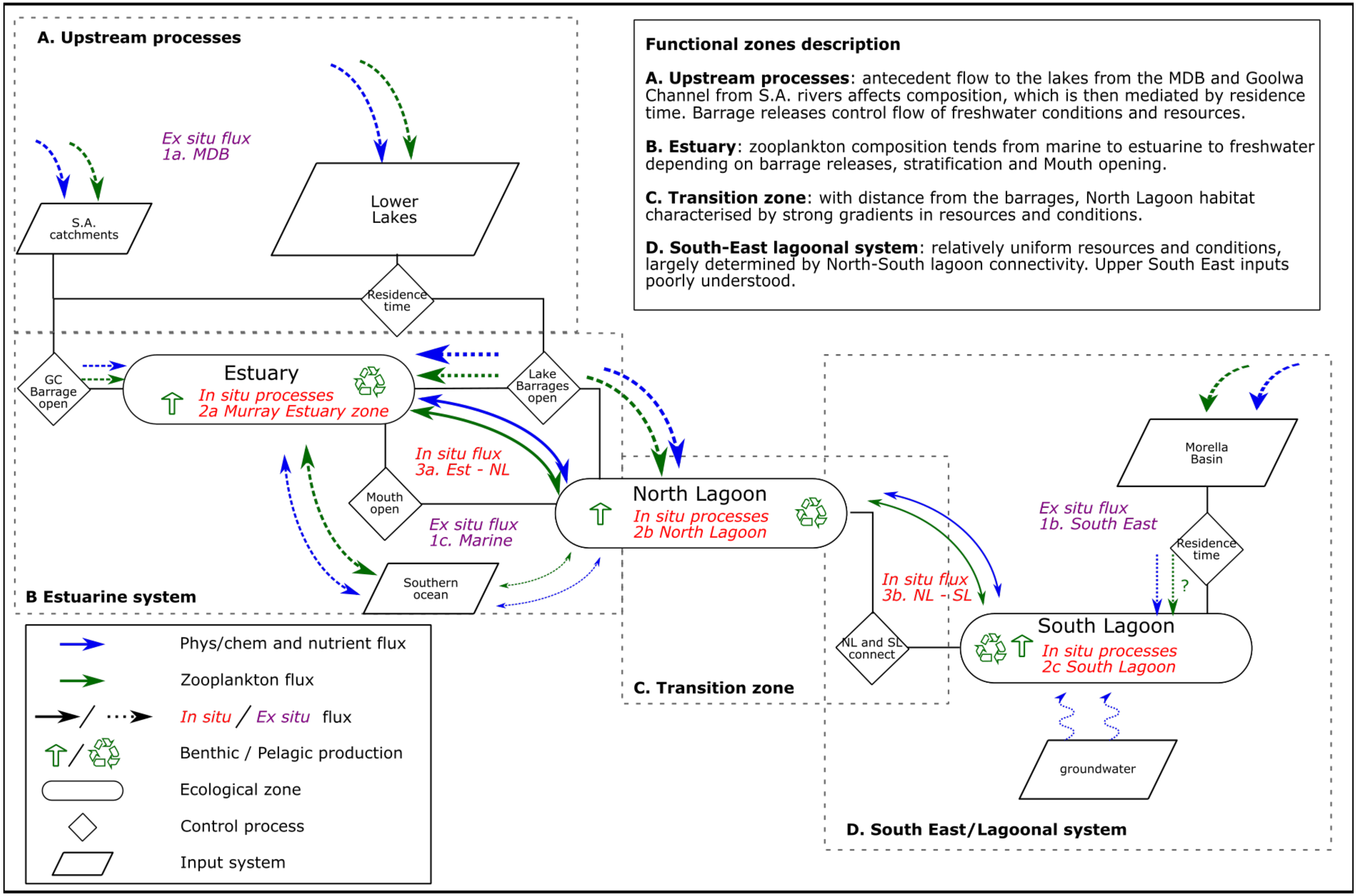
No set of conditions included in the classification tree (Figure 11) favoured the development of Group 5 assemblage, which had the most indicator species, predominantly freshwater and estuarine rotifers (Table 12). As the samples classified as Group 5 were primarily summer–autumn samples obtained during 2011-12, it is probable they represent samples including species emerging from egg banks following re-inundation of the Lower Lakes fringes post drought, hypothesised as an explanation for the increase in taxonomic richness during that year (Shiel and Tan 2013a).

To summarise, all studies have found zooplankton species composition and abundance is highly dynamic with consistent evidence in studies of Coorong zooplankton of rapid change in species composition, not only in space, but also over time at a given site (Shiel and Tan 2013a, 2013b, Oliver et al. 2014). To distinguish natural successional or trophic changes in composition due to flow or other abiotic changes (e.g. water quality), the sampling interval must be shorter than the period over which such changes occur (Shiel and Tan 2013b). It seems likely that sampling at four weekly intervals might be too infrequent to achieve this given the dynamic nature of the Coorong. The same arguably applies to our understanding of Coorong food webs, where prey selectivity is also highly dynamic, being influenced by – and probably influencing – the distribution of zooplankton in space and time (Brookes et al. 2015, Bice et al. 2016a, Hemraj et al. 2017a).

3.2.3 Main influences on Coorong zooplankton

The most often reported abiotic determinants of composition of zooplankton in the Coorong are flow, salinity, pH and water temperature (Oliver et al. 2013, Shiel and Tan 2013a, b, Oliver et al. 2014, Geddes et al. 2016, Hemraj et al. 2017b). Biotic determinants are also important with the density and composition of the phytoplankton community linked to zooplankton assemblage type (Hemraj et al. 2017a, Hemraj et al. 2017b), and top-down predation implied by the lack of adult copepods despite high density of nauplii (Bice et al. 2016a, Geddes et al. 2016, Furst et al. 2019). Predation pressure could become more important at low flow due to reduced turbidity (Geddes et al. 2016, Furst et al. 2019). However, water quality or phytoplankton composition could also be implicated in impeding completion of zooplankton life cycles (Hemraj et al. 2017a, Hemraj et al. 2018).

More generally, it is necessary to consider how both internal (e.g. water quality in the Coorong) and external (e.g. zooplankton influx from the Lower Lakes) factors contribute to the state of the Coorong system, including the zooplankton community (Figure 12). Most, if not all, of these factors are determined by the relative contribution of different water sources to the different regions of the Coorong, due to their contrasting abiotic and biotic characteristics. As a result of the differential connectivity to external sources, the three regions of the Coorong have distinct characteristics, resulting in reasonably stable patterns of water quality variation (Oliver et al. 2013). Among Coorong regions, the Murray Estuary is the most influenced by barrage flows and is well connected to the Southern Ocean and therefore zooplankton are most likely to respond rapidly to changing contributions from each. The South Lagoon is the opposite, receiving only limited inflows and changing slowly over time and with a more stable zooplankton composition, at least during 2010–2014 (Oliver et al. 2014). The North Lagoon is a transition region, being highly connected to freshwater or marine sources at the top of the lagoon, but with a more tenuous exchange with the more saline South Lagoon. As a result, it has the strongest gradients in water quality (Hemraj et al. 2017a), and also the most dynamic, though not most speciose, zooplankton assemblages (Oliver et al. 2014). Figure 12 hypothesises the main influences on zooplankton communities in the Coorong based on a literature review and is discussed further below.



Functional zones description

A. Upstream processes: antecedent flow to the lakes from the MDB and Goolwa Channel from S.A. rivers affects composition, which is then mediated by residence time. Barrage releases control flow of freshwater conditions and resources.

B. Estuary: zooplankton composition tends from marine to estuarine to freshwater depending on barrage releases, stratification and Mouth opening.

C. Transition zone: with distance from the barrages, North Lagoon habitat characterised by strong gradients in resources and conditions.

D. South-East lagoonal system: relatively uniform resources and conditions, largely determined by North-South lagoon connectivity. Upper South East inputs poorly understood.

Figure 12. Hypothesised influences on zooplankton composition and abundance in the Coorong estuary and lagoonal system.

Ex situ fluxes and controls on their influence

The most important determinant of the ecological state of the Coorong is antecedent barrage flow (Brookes et al. 2009b, Lester and Fairweather 2009, Geddes et al. 2016, Hemraj et al. 2017b). For zooplankton, this has the direct effect of transporting zooplankton taxa and phytoplankton blooms from upstream (Shiel and Aldridge 2011, Oliver et al. 2013) and indirect effects on conditions, particularly salinity but also influencing the availability of resources that fuel primary productivity within the system (Oliver et al. 2013, Oliver et al. 2014, Bice et al. 2016a, Brookes et al. 2015, Hemraj et al. 2017a, 2017b).

The composition of zooplankton transported to the Coorong by barrage flows reflects populations within Lakes Alexandrina and Albert and the Goolwa channel. These depend on antecedent flow regimes and flood history in the MDB, because different river systems provide distinct taxa to the water bodies upstream of the barrages (Shiel et al. 1982, Shiel and Aldridge 2011, Shiel and Tan 2013a). Darling River zooplankton are characterised as being dominated by warm-water rotifers, contrasting with a more typical lacustrine (lake adapted) microcrustacean community found in the Murray River as a result of the impoundments (Shiel and Aldridge 2011). Floodplain (and presumably riverine wetland) recession flows transport high zooplankton densities to the river, fuelling downstream productivity (Furst et al. 2014) and transporting a diverse range of zooplankton taxa downstream to the lake system. These are then transported to the Coorong via barrage releases (Shiel and Aldridge 2011). Watercourses within the South Australian MDB such as Finniss River and Currency Creek also provide specific taxa, including microcrustaceans along with riparian, epiphytic, epibenthic or littoral microfauna including protists such as *Difflugia* and other Rhizopoda that increase taxonomic diversity - at least within the Goolwa channel (Shiel and Tan 2013a, Oliver et al. 2014).

Antecedent water level history within the Lower Lakes and channel environment could also be reflected in zooplankton delivered to the Coorong. For example, Shiel and Tan (2013a) ascribed increased diversity and abundance in the year following the drought-breaking 2010 flood event as potentially a result of increased emergence from egg banks within re-inundated sediments.

Barrage closure and residence time

Once zooplankton reach the Lower Lakes, their composition and abundance, and therefore their contribution to Coorong food webs, depend in part on residence time of water within the Lower Lakes before release to the Murray Estuary and North Lagoon. Increased residence time within the Lower Lakes is thought to increase abundance of zooplankton, and has also been thought to favour development of assemblages dominated by copepods and cladocerans rather than rotifers (Bice et al. 2016a, Geddes et al. 2016, Leterme et al. 2018). Given the preferred-prey status of calanoid copepods and cladoceran species for several important fish species in the Coorong (Section 2.1), and the apparent change in annual barrage closure patterns post the onset of the Millennium Drought (presumably decreasing residence time, see Section 3.2.4), additional research effort is warranted to understand the role of lake residence time in moderating zooplankton flux to the Coorong.

Preliminary data analysis testing this effect suggests that the volume of freshwater discharge increases zooplankton abundance in an approximately proportional (linear) manner, while the effects of residence time appear to be more unimodal (hump shaped), and pronounced in the Murray Estuary (Figure 13). As with all information in this sub-section, the data warrant caution in interpretation. For example, as these data include samples taken during the large barrage release period following near-record low inflows to the lower MDB (Shiel and Aldridge 2011), high abundance and richness values at short-residence times might reflect increased channel density of zooplankton during the receding limb of flood flows due to floodplain productivity (Furst et al. 2014) rather than high productivity within the Lower Lakes. The relationship between upstream floodplain inundation, lake/channel residence time and zooplankton flux to the Murray Estuary and Coorong lagoons via the barrages warrants additional research. Any zooplankton monitoring undertaken within the Coorong system probably requires this context to be correctly interpreted.

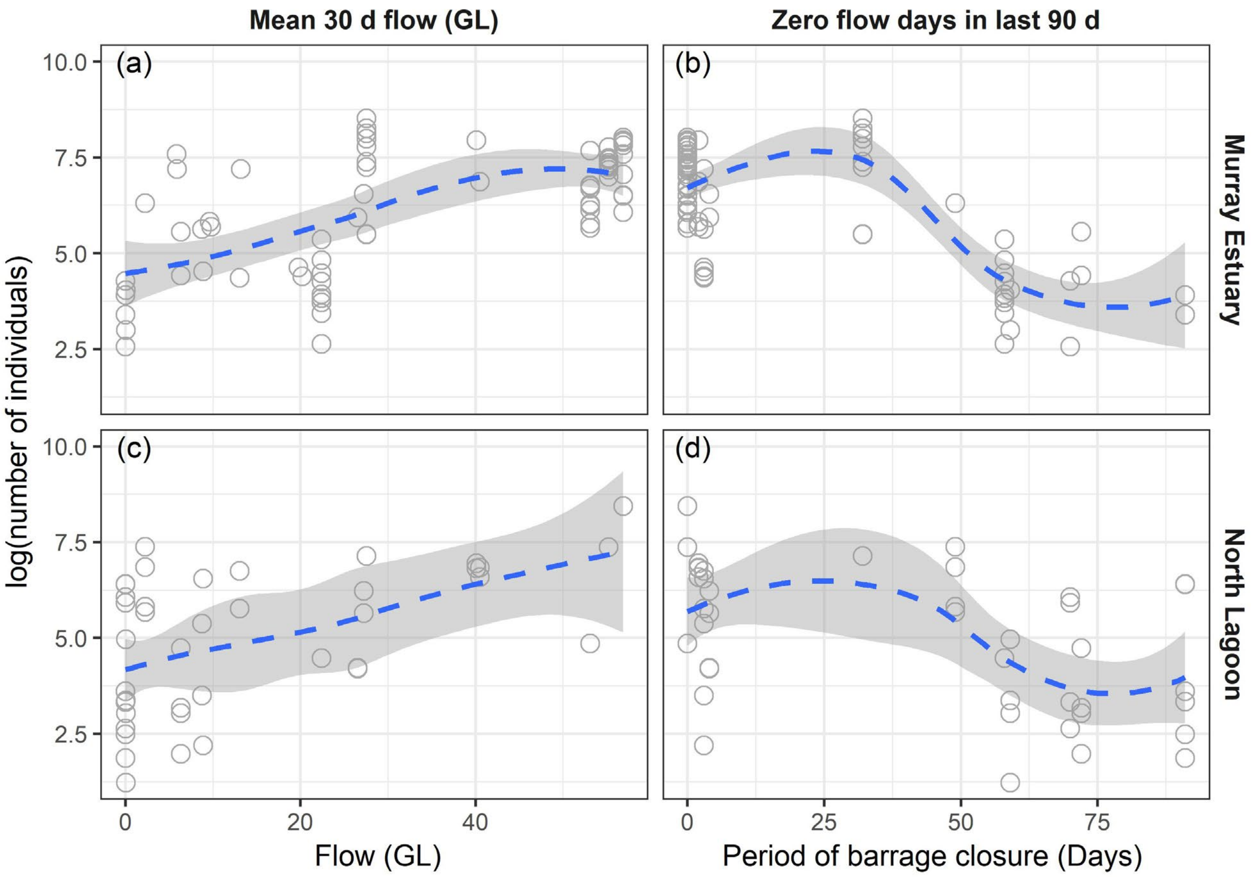


Figure 13. Effects of mean 30-day discharge through the barrage system (a, c) and the period of barrage closure (b, d) on the abundance of zooplankton from the Murray Estuary (top row) and the North Lagoon (bottom row). Period of barrage closure used as a proxy for lake residence time. Data sources: Geddes et al. (2016), Shiel and Aldridge (2011).

Upper South East Drainage Scheme and groundwater

While MDB flow via the barrages is the main determinant of the ecological state of the Coorong, the Upper South East Drainage Scheme also appears to present considerable, but largely unexplored influence on the conditions and resources pertinent to zooplankton assemblages in the South Lagoon. For example, flow release of ~20 GL during 2014 prevented worsening of – and even reversed – a salinity gradient along the South Lagoon (Hamilton et al. 2014), maintaining salinity at less than twice that of sea water, thought to be an upper salinity tolerance threshold for most fish species (Brookes et al. 2009b) and also limiting for zooplankton composition (e.g. Figure 10). This same release also improved connectivity between the South and North lagoons (Hamilton et al. 2014).

The potential for delivery of zooplankton from Morella Basin via the Upper South East Drainage Scheme also warrants some investigation, with Hemraj et al. (2017b) detecting several zooplankton species, including freshwater dependent and high quality prey species (*Filinia pejleri*, *Keratella australis*, *Bosmina meridionalis*, *Daphnia lumholtzi*, and *Boeckella triarticulata*), only once in Salt Creek, concurrent with the highest flow release volumes during August 2014. Despite typical salinities of approximately half that of sea water (Hamilton et al. 2014, Mosley et al. 2017), presumably, these taxa originated from Morella Basin.

Within the South Lagoon, groundwater seepage might be locally influential, via nutrient fluxes including biologically available nitrogen (Haese et al. 2009), which could contribute to productivity (Brookes et al. 2009b). Being brackish in nature (~5–7 psu), regional groundwater is unlikely to be influential on the South Lagoon salt balance during hypersaline periods (Mosley et al. 2018). However, if future management interventions could successfully reduce the salinity of the South Lagoon closer to that of marine salinity, groundwater could arguably become a more influential component of the salt balance, particularly in areas where seeps were concentrated.

Murray Mouth closure

The state of openness of the Murray Mouth determines whether water from the Southern Ocean enters the Coorong estuary. This is critical for maintaining salinity within the Murray Estuary and North Lagoon close to marine salinities. Mouth closure during the Millennium Drought led to significant increases in salinity throughout the Coorong that were highly limiting of ecological processes, food web complexity and taxonomic diversity (Brookes et al. 2009b), including zooplankton.

The role of zooplankton egg banks

Many freshwater zooplankton produce a resting stage, which can either hatch in the following year or become part of a persistent egg bank, where, on later emergence, they contribute to local diversity (Brendonck and De Meester 2003). The impacts of the drought on the state of egg banks in both the Lower Lakes and the Coorong are unknown, but emergence from re-inundated sediments is thought to have contributed to high zooplankton diversity in the region during sampling in 2011-12 (Shiel and Tan 2013a). As these species were not present in later years, it is possible egg banks were depleted. Egg banks might not be as important for resident estuarine taxa in the Coorong, although *Acartia* cf. *fancetti* eggs appear to remain viable even in hypersaline water, with emergence from dormant eggs potentially explaining their presence in the South Lagoon in 2014 (Hemraj et al. 2017b). Nonetheless, it seems likely that zooplankton egg banks in the Lower Lakes (and possibly Coorong lagoons) would have become depleted in both diversity and abundance in comparison to their state prior to the Millennium Drought. This could still be affecting the flux of zooplankton to the Coorong. The resulting lower abundance or difference in species composition of zooplankton would then be reflected in their role in food web studies that have occurred since the drought period. Such an impact is an example of a hysteresis effect, where returning the flow regime to pre-drought levels does not reverse ecological impacts. For example, 2010–2014 phytoplankton assemblages appeared not to have returned to pre-drought composition, despite return of comparable water quality (Oliver et al. 2014).

In situ biotic and abiotic processes (connectivity, water quality gradients, productivity, predation)

With relative contributions of different water sources largely dictating the prevailing conditions and available resources within the Coorong, *in situ* processes then alter the observed zooplankton community. Variable connectivity to external flow results in gradients in water quality, which set constraints on taxonomic diversity and are spatially most pronounced in the North Lagoon (Hemraj et al. 2017a) although stratification of layers in the Murray Estuary driven by differences in salinity can also create sharp transitions in water quality that moderate benthic productivity (Bice et al. 2016a). The important *in situ* processes affecting zooplankton are autotrophic productivity and predation. As zooplankton themselves consume autotrophic taxa, their composition and abundance can also moderate these *in situ* processes.

During periods of low or zero-flow from the barrages, salinity increases throughout the system with the Murray Estuary likely to attain a maximum of marine salinities (providing the mouth is open). With the onset of flow, the zooplankton assemblage in the Murray Estuary will increasingly reflect that of Lake Alexandrina (Oliver et al. 2013, Shiel and Tan 2013a). For example, the large flood release in 2010 shifted the estuarine microcrustacean zooplankton assemblage that had emerged during drought periods to one dominated by protists and rotifers (Shiel and Aldridge 2011).

Productivity and bottom up control on zooplankton

Productivity within the Coorong depends on freshwater flows to reduce salinity and provide nutrients fuelling primary production (Brookes et al. 2015). This will affect zooplankton by altering the abundance and composition of phytoplankton and other food resources (Hemraj et al. 2017a). In addition to salinity and pH, Hemraj et al. (2017b) found zooplankton community composition was linked to the concentration of chlorophyll *a* and to the presence of cryptophytes. Phytoplankton will be influenced by nutrient availability and turbidity (Leterme et al. 2018), suggesting indirect impacts on zooplankton will arise from variations in these parameters.

Benthic productivity has been consistently found to be important in Coorong food web studies (Bice et al. 2016a, Hossain et al. 2017). In the Murray Estuary, the development of salt wedge conditions during freshwater releases favours increased flux of detritus to the benthos via flocculation, resulting in increased abundance of harpacticoid copepods (Bice et al. 2016a, Furst et al. 2019), providing an important link between benthic and pelagic productivity.

Predation and top down controls on zooplankton

A feature of the Coorong zooplankton, particularly copepods, is the presence of juveniles (nauplii and copepodites). Several authors have interpreted the abundance of these immature stages as possibly a result of top-down predation selectively removing adults (Bice et al. 2016a, Geddes et al. 2016, Furst et al. 2019). Such pressure could be amplified during low or zero flow periods, as decreasing turbidity could increase predation (Geddes et al. 2016). However, water quality can also affect zooplankton development and Hemraj et al. (2018) showed that high salinity can suppress development of immature *Acartia fancetti*, particularly as temperature increases. Nonetheless, several important copepod prey species, such as *Gladioferens* sp., have been notably absent, or rare, from the Coorong despite being common in other southern Australian estuaries (Geddes et al. 2016). As data prior to the drought are lacking, it is possible that their absence reflects incomplete recovery of their populations, which could be further constrained by selective predation of zooplankton by fish species.

More speculatively, release from top down pressure could possibly be occurring within zooplankton taxa. Both calanoid and cyclopoid copepods graze on soft-bodied rotifers including genus *Synchaeta* (Furst et al. 2019, and references cited therein). *Synchaeta* are commonly recorded in higher salinity samples from the Coorong lagoons (Oliver et al. 2014), but are selectively avoided as a prey by forage fish such as sandy sprat (Bice et al. 2016a). It is unusual for an available resource not to be exploited and it is tempting to question whether high *Synchaeta* abundance could be partially associated with a lack of copepod predators, although clearly their abundance could be due to other factors, e.g. salinity tolerance, rather than release from predation.

Loss of North-South Lagoon connection

In the absence of adequate barrage flow or marine inflows to replenish water in Coorong lagoons lost from evaporation, the connection between the North and South lagoons can be lost. Subsequent increases in salinity from evaporation create extremely limiting conditions for all aquatic taxa except obligate halophiles. As salinity increases, only highly tolerant or salt lake adapted species are likely to be present in the South Lagoon and the North Lagoon develops strong longitudinal salinity gradients reflecting connectivity with the Murray Mouth.

3.2.4 Uncertainties relating to zooplankton spatio-temporal sampling distribution

There are two major sources of uncertainty limiting our current understanding of the role of zooplankton population dynamics in Coorong food webs. Most important is lack of a pre-drought baseline understanding of variability in the composition and population dynamics of zooplankton prior to the Millennium Drought. This limits our ability to interpret existing patterns within the context of natural variability in ecosystem function that existed prior to the Millennium Drought. The second source of uncertainty is the unbalanced spatio-temporal sampling effort and limited duration of most studies (see Section 3.2.1), which limits our understanding of even contemporary zooplankton dynamics.

Comparison of pre-Millennium Drought and zooplankton-sampling-period barrage flow data illustrate the first problem relating to the lack of baseline understanding of ecosystem dynamics (Figure 14). Despite some tendency for above and below average years to follow one another, prior to the drought, both annual barrage closure days (Figure 14a) and total flow volumes (Figure 14b) were highly variable from year to year. Post

Millennium Drought there has been positive temporal autocorrelation (the tendency for high, or low-flow years to follow one another) in zero flow days over short-periods (2-year lag correlation = 0.51; $p < 0.05$), and no evidence of a long-period negative autocorrelation in annual flow volumes typical of cyclical climatic dynamics (e.g. pre-drought 8-year lag = -0.38; $p < 0.05$).

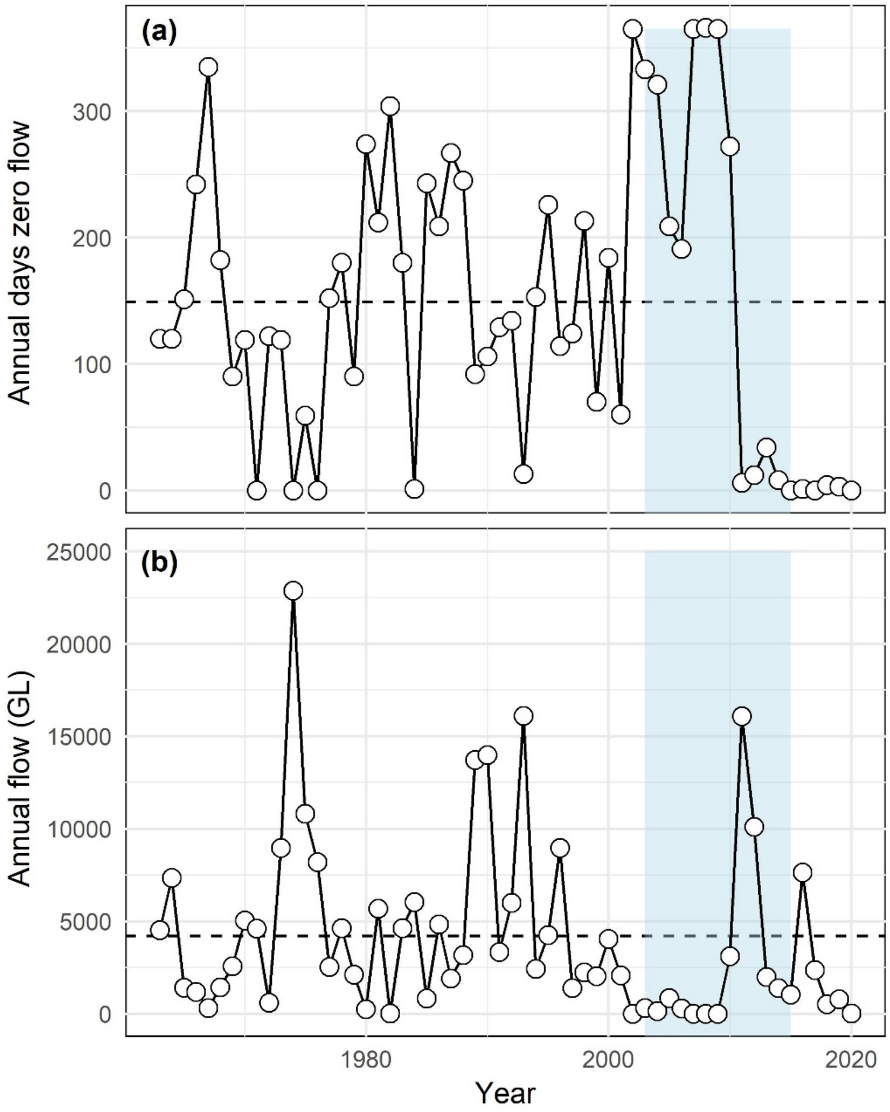


Figure 14. Period of Zooplankton community characterisation compared to temporal changes in (a) total cease-to-flow days; and (b) annual barrage flow showing period. Horizontal dashed line shows mean for time series. Shading indicates the period over which zooplankton communities have been characterised. Total cease-to-flow days used as a proxy for lake residence time. Data source: Department for Environment and Water.

Over the monitoring period, flow seasonality has also been altered, becoming less variable month-to-month and almost reversed in terms of the peak mean flow months (Figure 15). The ecological consequences of this change in seasonal and inter-annual variability and autocorrelation in flow conditions are unknown. However, it seems unlikely that population dynamics would currently reflect pre-drought patterns. Zooplankton data reflect communities over a period during the middle of the worst drought on record with above average residence times in the Lower Lakes, or following one of the wettest periods on record and following historically unprecedented low residence times in the Lower Lakes (Figure 14). Mean daily flow calculated by month shows that annual barrage flow signals during the period were the reverse of historical trends, with flows April-May – historically among the driest months – greater than during October-December – historically among the wettest months (Figure 15).

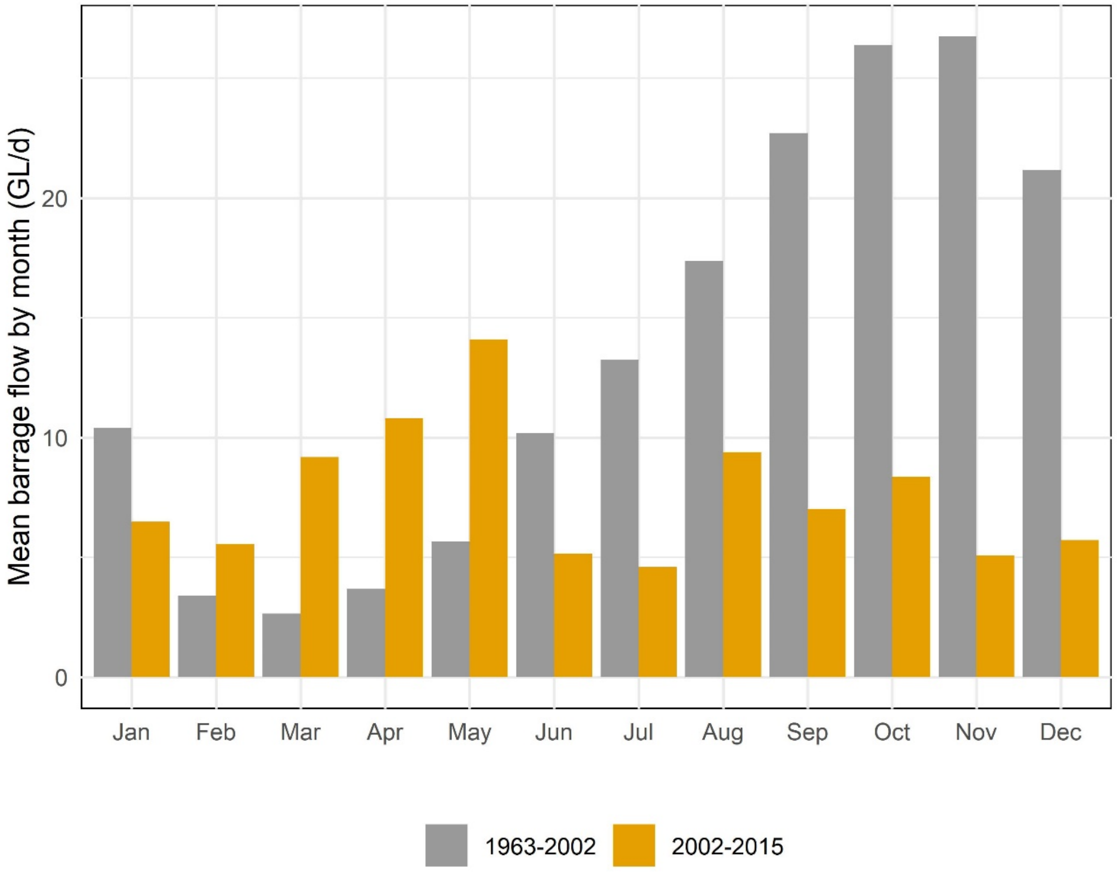


Figure 15. Comparison of mean monthly barrage flow patterns comparing historical records from 1963–2002 with the period over which most zooplankton sampling occurred (2003–2015). Data source: Department for Environment and Water.

3.2.5 Conclusions

Spatio-temporal patterns in zooplankton abundance and composition in the Coorong reflect variation in the distribution and availability of conditions and resources. Both depend primarily on the relative contribution of freshwater and marine inflows and the way these influences are moderated by connectivity within and among the Coorong regions. Depending on proximity to the barrages, inflows not only homogenise Coorong zooplankton composition with upstream sources but set the conditions that determine where within the Coorong different zooplankton taxa can persist. Flow, salinity, pH and water temperature are the abiotic factors with the strongest correlation with zooplankton abundance and composition. Nutrients and turbidity also likely contribute, if only via effects on phytoplankton density and composition. However, biotic factors are perhaps as critical for zooplankton in the Coorong, with bottom up and top down controls on composition and abundance implied, although poorly understood.

Importantly, freshwater flows to the Coorong reflect the antecedent upstream flow and flood history of the MDB, which varies over monthly to decadal scales. Zooplankton population dynamics within the Coorong must be understood in the context of these external influences. This is also important for understanding the multiple trophic-level interactions in which zooplankton are involved. Coorong food web studies have found the most common zooplankton fish prey species have been harpacticoid copepods (Section 2.1); but as they have generally coincided with relatively low flow periods, they might not have captured episodic contributions to estuarine productivity during high flow events. When present, freshwater calanoid copepods, cladocerans and rotifers are opportunistically consumed prey, but such taxa have been present in low densities in studies to date. Additionally, some estuarine calanoid copepods such as *Gladioferens* sp., potentially important prey for larval black bream, have appeared only sporadically, while they are common in other southern Australian estuaries. It is not known whether this represents a natural pattern or incomplete recovery of these species, as no pre-drought data are available for comparison.

A key uncertainty remains whether zooplankton composition or their role in Coorong food webs inferred from research over the period 2003–2019 reflects their role prior to the Millennium Drought. It is possible that zooplankton dynamics that were typical of pre-drought conditions might not yet be restored. For example, it may take many years of more typical pre-drought barrage release and riverine flow patterns to replenish egg banks. Comparison of flow data from the period 1963–2002 with the period 2003–2015 during which time zooplankton data have been collected, shows markedly different hydrological characteristics. This is compounded by uncertainties associated with inconsistent methodology (e.g. net mesh, boat versus wading, different enumeration methods) and unbalanced spatio-temporal sampling effort, making reliable inference on zooplankton abundance and composition in the Coorong challenging. Therefore, caution is warranted in making assumptions about the role of zooplankton in the ecology of the Coorong based on available information. Further research sampling is being conducted, as part of *Component 3 Food web* of the T&I Project (Table 1), to increase time series data and improve our understanding of seasonal dynamics of zooplankton assemblage in the Coorong and their role in the food web.

3.3 Macroinvertebrates

3.3.1 Review of the Coorong macroinvertebrate studies

The earliest macroinvertebrate studies in the Coorong were conducted in the 1980's with assessments of taxa associated with different salinities, *Ruppia* habitat and their role as food items. These studies were predominately qualitative (Snoeijs and van der Ster 1982, Paton 1982, Geddes 1987, Geddes and Butler 1984). Since the early 2000's, annual quantitative macroinvertebrate sampling occurred from the Murray Estuary to Salt Creek in the South Lagoon as part of 'The Living Murray' (TLM) program, which established the macroinvertebrate response to the Millennium Drought and post-drought floods with water release through the barrages (Dittmann *et al*. 2015). During the National Research Flagship CLLAMMecology, patterns in distribution and abundance of adult and juvenile macroinvertebrates were investigated, and their recolonisation potential experimentally assessed (Rolston and Dittmann 2009). From 2010 to 2014, the most intensive macroinvertebrate sampling in the Coorong occurred as part of the Murray Futures program, sometimes at monthly intervals in the intertidal and subtidal zones around the Murray Estuary and in both the North and South Lagoons (Dittmann et al. 2016). The ongoing monitoring programs throughout the Murray Estuary and Coorong lagoons have provided long-term datasets that are integral to our understanding of macroinvertebrate community dynamics through drought and flood events. In the Murray Estuary and North Lagoon region of the Coorong, some studies have also focused on the distribution and ecology of the tube-reef building polychaete *Ficopomatus enigmaticus* (Dittmann et al. 2009, Goldschmidt 2010, Kirkpatrick 2011, Moyle 2016). The focused studies on those tube-worm reefs have provided new knowledge of the settlement dynamics and formation of reefs and their added structural complexity as habitat provision for some macroinvertebrate communities.

Across the Murray Estuary and Coorong lagoons, over 60 macroinvertebrate species have been recorded, mostly in the Murray Estuary (from the Goolwa Barrage to Pelican Point) and North Lagoon (from Mark Point to Parnka Point) and the less speciose South Lagoon (Parnka Point to Salt Creek) which is dominated by insect larvae (Dittmann *et al.* 2018). The Murray Estuary and North Lagoon regions of the Coorong share many macroinvertebrate species, but in comparison fewer species in the South Lagoon have overlapping ranges with the two northern regions (Dittmann *et al.* 2018). Seawater and freshwater inflows through the Murray Mouth and barrages respectively, are strong hydrodynamic drivers linked to the environmental conditions that influence species ranges throughout the Coorong.

Changes to ecosystem condition across recent decades (i.e. 2004 to 2020), and the alignment of ongoing macroinvertebrate monitoring programs have enabled us to establish baseline understanding of benthic functioning under dominant environmental conditions (i.e. low flow and hypersaline, high flow and estuarine-marine) (Dittmann *et al.* 2018; Figure 16). The benthic response to drought, with depauperate macroinvertebrate communities, through to high abundances of opportunistic species during flood events, and highly biodiverse communities under estuarine conditions, has matched classic ecological theory of estuaries and has been recorded in other hypersaline systems (Whitfield et al. 2012, Tweedley et al. 2019).

To support the food web investigations around ecological restoration of the South Lagoon, we explored and summarised the long-term datasets from TLM, CLLAMMecology, and Murray Futures benthic macroinvertebrate monitoring programs. Since 2004, standardised field and laboratory methodology has enabled us to investigate the spatial-temporal patterns of benthic macroinvertebrates throughout the Coorong. Here, we summarise the patterns in benthic species richness, total abundances, key macroinvertebrates, biomass and communities. In the context of the ecological restoration plans for the Coorong we also discuss environmental drivers of change to benthic macroinvertebrate distribution in recent decades.

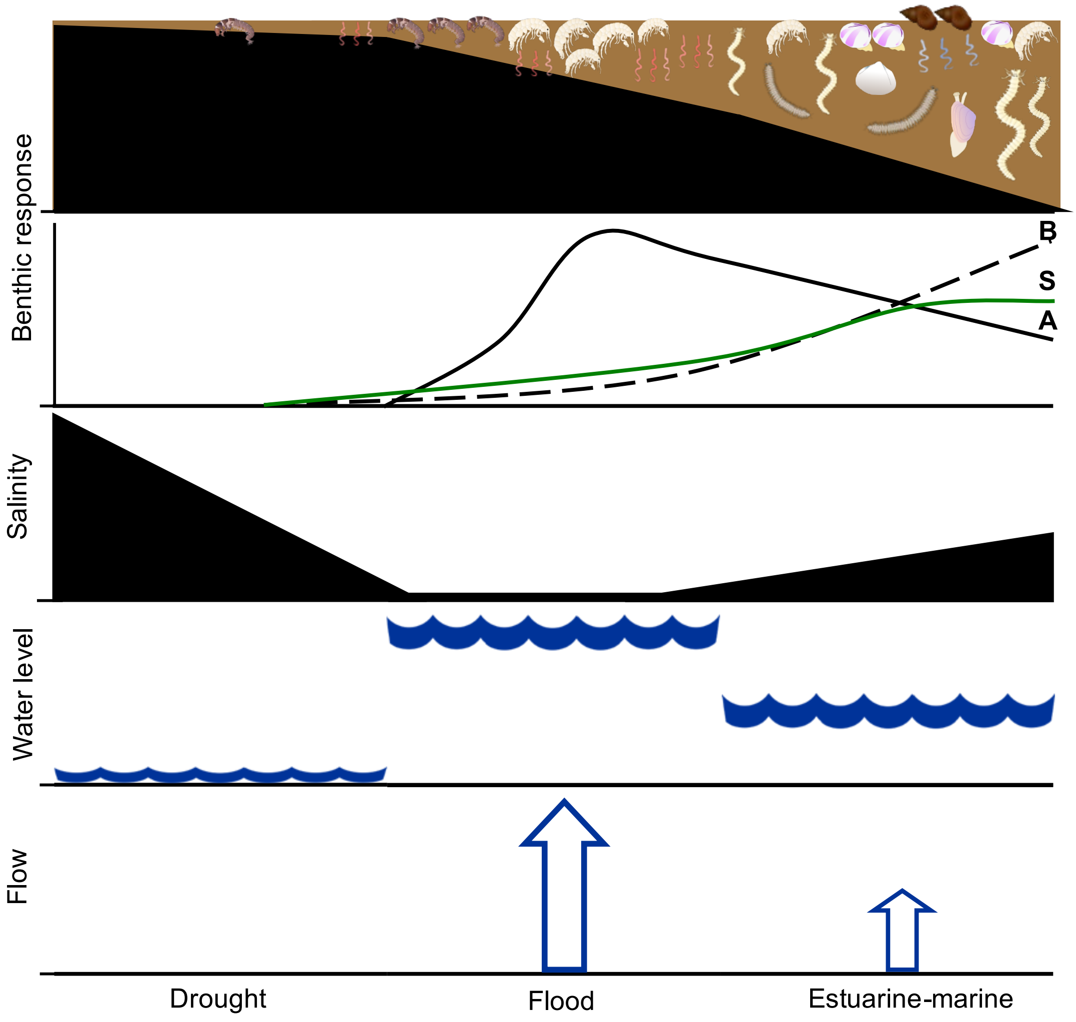


Figure 16. Conceptual diagram of changes to the main environmental drivers (water level and salinity) and response of benthic macroinvertebrates occurring in sand or mud of the Coorong and Murray Estuary during drought, flood, and estuarine-marine conditions. The black and brown shading in the top diagram indicate anoxic and oxic sediment layers respectively. B = Biomass; S = Species richness; A = Abundance. The conceptual diagram can also be seen in a spatial context, with conditions under drought characteristic for the South Lagoon, and estuarine-marine conditions for the North Lagoon and Murray Estuary. Source: Dittmann et al. 2018.

3.3.2 Spatio-temporal patterns in macroinvertebrate species richness, abundance, biomass and assemblage dynamics

There are some clear and consistent species patterns from the macroinvertebrate monitoring in the Coorong between 2004 to 2020. Across the Murray Estuary and North Lagoon regions, the presence of macroinvertebrate species has consisted of >40% Molluscs and >35% Annelid worms. In comparison, 50–70% of the species found in the South Lagoon have been insect larvae (Dittmann et al. 2018). Particularly common taxa were identified in the early stages of monitoring programs and are now used annually as key estuarine-lagoonal species and indicators of environmental change (e.g. Amphipoda, *Simplisetia aequisetis*, *Capitella capitata*, Chironomidae larvae, *Arthritica semen*, Hydrobiidae).

Species richness and abundance

Since 2004, macroinvertebrate species richness has fluctuated throughout all three regions of the Coorong (Figure 17, Table 13). The Murray Estuary and North Lagoon had low (5-11) numbers of species present during the Millennium Drought, and species richness and species density increased after the water release in 2010 (Figure 17). Since return to regular flows through the barrages post 2010, higher species numbers are regularly recorded in the Murray Mouth and North Lagoon (up to 17 and 18 species, respectively). In the South Lagoon, macroinvertebrate species richness is low across most years and usually <4 species are present (except in 2005 and 2013) (Figure 17). In recent years (2018-2019) the occurrence of macroinvertebrate species throughout the Coorong has extended across more sites in the Murray Estuary and North Lagoon, and key species are now more constant and becoming less rare (Dittmann et al. 2020) (Figure 18).

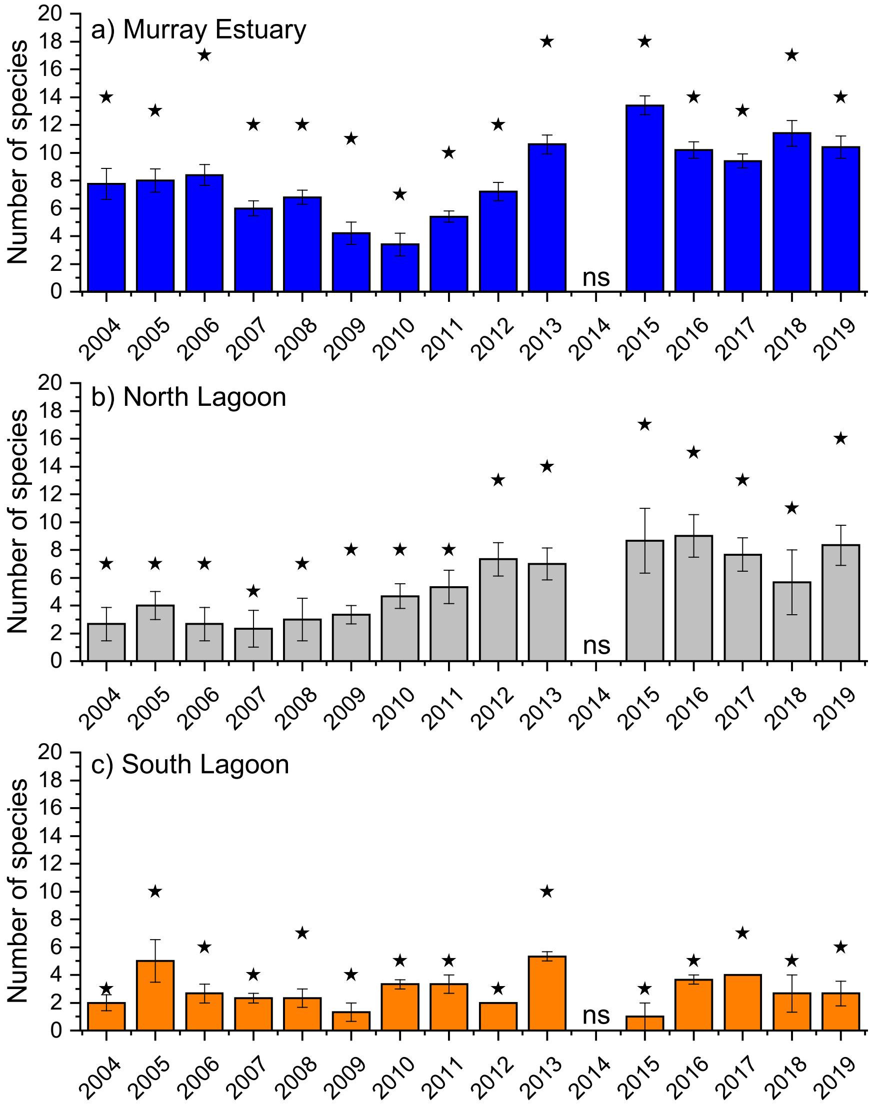


Figure 17. Number of macroinvertebrate species (stars) and species density (average ± standard error) by region in the Murray Estuary, North and South Lagoon of the Coorong in all years of The Living Murray monitoring, based on surveys in spring/early summer No survey (ns) was carried out in 2014. Data source: Dittmann et al. 2020.

Table 13. Test results from permutational ANOVA (PERMANOVA) on differences of macroinvertebrate species density, abundances (all species combined), biomass and assemblages for years of 2004–2019 and across the regions, based on annual monitoring for The Living Murray. Significant *P* values are in bold.

		SPECIES DENSITY	TOTAL ABUNDANCE	BIOMASS	ASSEMBLAGE
MAIN TEST	df	*P(PERM)*	*P(PERM)*	*P(PERM)*	*P(PERM)*
Year	14	**0.0001**	**0.0001**	**0.0001**	**0.0001**
Region	2	**0.0001**	**0.0001**	**0.0001**	**0.0001**
Year x Region	28	**0.0001**	**0.0001**	**0.0001**	**0.0001**
Residual	118	118	1584	1584	1584

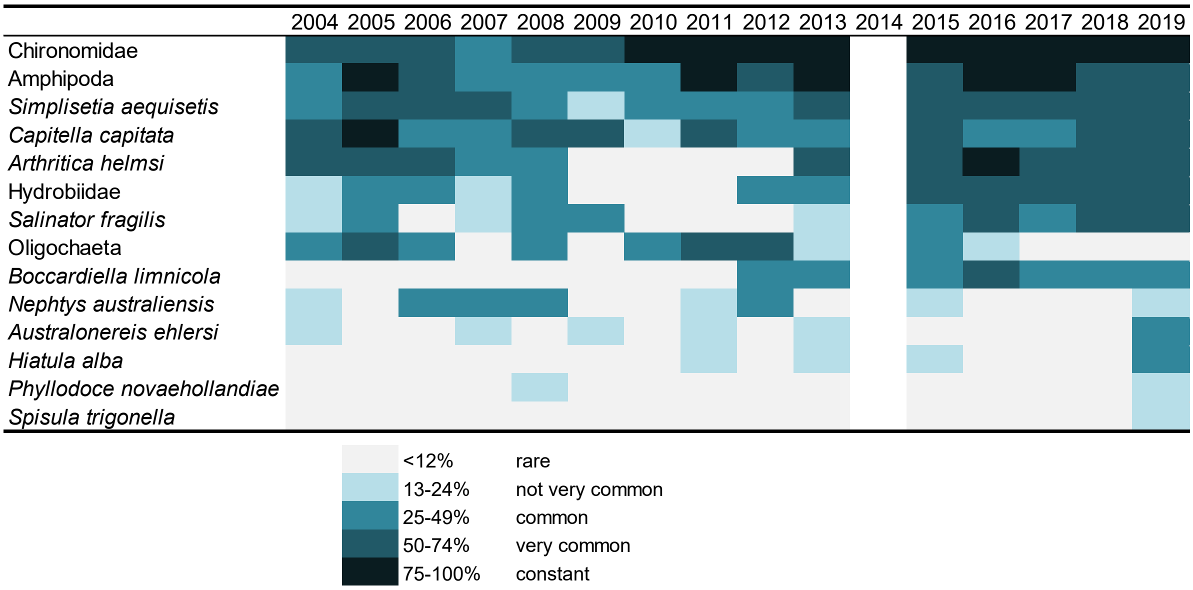


Figure 18. Constancy Index showing the occurrence of some key macroinvertebrate species across the monitoring sites in the Murray Estuary and Coorong lagoons over The Living Murray monitoring years since 2004. The darker the colour, the more widespread a species is recorded. The Constancy Index reflects presence only, not the abundance of species across sites. No survey occurred in 2014. Source: Dittmann et al. 2020.

Individual densities of macroinvertebrates are several orders of magnitude higher in the Murray Estuary and North Lagoon than in the South Lagoon, and varied significantly over the years and regions (Figure 19, Table 13). Only during the Millennium Drought were abundances as low in the Murray Estuary and North Lagoon as in the South Lagoon. In recent annual surveys, total macroinvertebrate abundances in the Murray Estuary and North Lagoon were similar across years, and higher since regular flow over the barrages commenced in 2010/2011. In the Murray Estuary, high abundances were also recorded following a smaller barrage release in 2005, before the Millennium Drought started to impact (Figure 19). In the North Lagoon, macroinvertebrate abundances have steadily increased since flows resumed (Figure 19). The total macroinvertebrate abundances in the South Lagoon have been consistently low over the years, except for a peak abundance due to chironomid larvae at the time of the flood event in late 2010 (Figure 19).

These long-term patterns of macroinvertebrate abundances are based on annual monitoring under The Living Murray (DEWNR 2017, Dittmann et al. 2020), but abundances can also vary within a year, although he only monthly data available for an entire year are from three sites in the Murray Estuary from a study carried out during the Millennium Drought (Keuning 2011). The Murray Futures program also allowed a higher spatial and temporal sampling frequency, yet this occurred in an adaptive approach which caused changes in the sampling design for almost every survey with regards to sampling sites and frequencies over the study period (Dittmann et al. 2016). While some finer scale resolution of spatial and temporal data were collected around periods of flow over the barrages (Figure 20) and some immediate effects of flows appear, any short- term variation in abundance is to be interpreted with caution due to the patchiness of data.

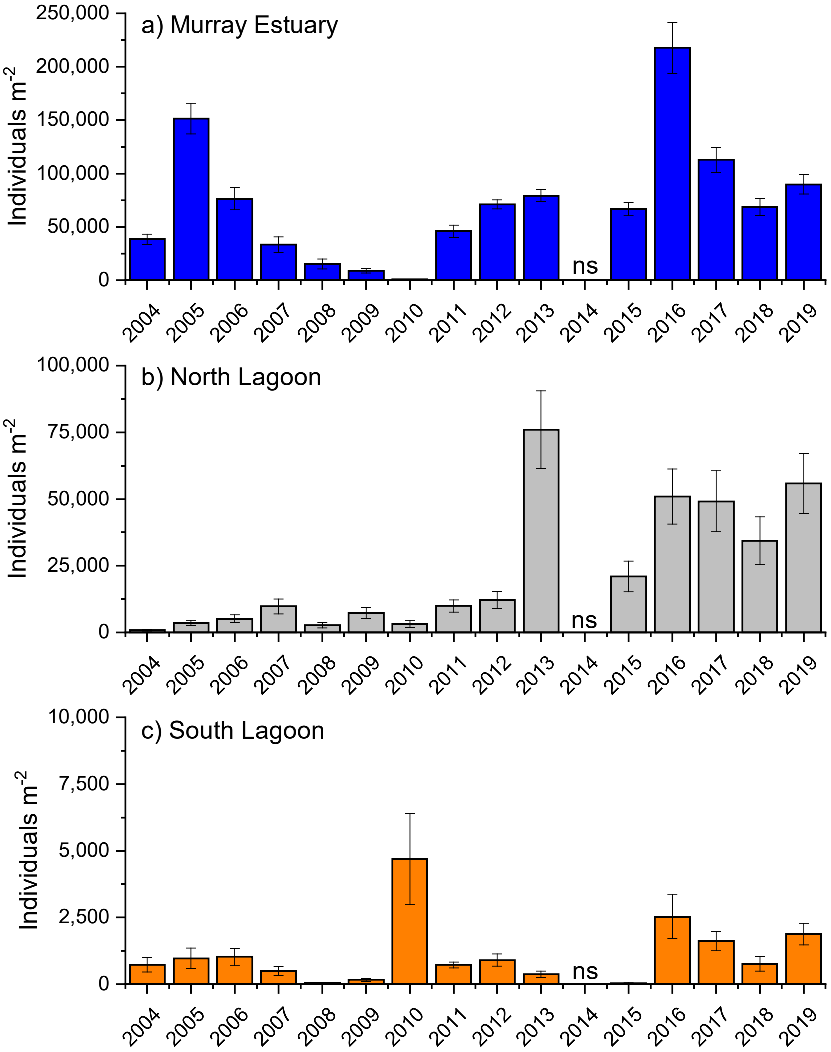


Figure 19. Individual densities (mean ± standard error) for total macroinvertebrates (all species) for a) the Murray Estuary (4-5 sites); b) the North Lagoon (2-3 sites); and c) the South Lagoon (3 sites). No sampling occurred in 2014 (ns). Note the different y-axes scales. Data source: annual monitoring for The Living Murray macroinvertebrate condition monitoring, Dittmann et al. 2020.

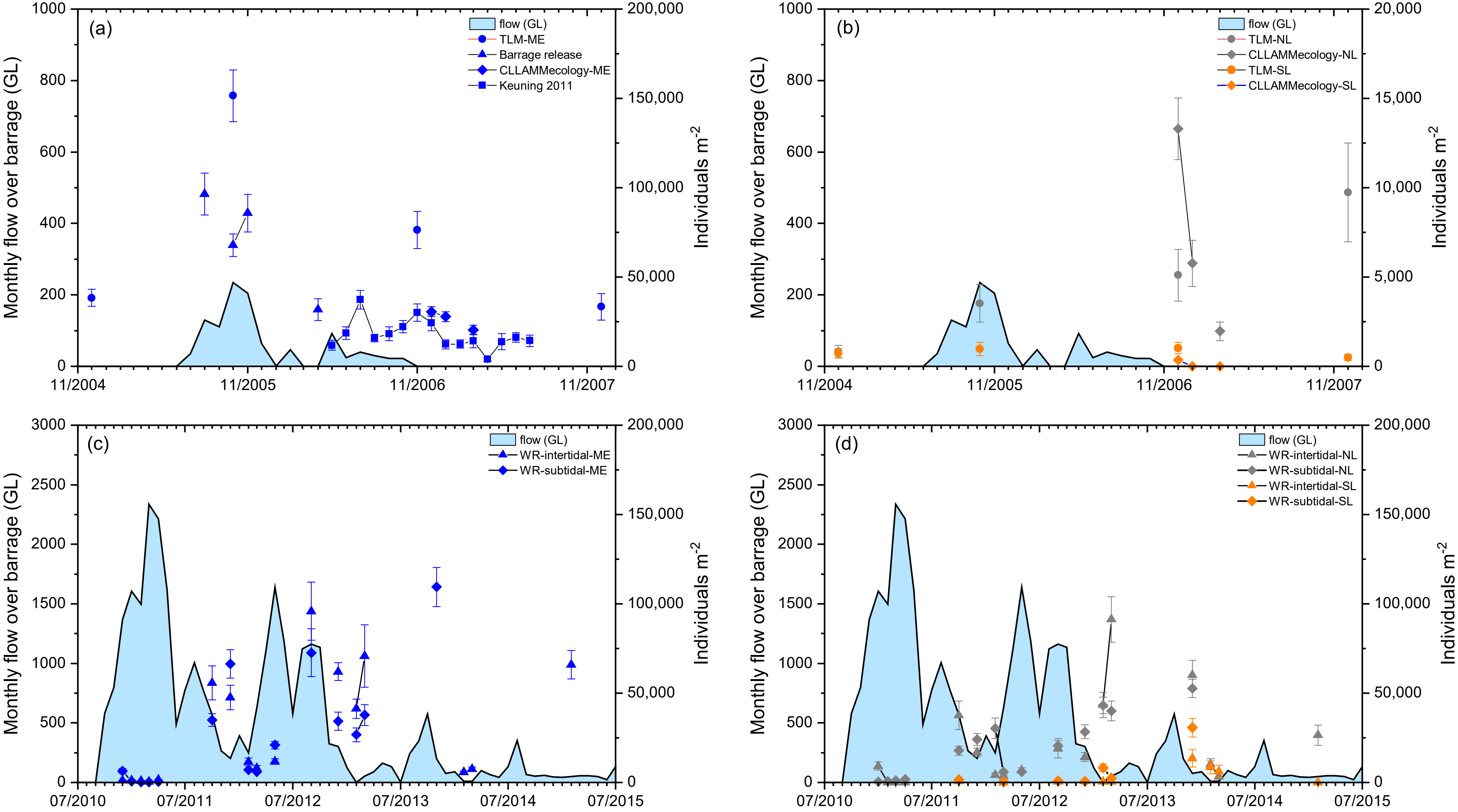


Figure 20. Short-term changes in macroinvertebrate abundances and flow. (a) and (b) show the small barrage release in late 2005, and (c) and (d) the period of commencement of flow since late 2010. (a) and (c) show the Murray Estuary, and (b) and (d) the North and South Lagoon. Note the differences in y-axes between flow periods, as well as for abundances (b). Data sources: condition monitoring for The Living Murray, Rolston and Dittmann 2009, Keuning 2011, Dittmann et al. 2006, 2016. The sampling effort and design varied between and within these studies.

Change in macroinvertebrate abundances were identified through the years for key taxa in the Coorong. For amphipods, the polychaete *Simplisetia aequisetis*, and the micro-bivalve *Arthritica semen*, abundances have recovered from the Millennium Drought since flows returned in late 2010 (Figure 21). In recent years, abundances of these species has significantly increased in the Murray Estuary and also in the North Lagoon (Figure 21). Small hydrobiid snails are now also more abundant than over the previous decade. In comparison, abundances of the small, opportunistic polychaete *Capitella capitata* significantly decreased in the Murray Estuary since flows resumed, but have increased in the North Lagoon (Figure 21). This species has also been found occasionally in the South Lagoon. Chironomid larvae are the only invertebrates found consistently in all three regions, and have fluctuated in abundance following flows (Figure 21).

At a longer timeframe, comparisons of individual densities are possible with quantitative data by Snoeijs and van der Steer (1981) for Noonameena, which provide a valuable benchmark (Figure 22). For two polychaete species (*C. capitata* and *S. aequisetis*), the abundances recorded in 1981 were only reached again in the last few years since flows resumed. Chironomid larval abundance was variable between the two survey months in 1981, and continues to be variable, which can be in relation to flows and the life cycle of these midges. Three mollusc species were abundant in 1981 but have rarely been found at Noonameena in annual monitoring since 2004. These small bivalves and snails can be food items for waterbirds and fish, and were once available at Noonameena, but missing as a prey choice in the last 15 years.

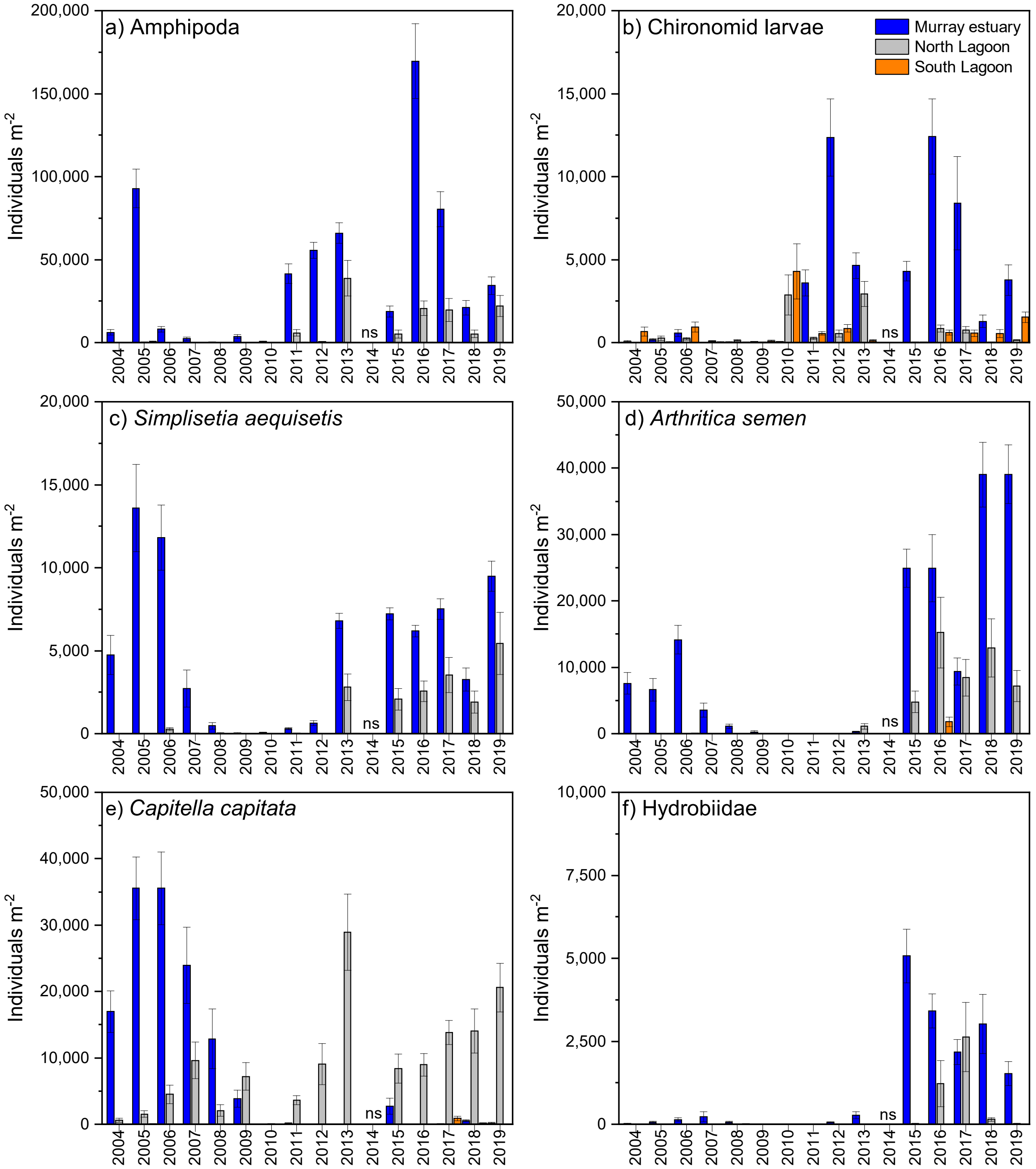


Figure 21. Individual densities (mean ± standard error) of several key macroinvertebrate species in the three regions of the Coorong. Data source: The Living Murray program macroinvertebrate monitoring, Dittmann et al. 2020. No sampling (ns) for the TLM monitoring occurred in 2014.

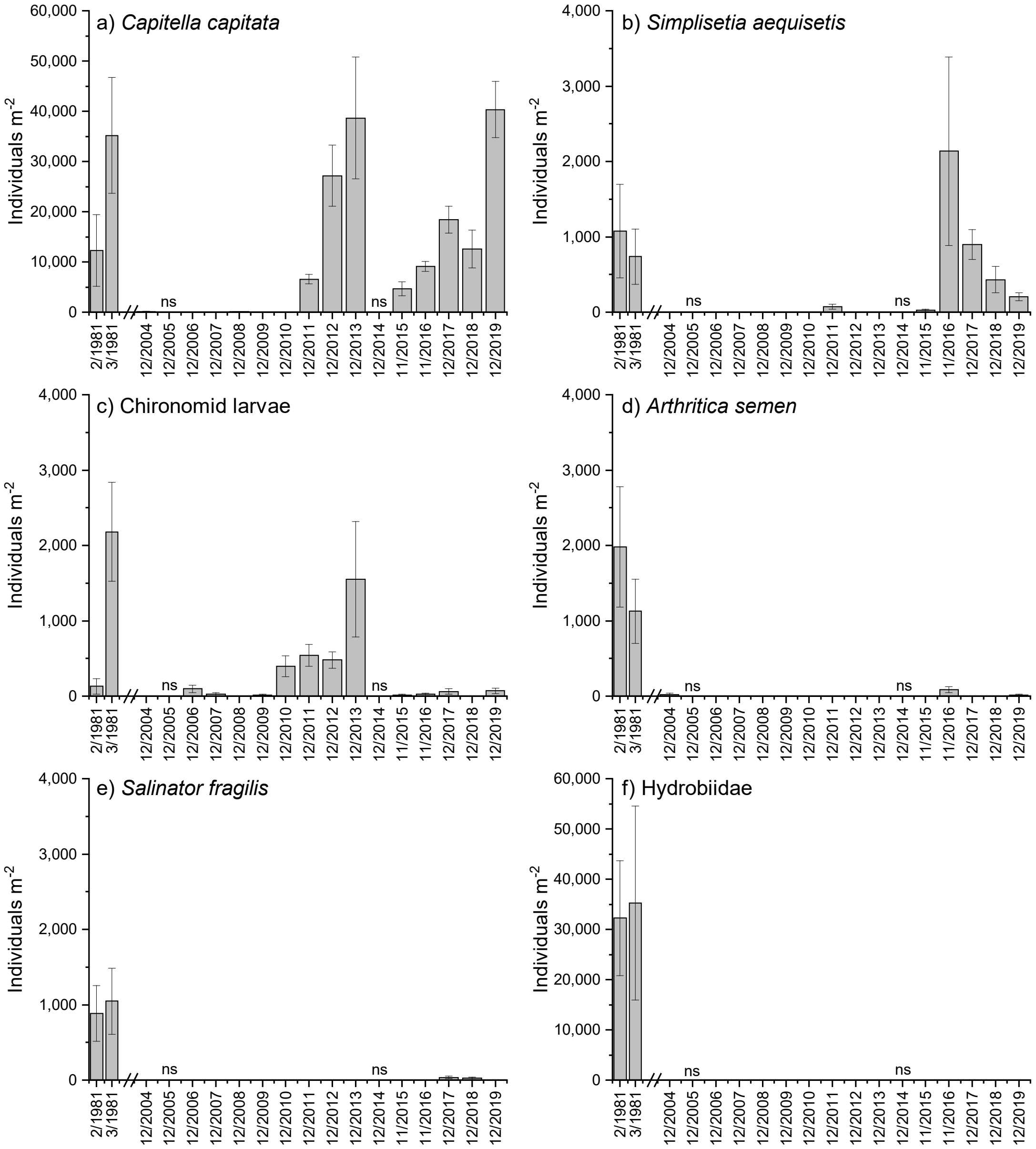


Figure 22. Individual densities (mean ± standard error) of several key macroinvertebrate species at Noonameena in the North Lagoon, for which quantitative data are available for 1981. Data sources: Snoeijs and van der Ster (1981), and The Living Murray program (Dittmann et al. 2020). No sampling (ns) occurred at Noonameena for the TLM monitoring in 2005 and 2014.

Total macroinvertebrate biomass increased in recent years in the Murray Estuary and North Lagoon regions, coinciding with continuous flows into the Coorong. However, macroinvertebrate biomass is consistently low in the South Lagoon, except for relatively higher biomass found for this region in 2017 and 2018, possible as some capitellid polychaetes were found at one site (Jack Point) (Figure 23).

Macroinvertebrate assemblage structure

Macroinvertebrate assemblages between the three regions are structurally very different and are kept separate in assessments of changes to assemblages through the years. The macroinvertebrate assemblage in the Murray Estuary has significantly changed (*P*<0.05, SIMPROF tests) in structure between drought (2004 to 2009), flood (2010), water release post-flood (2011-2012) and regular flow (2013 to 2019) conditions (Figure 24a). Similar changes emerged for the macroinvertebrate assemblage in the North Lagoon, which differed significantly for the period during drought and flood, and the regular flow period since 2013 (Figure 24b). During the drought years, some opportunistic species were persistent and faired quite well, which included insect larvae, the polychaete *C. capitata* and amphipods. After the floods in 2010, the inflow of freshwater through the barrages brought freshwater oligochaete worms and amphipods, which were particularly abundant in the Murray Estuary and North Lagoon during that time. Since the change to regular flows through the barrages into the Coorong, many species have improved in their spatial distribution and abundance, which have included large polychaete worms (*Simplisetia aequesetis*, *Boccardiella limnicola*), micro-gastropods (Hydrobiidae) and large grazing snails (*Salinator fragilis*) (Dittmann et al. 2020).

In the South Lagoon, macroinvertebrate assemblage structure showed no clear pattern of variation across the years (Figure 24c). The main contributors to the macroinvertebrate assemblages in most years have been insect larvae, but during recent years other species have started to appear in low abundances (e.g. ostracods, the isopod species *Haloniscus searlei* and the polychaete *C. capitata*).

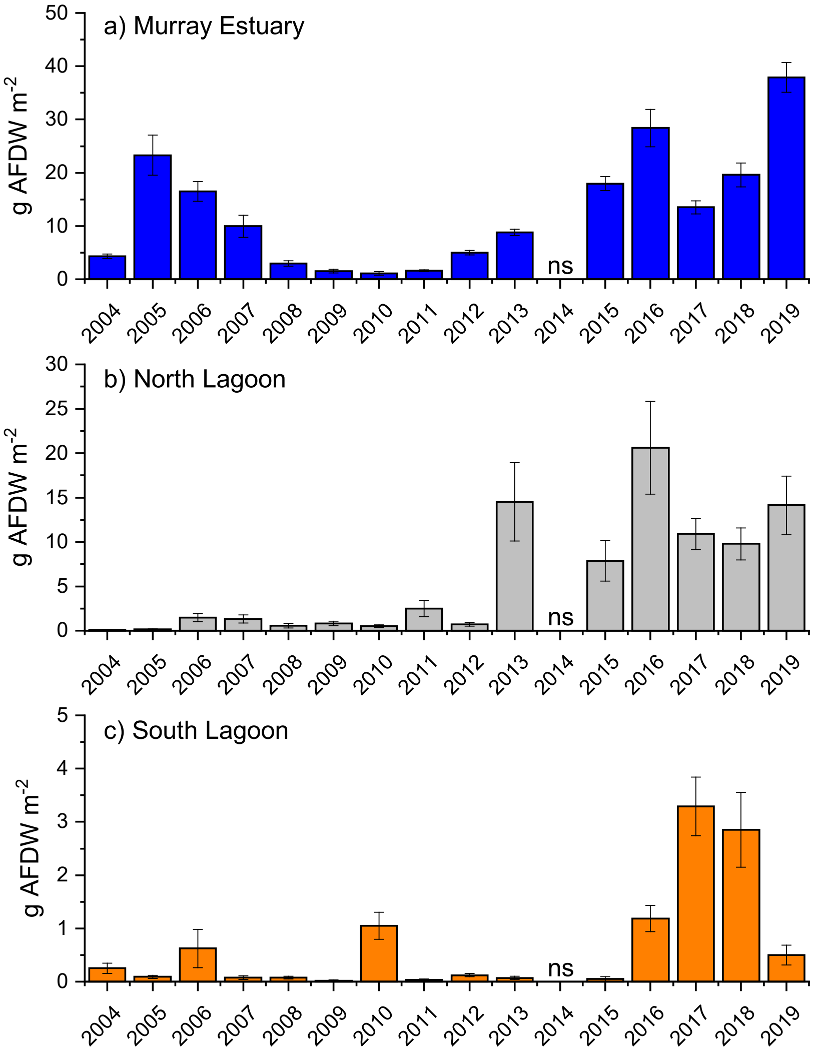
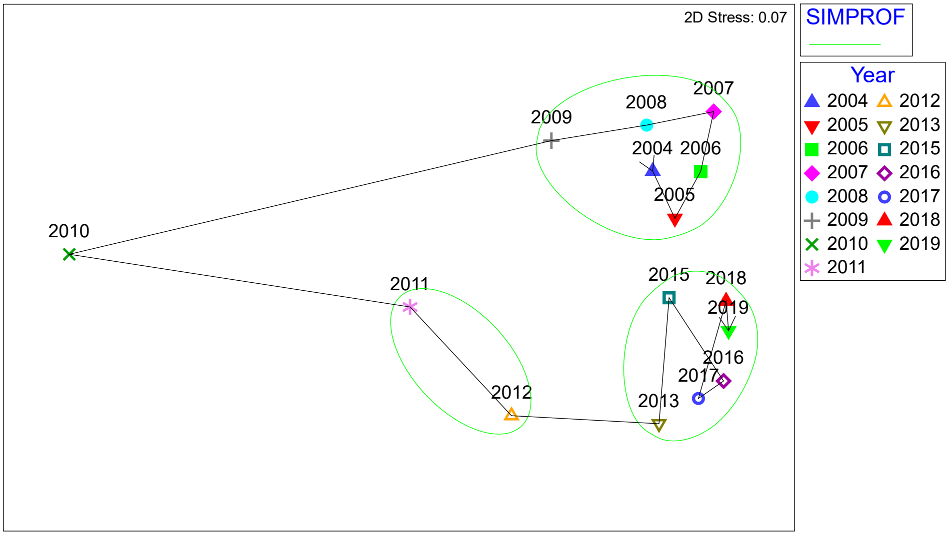
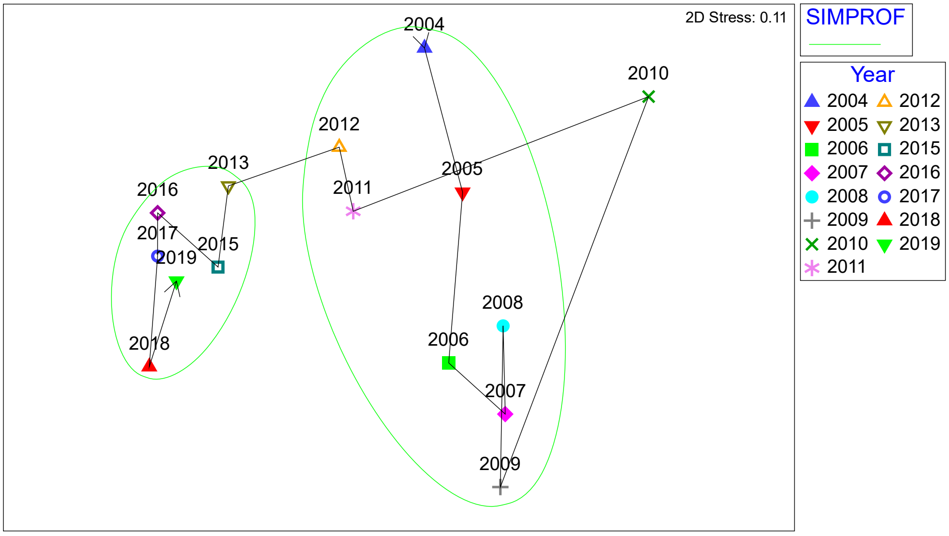


Figure 23. Biomass (ash-free dry weight AFDW) of macroinvertebrates (mean ± standard error) for a) the Murray Estuary (4–5 sites), b) the North Lagoon (2–3 sites), and c) the South Lagoon (3 sites). Note the different y-axes scales. Data source: The Living Murray macroinvertebrate monitoring, Dittmann et al. 2020. No sampling occurred in 2014 (ns).

(a) Murray Estuary



(b) North Lagoon



(c) South Lagoon

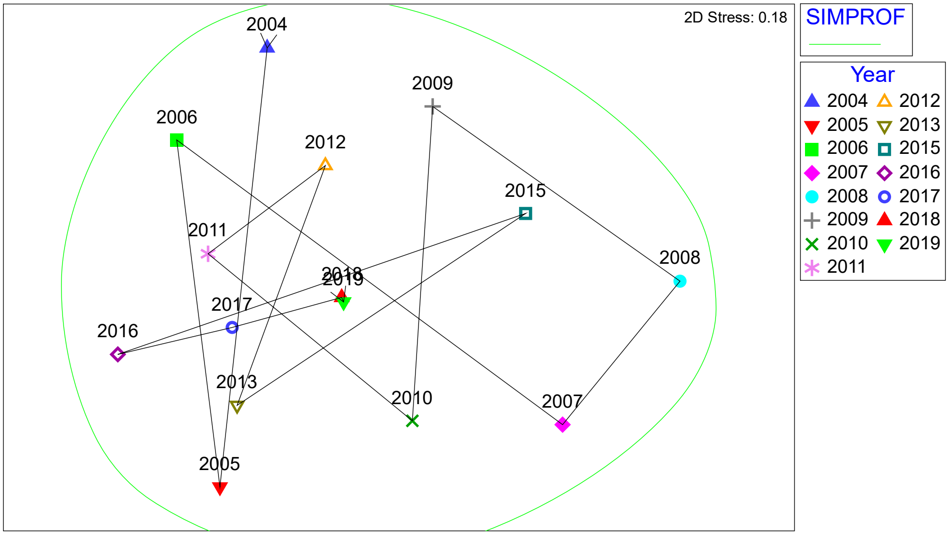


Figure 24. Non-metric multidimensional scaling plots for macroinvertebrate communities in a) the Murray Estuary, b) the North Lagoon, and C) South Lagoon. Data are based on averages per year and region. The green circles show significantly different groupings based on SIMPROF tests (*P* < 0.05). The direction of the connecting black lines shows a trajectory over consecutive monitoring years. No surveys occurred in 2014. Data source: The Living Murray monitoring macroinvertebrate monitoring, Dittmann et al. 2020.

3.3.3 Linking macroinvertebrate assemblage dynamics with key environmental drivers

Temporal and spatial changes in macroinvertebrate species richness, abundances, biomass, and assemblage structure have been strongly influenced by flow through the barrages, particularly in the Murray Estuary and North Lagoon. The fluctuations in flow have resulted in various environmental condition changes including salinity, dissolved oxygen and sediment conditions. The environmental parameters that contribute most to the distribution of macroinvertebrate assemblages between the Murray Estuary, North and South Lagoon are salinity and sediment conditions (e.g. grain size, particle size sorting and organic matter), while dissolved oxygen saturation has played less of a role (Figure 25).

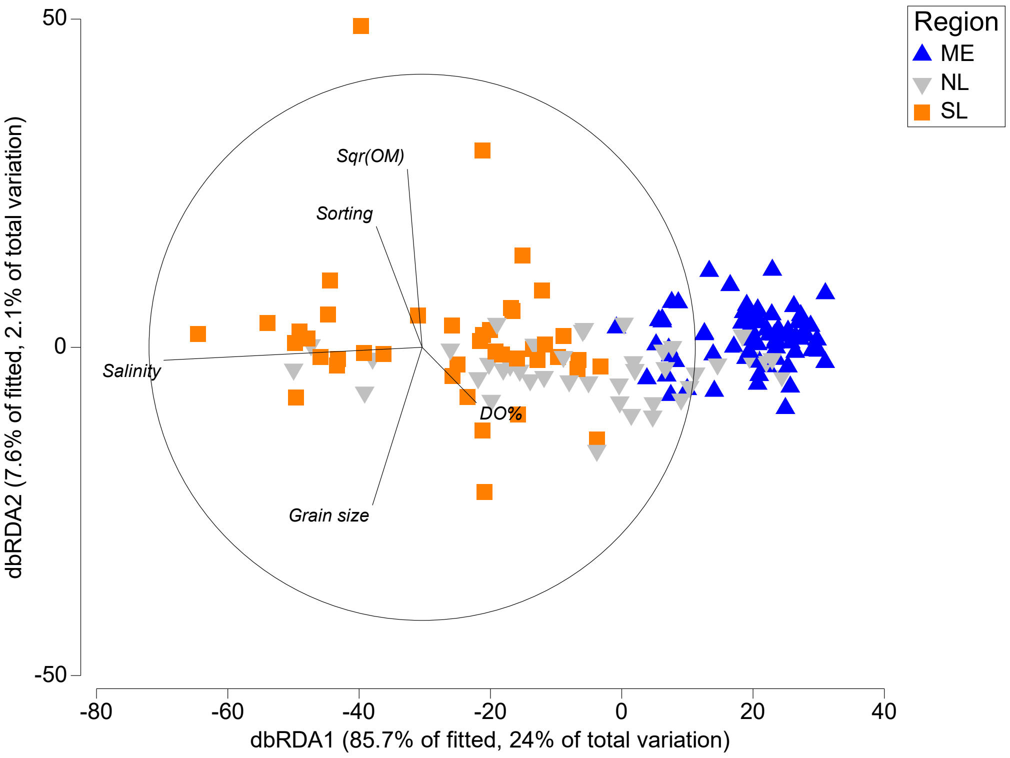


Figure 25. Plot of distance-based redundancy analysis (dbRDA) for monitoring years from 2005 to 2019. Environmental variables recorded in each monitoring are included here, except for chlorophyll-*a* which was only measured since 2007. The regional differentiation shown are Murray Estuary (ME), North Lagoon (NL) and South Lagoon (SL) . The plots show a constrained ordination of macroinvertebrate communities subject to the environmental predictor variables displayed in the vector overlays. Data source: The Living Murray Program (Dittmann et al. 2020).

The defining separation in macroinvertebrate assemblage structure between the Murray Estuary, North and South Lagoons across the years has been related to salinity with 67 psu identified as a possible threshold for many taxa (Figure 26). A similar threshold was also identified through modelling by Lester and Fairweather (2009). In all regions of the Coorong, the environmental variable contributing most to significant macroinvertebrate assemblage changes has been the variation in salinity between drought and post-drought years, which in particular resulted in a separation of the scarce macroinvertebrate assemblage found in ultrahaline conditions (>96 psu) in the South Lagoon during the Millennium Drought (Figure 26). Some of the flood years had other environmental parameters influencing macroinvertebrate assemblage structure in the North Lagoon (e.g. dissolved oxygen, organic matter and sediment grain size), but they were particularly unique years with large environmental flows through the barrages (Figure 26).

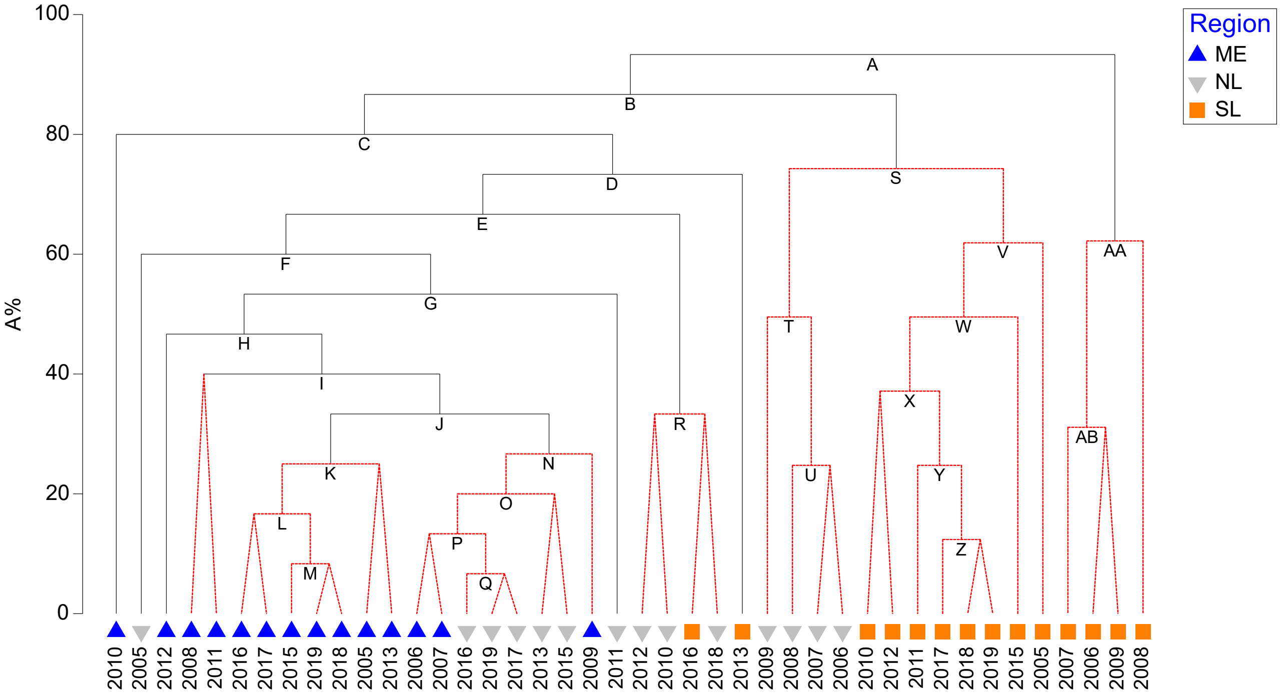


Figure 26. LINKTREE of macroinvertebrate community for 2005–2019 in the Coorong. Analysis based on average values per region by year (ME = Murray Estuary, NL = North Lagoon, and SL = South Lagoon). Black lines separate significantly different groups based on SIMPROF tests. The splits are explained by environmental variables, with significant splits at A: Salinity <96.1(>122) P=0.001; B: Salinity <67.4(>69.5) P=0.001; C: Dissolved oxygen Saturation (DO%) <71.2(>80.8) P=0.001; D: Organic matter (OM) <2.77 (>3.28) or DO% <141 (>146), P=0.001; E: Grain size µm <235 (>274), P=0.001; F: <0.77 (>0.94), P=0.001; G: DO%>84.7(<80.8) or Grain size <228(>235) or Salinity <65.7(>67.4) P=0.006; H: Grain size <105(>150) P=0.006; I: OM <0.99(>1.04) P=0.003; J: Salinity <21.7(>23.2) P=0.004. Red lines indicate groups that are not significantly different. The A% scale splits groups equally spaced. Data source: The Living Murray Program macroinvertebrate monitoring, Dittmann et al. 2020.

Salinity is a large contributor to temporal changes in macroinvertebrate assemblage , particularly in the North Lagoon. With ongoing monitoring from 2004 to 2019, we have been able to establish maximum average abundances of key macroinvertebrate taxa with favourable salinity conditions and tolerance ranges. Most of those taxa fit into favouring mesohaline or polyhaline conditions and only one species (the polychaete species *C. capitata*) prefers the euhaline salinity range (Figure 27). None of the key taxa favour hyperhaline conditions, but some species do have ranges within those salinity bounds of >40 psu, and can be found in higher salinities at low abundances (Figure 27).

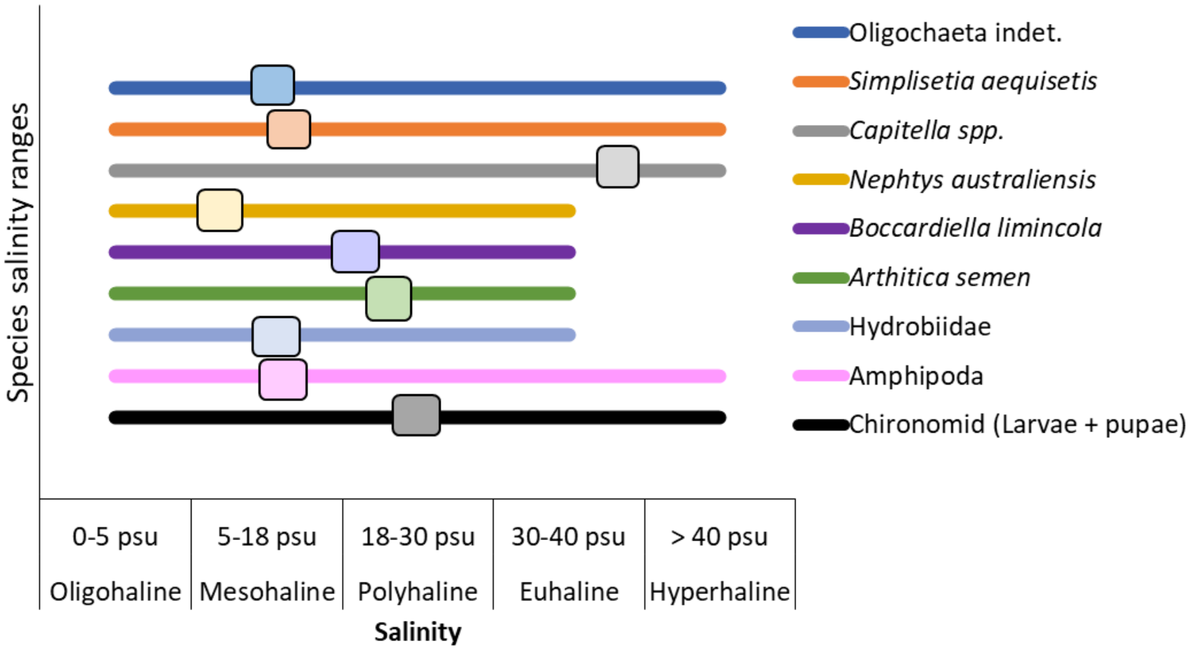


Figure 27. Key macroinvertebrate taxa found in the Coorong with salinity ranges and boxes representing average salinites with greatest abundances of individuals for those representative taxa. Data includes samples from intertidal and subtidal sites from the Murray Estuary to South Lagoon regions during 2010 to 2015. Data source: Dittmann et al. (2016).

3.3.4 Conclusion

Long-term monitoring in the Coorong has provided the opportunity to identify long-term trends in benthic macroinvertebrate species richness, abundance, biomass, and assemblage structure. Declines in macroinvertebrate abundances occurred during the Millennium Drought, particularly in the Murray Estuary and North Lagoon, but increased again after floods and post-drought water release through the barrages. Macroinvertebrate assemblages in the Murray Estuary and North Lagoon have shifted in their structure through the drought, flood and water release phases, and have settled into a similar structural pattern for the last six years (i.e. since 2013). In comparison, the South Lagoon has not changed as much in macroinvertebrate structure post-drought and remains dominated by insect larvae. The dynamics of macroinvertebrate assemblage structure has strongly followed patterns in flow through the barrages which was particularly noticeable in fine-temporal scale surveys during the water release period of 2010 to early 2014. Yet, these investigations were largely confined to the Murray Estuary and North Lagoon of the Coorong, and knowledge gaps persist on seasonal variability and macroinvertebrates associated to specific habitats, or groundwater seeps. Salinity due to barrage flows, or no flows, is the main environmental contributor to patterns in macroinvertebrate assemblages. Most of the macroinvertebrate surveys have occurred across intertidal mudflats in the Coorong, with some subtidal benthic sampling occurring post-flood (e.g. 2010 to 2013). However, further investigation into subtidal benthic macroinvertebrate assemblage structure and some of the more mobile macroinvertebrates (e.g. crabs) would be beneficial for a more complete understanding of macroinvertebrates available to predatory fish in deeper sections of the Coorong.

3.4 Fish

3.4.1 Review of the Coorong fish studies

As the dynamic interface between the lower Murray River and Lower Lakes, and the Southern Ocean, the Coorong provides important estuarine and hypersaline habitats to support a diverse assemblage of fish species, unique in the MDB (Bice et al. 2018). These include species that are of significant commercial and recreational values for fisheries (Ferguson et al. 2018), important to the Ngarrindjeri people (Phillips and Muller 2006), and/or critical in supporting biodiversity and ecological function including the Coorong food webs (Ye et al. 2016).

Most fish-related research and monitoring in the Coorong prior to 2005, had focused on commercial fishery species (e.g. Hall 1986, Olsen and Evans 1991), with a few ecological studies on small-bodied fish or fish assemblages (Geddes and Butler 1984, Geddes 1987, Molshel et al. 1994). Since 2005, a range of research and monitoring programs have been undertaken on fish assemblages in this region. These include CLLAMMecology fish research (2006–2009) (Noell et al. 2009, Bucater et al. 2013, Ye et al. 2013), Murray Futures CLLMM Recovery Program fish intervention monitoring (2010–2014) (Ye et al. 2015a, 2016), TLM fish condition monitoring (2008–2020) (Ye et al. 2018, 2020), TLM barrage fishway monitoring (2006–2020) (Zampatti et al. 2010, Bice et al. 2016b, Bice et al. 2020), and TLM fish intervention monitoring (various years between 2006–2020) (e.g. Bice et al. 2017, Ye et al. 2015b, 2019a, 2019b). A number of PhD student projects (e.g. Ferguson et al. 2008, 2013, 2014, Earl 2014, Earl et al. 2014, 2017, Barnes et al. 2015), other ecological research (e.g. Doubleday et al. 2015, Gillanders et al. 2015, Izzo et al. 2016) and fisheries assessments (e.g. Earl and Ferguson 2013, Earl and Ye 2016, Earl et al. 2016, Earl 2020) have also occurred in the Coorong, along with fish diet studies (see Section 2.1). These studies have improved knowledge of fish ecology and population dynamics in the Coorong. Importantly, several monitoring programs provide long-term data incorporating a period of hydrological extremes and varying conditions (drought – high flow – moderate flow – low flow), which allow us to explore the trend and develop the understanding of how flow regime and river discharge influences fish species of different life-histories and the assemblages in the Coorong.

Based on similarities in biology and ecology, Bice et al. (2018) allocated 93 fish species from the Coorong under four broad life-history categories, defined primarily by the environment in which spawning occurs, namely: 1) freshwater; 2) diadromous; 3) estuarine; and 4) marine. Each category comprises two or more ‘estuarine use functional guilds’ (Figure 28) defined by specific locations of spawning, feeding and/or refuge, and the nature of migratory movements between marine, estuarine and freshwater ecosystems. This followed the approach by Elliott et al. (2007) and refinement by Potter et al. (2015). The classification helps to investigate similar species (i.e. guild) response and assists management by simplifying complex assemblages.

Freshwater inflows (particularly the Murray River discharge) impact fishes in the Coorong by influencing the following critical factors: (1) connectivity within, and between, marine, estuarine and lake environments; (2) salinity; and (3) productivity by transporting carbon, nutrients and microbiota from upstream. Recent research and monitoring have improved our understanding of the effects of these key factors on fish ecology and populations in the Coorong (Ye et al. 2016).

Specifically, for food web investigations (T&I Project *Component 3 Food web*) to support the South Lagoon ecological restoration, we explored the long-term fish datasets from relevant research and monitoring programs, including CLLAMMecology (Noell et al. 2009), CLLMM Recovery fish intervention monitoring (Ye et al. 2016) and TLM Coorong fish condition monitoring (Ye et al. 2020). These programs used a consistent, standardised and quantifiable sampling method (i.e. standard seine net with similar effort) and covered multiple sites in the Murray Estuary, North Lagoon and South Lagoon. Further analyses were conducted on this consolidated dataset from 2007–2020 (sampling annually in March) to explore spatio-temporal patterns of fish species richness/diversity, abundance, distribution and assemblage structure, and key environmental drivers and relationships. The results are presented here and discussed in the context of contemporary understanding of fish ecology based on recent research in this region.

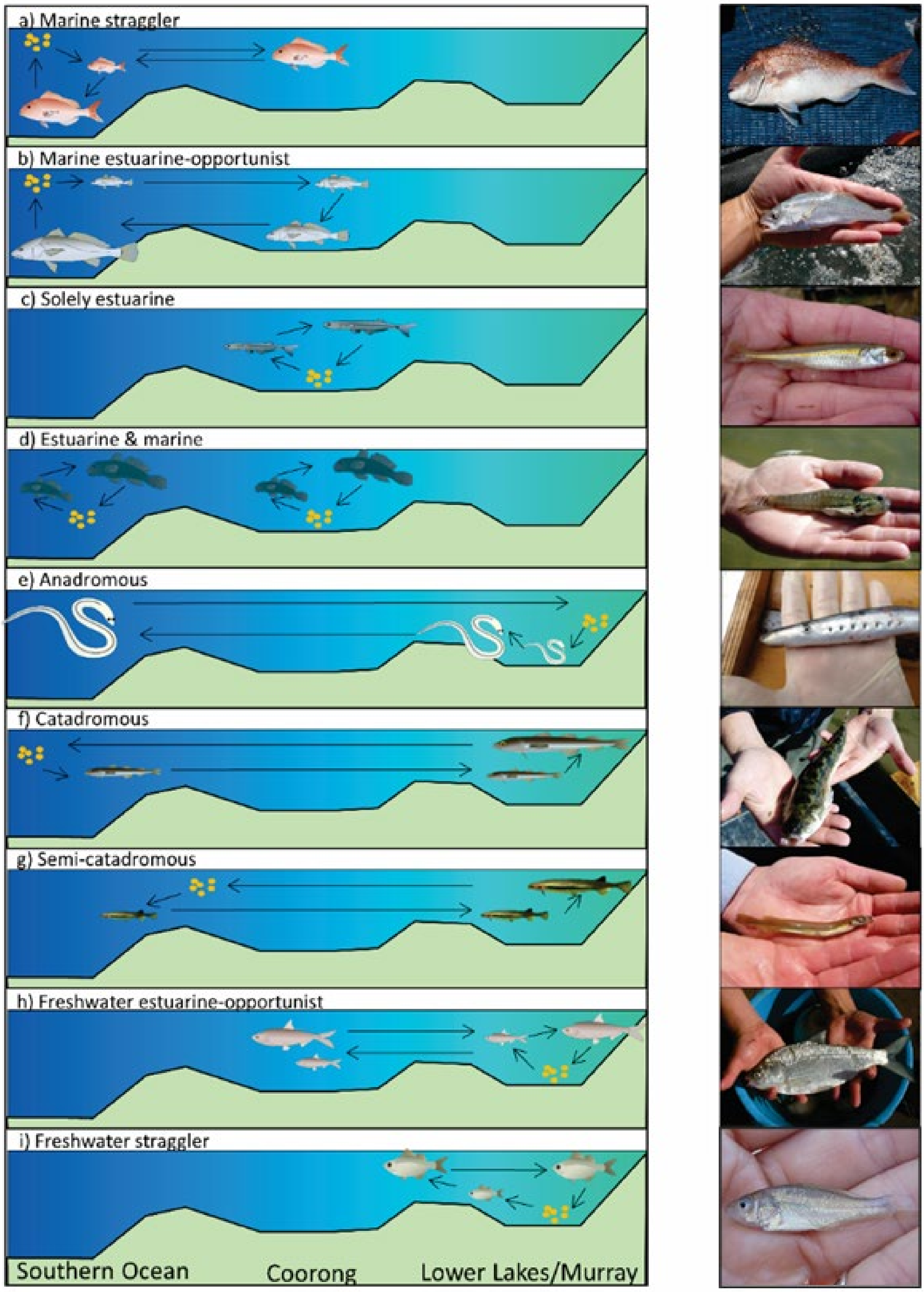


Figure 28. Conceptual diagrams of the life-histories of different estuarine use functional guilds and representative fish species from the Coorong. Shown guilds and species are (a) Marine straggler — snapper, (b) marine estuarine-opportunist — mulloway, (c) solely estuarine — smallmouth hardyhead, (d) estuarine and marine — bridled goby, (e) anadromous — pouched lamprey, (f) catadromous — congolli, (g) semi-catadromous — common galaxias, (h) freshwater estuarine- opportunist — bony herring and (i) freshwater straggler — golden perch. Source: Bice et al. (2018).

3.4.2 Spatio-temporal patterns in fish species richness, abundance and assemblage structure

Between 2007 and 2020, a total of 36 species were present during March sampling in the Coorong, including twelve small-bodied and 24 medium- to large-bodied species (including species grouped in Tetraodontidae). Overall, small-bodied species were clearly the most abundant, representing 97% of total fish caught (by number). This was mainly due to the large contribution of sandy sprat (75%) collected in the Murray Estuary, sandy sprat and smallmouth hardyhead (96% combined) in the North Lagoon, and smallmouth hardyhead in the South Lagoon (98%). See detailed table in Appendix A.

For the medium- to large-bodied species, the overall numbers caught in the Murray Estuary were about five times greater than in the North Lagoon, and 60 times greater than in the South Lagoon. The commonly present species included yelloweye mullet and bony herring in the Murray Estuary, and congolli and yelloweye mullet in the North and South lagoons.

Species richness and abundance

Fish species richness (the number of species) and total abundance varied significantly across regions and years (Table 14; Figure 29). The Murray Estuary presented the highest species richness, followed by the North and South lagoons (Figure 29). The peak of species richness occurred in the Murray Estuary (mean 11 ± 0.5 SE) in 2011, following a significant flood. In all regions since 2011, species richness has been higher compared to the drought years (2007–2010). Despite this, mean species richness in the South Lagoon remained low (~3 species) post drought, associated with hypersaline conditions (42–120 psu). Only species with high salinity tolerance were regularly present in this region (e.g. smallmouth hardyhead, congolli and yelloweye mullet).

Total abundance (catch-per-unit-effort (CPUE) of combined fish number per seine net) was the highest in 2014 in the Murray Estuary (mean 6,255), however this was an isolated occurrence and was associated with high uncertainty (± 5,458 SE). Overall, mean total abundance was highest in the Murray Estuary (1,128 ± 475 SE), followed by South Lagoon (1,064 ± 98 SE) and North Lagoon (934 ± 128 SE), yet these abundances were not significantly different (Figure 29).

Table 14. Test results from permutational ANOVA (PERMANOVA) on differences of fish assemblage structure, total fish abundances (all species combined) and species richness among years from 2007–2020 and across the regions. Significant *P* values are in bold.

		SPECIES RICHNESS	TOTAL ABUNDANCE	FISH ASSEMBLAGE
MAIN TEST	df	$P_{(PERM)}$	$P_{(PERM)}$	$P_{(PERM)}$
Year	13	**0.001**	**0.001**	**0.001**
Region	2	**0.001**	**0.015**	**0.001**
Year x Region	24	**0.001**	**0.001**	**0.001**
Residual	401			

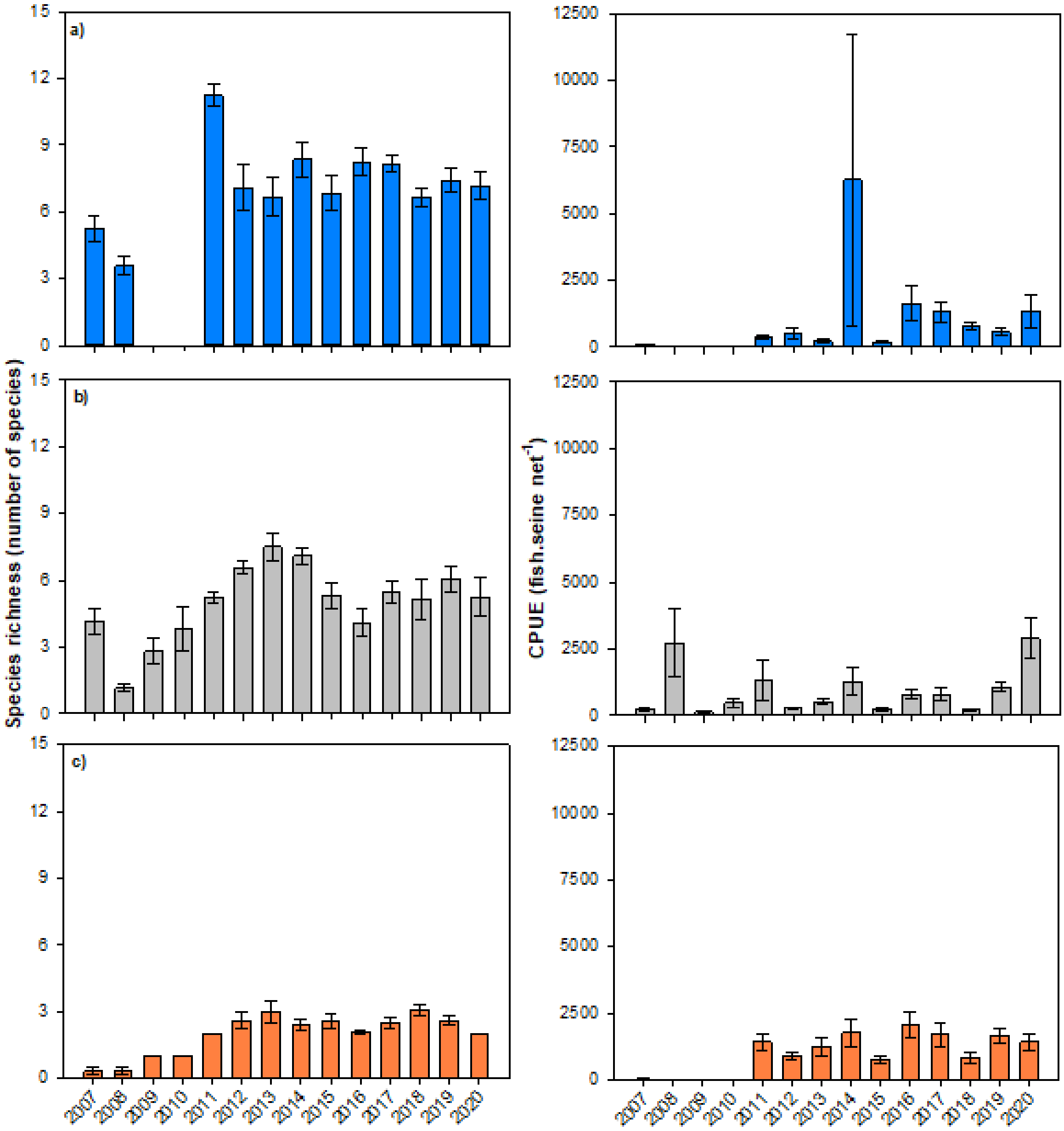


Figure 29. Mean species richness (number of fish species) (left) and mean total abundance (CPUE = catch-per-unit-effort) (right) of fish recorded at each region (a – Murray Estuary, b – North Lagoon and c – South Lagoon) from 2007 to 2020. Error bars are standard error.

Relative abundance (CPUE) of six key species, smallmouth hardyhead, sandy sprat, yelloweye mullet, congolli, Tamar and lagoon gobies varied significantly across regions and years from 2007–2020 (Table 15; Figure 30a-f). Abundances of smallmouth hardyhead were highest in the South Lagoon in most years after 2011, whereas they were highest in the North Lagoon and the species was absent in the South Lagoon during the late drought years (2008–2010) (Figure 30a). Smallmouth hardyhead were generally much more abundant in the North and South lagoons than in the Murray Estuary.

Contrastingly, abundances of sandy sprat were higher in the Murray Estuary than in the North and South lagoons in most years (Figure 30b). Notably the species was absent from the Coorong during the drought period of 2007–2010 and present in the South Lagoon during the period of 2012–2013 following flood/high inflows and a reduction in salinity to 76–79 psu in this region (Ye et al. 2015a). This range of salinity is quite high for sandy sprat, which suggests that the increase in spatial distribution may have partly related to displacement by high flows rather than active movement to preferred habitat conditions.

Abundance of yelloweye mullet varied between years and was generally more abundant in the Murray Estuary compared to other two regions (Figure 30c). This species occurred in low−moderate abundances in the North Lagoon in all years and was detected in the South Lagoon during the period of 2012–2015 and again from 2018–2019. Abundance of congolli also varied in time and space (Figure 30d) but showed a significant increase post-2011. This was likely attributed to enhanced recruitment associated with increased connectivity between the freshwater, estuarine and marine environments (Bice et al. 2018, 2020) and estuarine habitat improvement in the Coorong after restoring barrage releases post-2010 (Ye et al. 2016).

Tamar goby and lagoon goby were confined to the Murray Estuary and North Lagoon from 2007−2020, with highly variable abundances between years (Figure 30e-f). In some years, the abundances were relatively high (e.g. for Tamar goby, 2015 and 2017 in the Murray Estuary and 2015 in the North Lagoon; and for lagoon goby, 2014, 2019 and 2020 in the North Lagoon).

Examining spatio-temporal variability in abundance of key fish species, especially the most abundant prey species smallmouth hardyhead and sandy sprat, is crucial given they are an integral part of the Coorong food web. The time series data are critical for future determination of fish biomass and associated energy supply to support piscivorous fish and waterbirds in the Coorong.

Table 15. Test results from permutational ANOVA (PERMANOVA) on differences in abundances of key fish species across the regions and for years of 2007–2020. Significant *P* values are in bold.

		SMALLMOUTH HARDYHEAD	SANDY SPRAT	YELLOWEYE MULLET	CONGOLLI	TAMAR GOBY	LAGOON GOBY
MAIN TEST	df	$P_{(PERM)}$	$P_{(PERM)}$	$P_{(PERM)}$	$P_{(PERM)}$	$P_{(PERM)}$	$P_{(PERM)}$
Year	13	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**
Region	2	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**
Year x Region	24	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**
Residual	401						

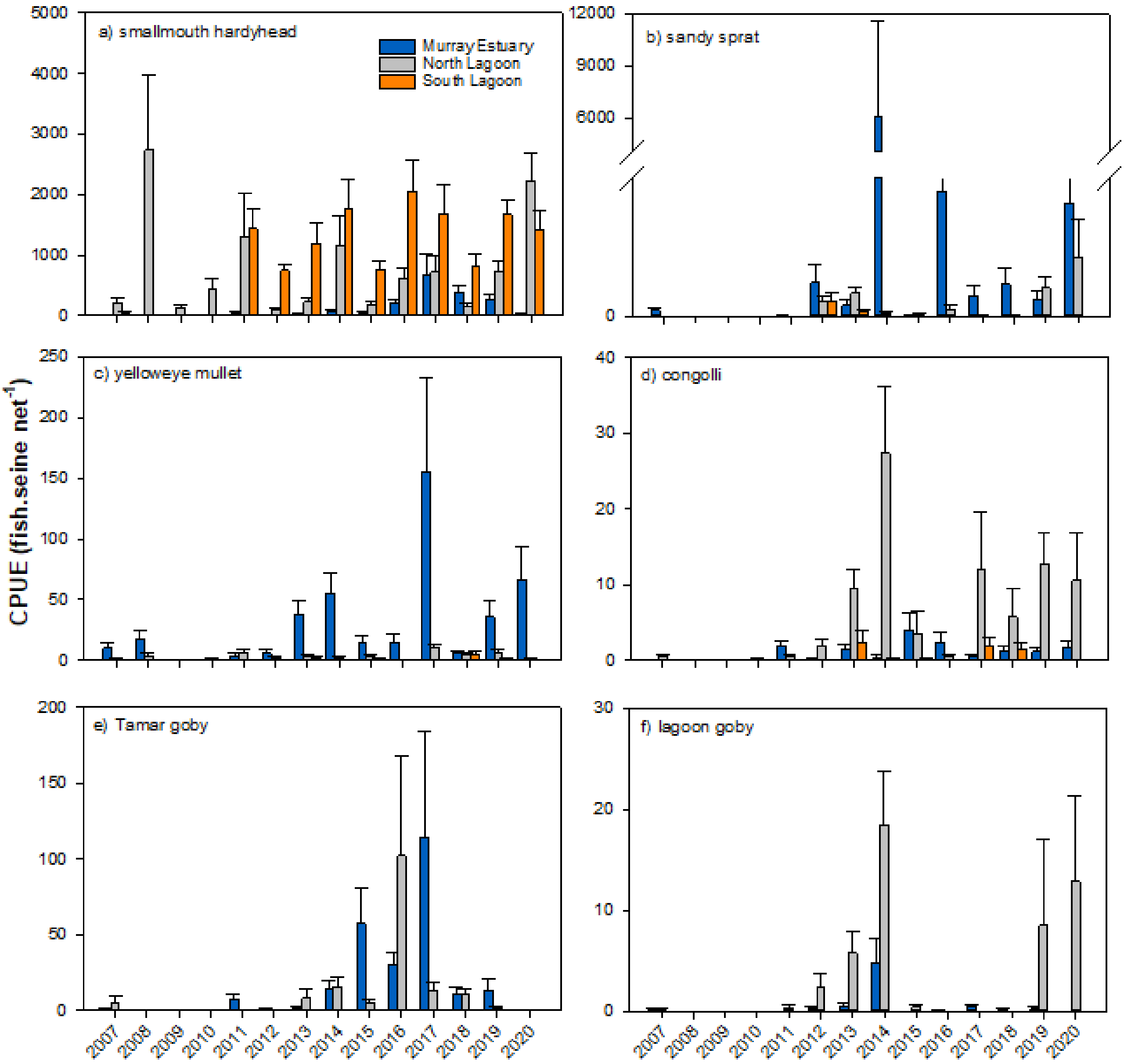


Figure 30. Relative abundance (CPUE = catch-per-unit-effort) (mean ± standard error) of key fish from 2007–2020 in the Coorong.

Fish assemblage structure

Fish assemblage structure showed significant variations across different regions of the Coorong and among years (2007–2020) (Table 14; Figure 31). Assemblages were consistently different across the three regions (Murray Estuary, North Lagoon and South Lagoon), although there were some interspersed data points (indicating annual average) between the North Lagoon and Murray Estuary, and the North Lagoon and South Lagoon. For instance, North Lagoon assemblages in 2012, 2013 and 2015, years immediately after the high or moderate flows, became more similar to those typical of the Murray Estuary, likely reflecting the effect of increased barrage flows into the Coorong and subsequent freshening the North Lagoon (Ye et al. 2015a). Correspondingly, North Lagoon assemblages during dry years (e.g. 2008–2010) were more similar to typical South Lagoon assemblages (Figure 31). Notably, the South Lagoon assemblages during the drought years (2007– 2010) were clearly distinct from the fish assemblage during post-drought years.

The spatio-temporal differences in fish assemblages were influenced mainly by highly abundant species (i.e. sandy sprat and smallmouth hardyhead) and the presence of less abundant species (e.g. yelloweye mullet and individual species from the tetraodontidae family). The Principal Coordinate Analysis (PCO) graph of fish assemblage data successfully accounted for 76.9% of the total variation in the first two axes (Figure 32). Sandy sprat is consistently highly abundant in the Murray Estuary, whilst smallmouth hardyhead dominated assemblages in the South Lagoon. Notably, both of these species were present in the North Lagoon with smallmouth hardyhead dominating the numbers throughout the period (2007–2020), except for 2012 and 2013 (Figure 33).

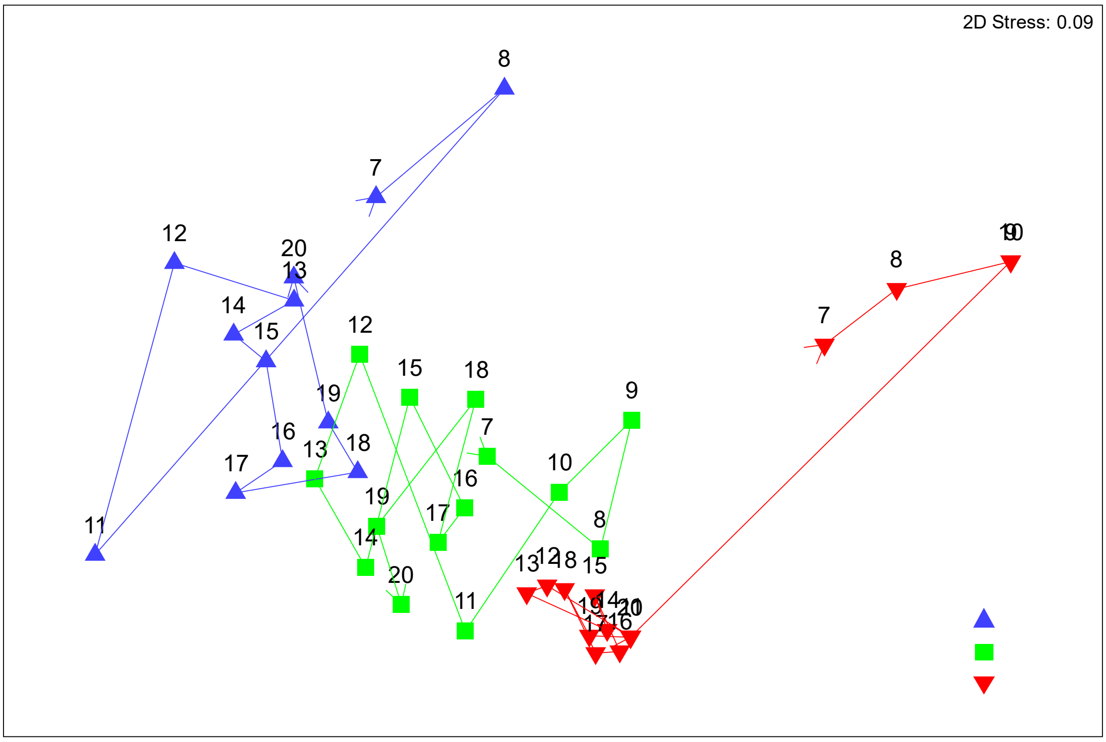


Figure 31. Multidimensional scaling ordination with SIMPROF (p <0.05) trajectory overlay showing grouping of fish assemblage by years and regions. ME = Murray Estuary, NL = North Lagoon, SL = South Lagoon.

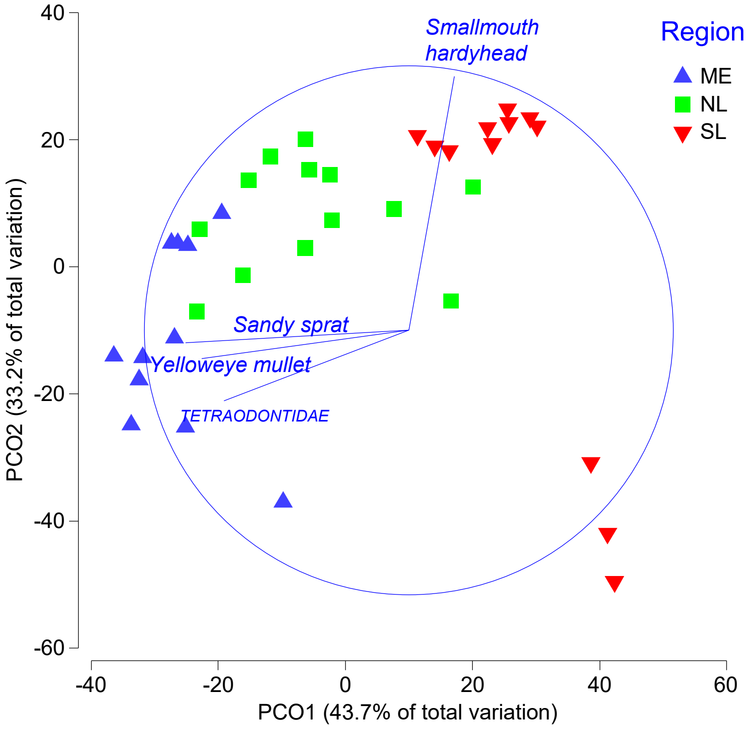


Figure 32. Principal Coordinate Analysis (PCO) of abundance samples of fish species collected by seine net in all years and regions. ME = Murray Estuary, NL = North Lagoon, SL = South Lagoon. The vectors overlay indicates Pearson rank correlations between species and PCO axes 1 and 2 (correlations >0.7, with respect to a unit circle).

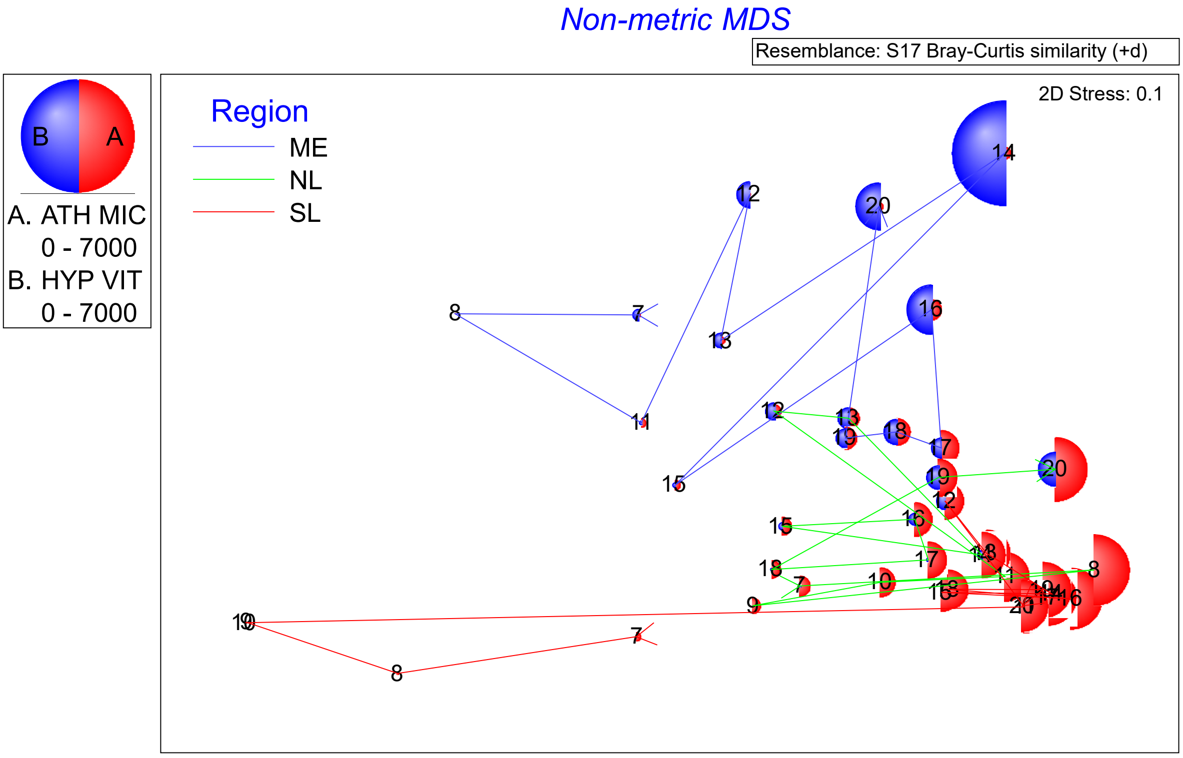


Figure 33. Multidimensional scaling ordination showing contribution of sandy sprat and smallmouth hardyhead to the distribution of assemblage data points across regions. ME = Murray Estuary, NL = North Lagoon, SL = South Lagoon. Trajectory lines with different colour for each region and all years.

3.4.3 Linking fish assemblage dynamics with key environmental drivers

The number of species sampled from different categories of estuarine use functional guilds has been influenced by barrage flow discharge into the Coorong since 2007 (Figure 34). During the late drought years with low or no barrage flow (i.e. 2007–2010), mean species richness was low and comprised mostly marine and estuarine species; the number of diadromous species was low and freshwater species were not detected (Figure 34). With increased flow from 2011 onwards, species richness as well as the contributions of freshwater, estuarine and diadromous species increased. Notably, during this period, two small-bodied and four medium- to large-bodied freshwater species entered the Coorong (refer to catch summary table, Appendix A), however only bony herring remained in the system until the last sampling event (March 2020). The species, alongside yelloweye mullet, was one of the most abundant medium- to large-bodied species in the Murray Estuary. The change in the composition of estuarine use functional guilds has likely been driven by reduced salinities, increased connectivity and enhanced productivity in the Coorong (Ye et al. 2016, Bice et al. 2018), facilitated by the increase of barrage flows.

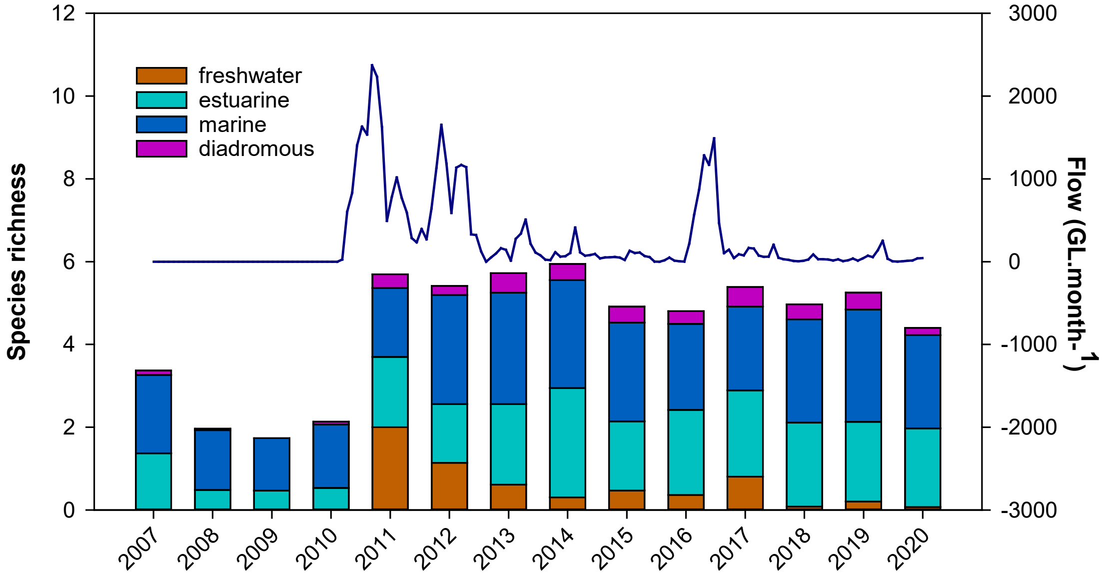


Figure 34. Total flow discharge over the barrages and species richness from 2006-2020. The contribution of fish species from different estuarine use functional guilds to species richness is shown. Freshwater = freshwater 'estuarine-opportunists' and 'straggler' combined; estuarine = 'solely estuarine' and 'estuarine and marine' combined; marine = marine 'estuarine opportunists' and 'straggler'; and diadromous = 'catadromous' and 'anadromous' combined. Guilds follow those proposed by Potter et al. (2015) and designated for Coorong and Lower Lakes by Bice et al. (2018).

Of four water quality parameters (water temperature, salinity, pH and transparency), salinity and transparency were the two parameters which significantly contributed to the differences in fish assemblage structure across the Coorong regions during 2007–2020 (Table 16). Together these two variables explained 46% of the total variation. Salinity best explained the horizontal separation of the samples (e.g. regional separation), with assemblages linking to increasing salinities from the Murray Estuary (left) to the South Lagoon (right), whilst transparency explained the vertical distribution of the data cloud, showing distinct assemblages associated with greater transparency during low flow years (e.g. 2008, 2016, 2018–2020), particularly in the Murray Estuary (Figure 35).

Table 16. Distance-based linear model (DistLM) sequential results indicating which environmental variable significantly contributed most to the relationship with the fish assemblage data (multivariate data cloud) collected by seine net. Sum of squares (SS), Proportion of the variation explained (Prop.), cumulative variation explained (Cumul.) and Residual degree of freedom (Res. DF).

VARIABLE	R^2	SS (TRACE)	PSEUDO-F	P VALUE	PROP.	CUMUL.	RES. DF
Salinity	0.36418	20555	21.765	**0.001**	0.36418	0.36418	38
Temperature	0.38974	1443.2	1.5503	0.173	0.025569	0.38974	37
Dissolved Oxygen	0.41593	1478	1.614	0.186	0.026185	0.41593	36
pH	0.42286	391.18	0.42029	0.837	0.006931	0.42286	35
Transparency	0.47902	3170.1	3.6654	**0.015**	0.056164	0.47902	34

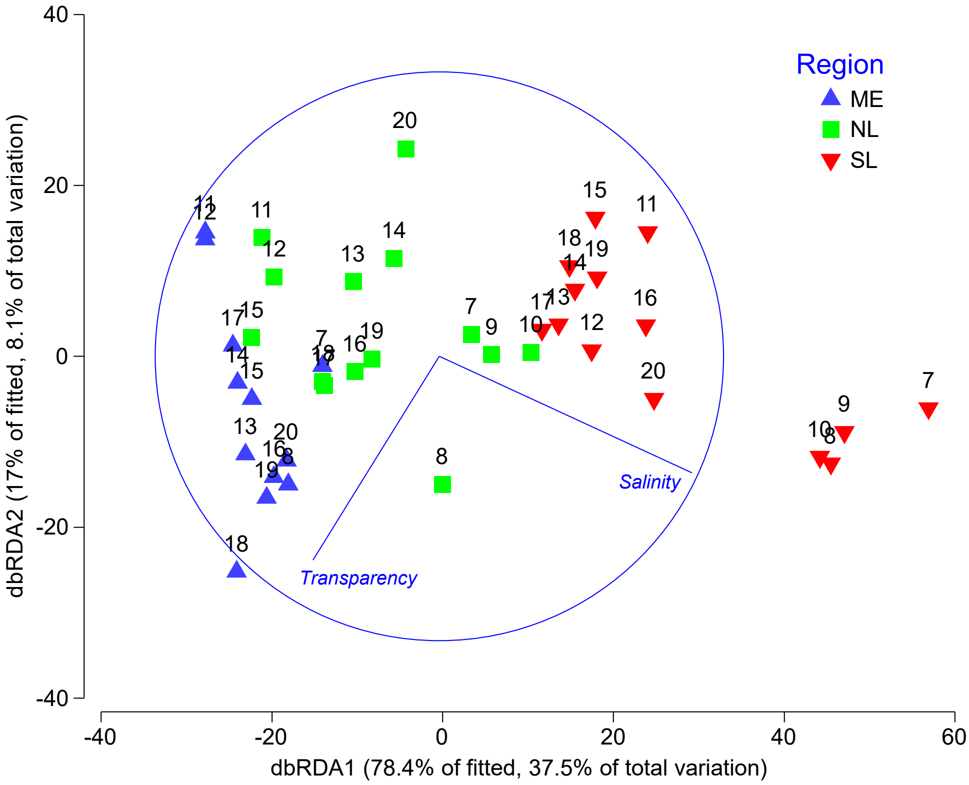


Figure 35. Distance-based redundancy analysis (dbRDA) ordination of the fitted model of species abundance data from different regions versus the predictor variables salinity and transparency. ME = Murray Estuary, NL = North Lagoon, SL = South Lagoon. The vectors overlay indicate multiple partial correlations between the predictor variables and dbRDA axes 1 and 2.

LINKTREE analysis was performed using a decision tree to identify subsets of samples from biological dataset (grouped by year and region) that were explained by threshold of the two significant environmental variables (i.e. salinity and transparency). The analysis resulted in six significant groups presented in black lines; insignificant groups (red lines) are presented, but not interpreted (Figure 36). The first separation (A) divided the early four drought years (2007–2010) of the South Lagoon samples, when salinity was >148 psu, whilst the remainder of the samples were associated with salinities <108 psu (Figure 36). The second separation (B) divided the samples to two groups: Group C included all Murray Estuary samples and North Lagoon samples of 2011, 2012, 2013, and 2015, linked with brackish to just above marine salinities (<37 psu), whereas Group L included remaining North Lagoon samples and South Lagoon samples post 2011 (with salinities >38).

Transparency and salinity influenced the separation of 2011 samples from the Murray Estuary (D), which was characterised by turbid (Secchi disc depth <233 mm) and fresher water (salinities <0.3 psu) in this flood year. For Group L, salinity once again was responsible for the separation with most of the North Lagoon samples (M – left leg) characterised by salinities (>37 and <70 psu), whilst post 2011 South Lagoon samples and 2008 and 2010 North Lagoon samples (R – right leg) were characterised by salinities >71 psu and <108 psu. Notably, transparency was the main driver, further dividing Group R to samples from South Lagoon (<415 mm) and North Lagoon samples (>595 mm).

Both significant environmental variables, salinity and water transparency, were directly influenced by flow discharge into the Coorong (Ye et al. 2015a, Bice et al. 2018). With increased inflows, salinity and water transparency decreased along the Coorong, although the response was delayed by one to two years in the North and South lagoons, respectively, compared to the Murray Estuary. The reverse response may also be plausible with reduced inflows. Due to the lagged responses in salinity and water transparency to barrage inflows along the spatial gradient of the Coorong, ecological responses in fish communities may take some time to become more apparent.

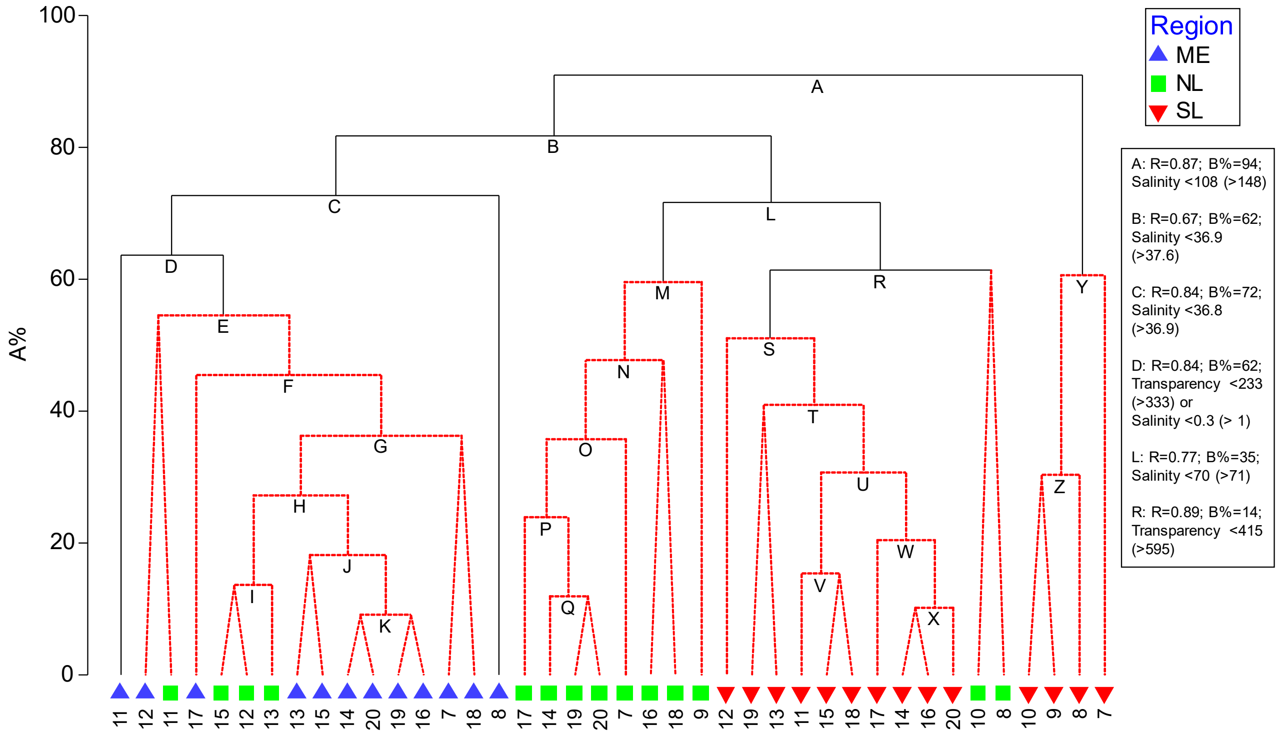


Figure 36. LINKTREE analysis using salinity and transparency (significant environmental parameters) showing divisive clustering of fish assemblages (above), constrained by inequalities in water quality variables (below). ME = Murray Estuary, NL = North Lagoon, SL = South Lagoon. Numbers below symbols refer to sampling year, e.g. 7 = 2007.

Salinity played a major role in influencing fish species richness, abundance, distribution and assemblage structure, whilst transparency did not influence at the same extent in the Coorong. Therefore, we graphed salinity with species richness and mean total abundance as dependable variables (Figure 37). The relationships between salinity and the abundances of the two most abundant species, sandy sprat and smallmouth hardy, were also developed.

The exponential decay curve indicates that species richness decreases as salinity increases in the Coorong, with no more than four species at salinities >70 psu (Figure 37a). This is probably driven by the greater osmoregulatory stress and diminishing food resources due to the increasing salinity, thus limiting the opportunity to only a few highly salt-tolerant species to extend their ecological niche (Whitfield 1999). This is best exemplified in this study, and previous fish studies (e.g. Noell et al. 2009), by the dominance of smallmouth hardyhead in the North Lagoon and their presence as the only fish species in the South Lagoon in most dry years. As for the salinity and mean total abundance relationship, the dome shape curve suggests that fish abundance reaches a maximum between 65–85 psu. This relationship is strongly influenced by the two most abundant species, particularly smallmouth hardyhead (Figure 37b).

Smallmouth hardyhead abundance peaked at approximately 80 psu and decreased dramatically when salinity levels were >110 psu (Figure 37c). This is explained by the species' broad salinity tolerances of 3.3–108 psu (lower-upper LD50) (Lui 1969). The abundance of sandy sprat presented its peak at around marine salinity (35 psu) and decreased with salinities over 50 psu (Figure 37d). It is noteworthy that the presence and abundance of both species in the Coorong is directly linked with salinity patterns (i.e. sandy sprat are most abundant in the Murray Estuary, smallmouth hardyhead in the South Lagoon and both species cohabit in the North Lagoon).

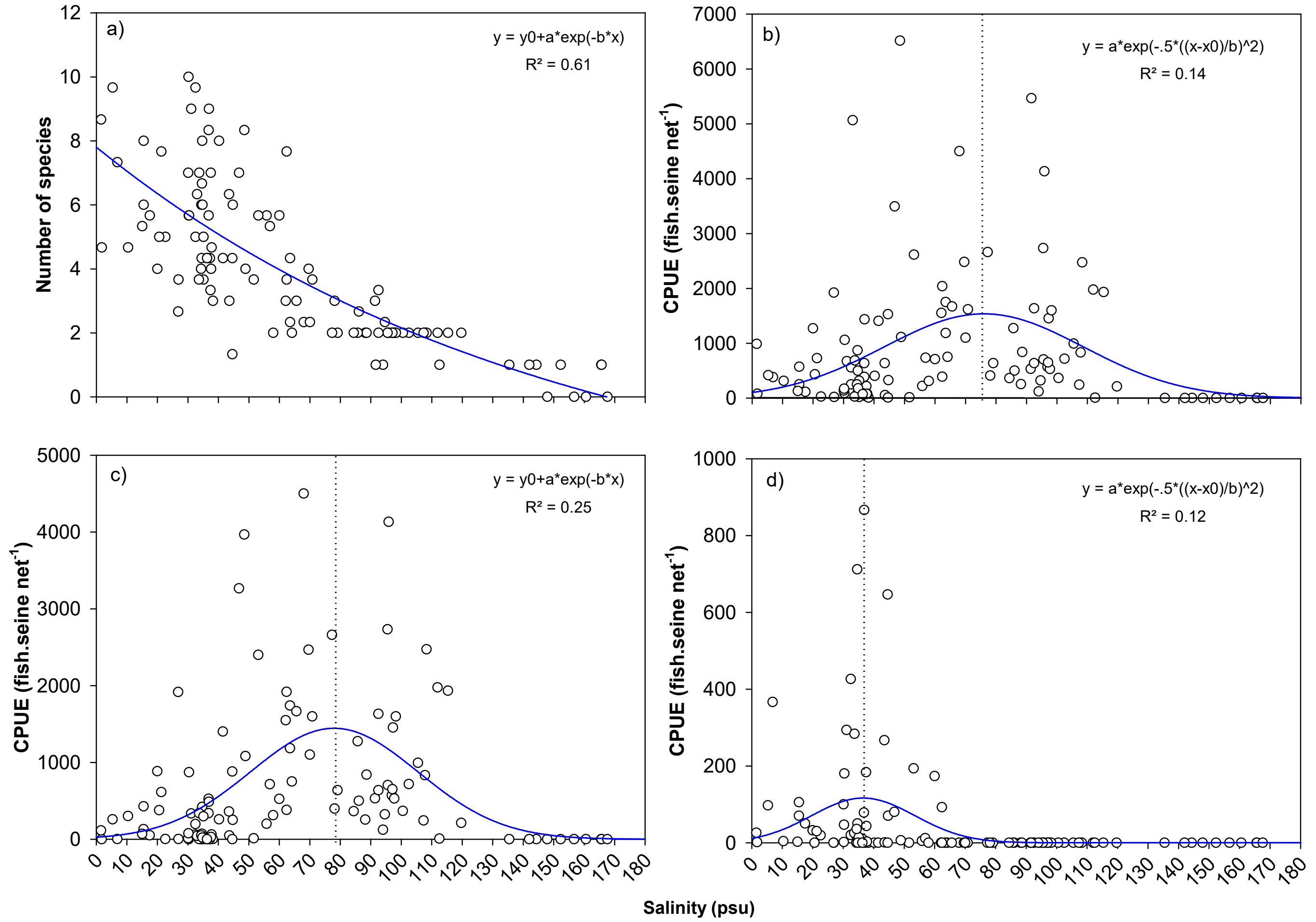


Figure 37. Changes in a) mean species richness (number of fish species), and b) mean total abundance, c) mean smallmouth hardyhead abundance and d) mean sandy sprat abundance with mean salinity. Abundance = catch-per-unit-effort (CPUE).

3.4.4 Conclusions

Our knowledge and understanding of the ecology and population dynamics of fish species in the Coorong has significantly improved, particularly with the long-term data collected under varying hydrological conditions over the last two decades. Freshwater inflow and salinity are the primary environmental drivers affecting the spatio-temporal variations in fish assemblage structure (composition and abundance) in the

Coorong although water transparency can also be influential in some years. Under drought or low flow conditions, fish species richness and abundance decrease in the Coorong, whilst the opposite occurs during high inflows mainly due to the increases in abundance of freshwater, estuarine and diadromous species. Species richness decreases along the increasing salinity gradient in the Coorong with ≤4 species at salinities >70 psu.

Two small-bodied prey fishes were the most abundant species in the Coorong from 2007–2020, with smallmouth hardyhead dominating the southern part and sandy sprat being more abundant in the northern part. Total fish abundance was highest between 65–85 psu, mainly driven by the above two species, particularly smallmouth hardyhead. In the South Lagoon, the prevalence of hypersaline (mean >80 psu) conditions limited the fish assemblage to a few highly salt tolerant species (e.g. smallmouth hardyhead, yelloweye mullet and congolli), although other species (e.g. bony herring and sandy sprat) also entered this region during and following high flows.

While understanding of long-term trends in fish assemblage structure and primary environmental drivers has improved over the past two decades, from a food web perspective, further research is required to examine patterns in fish biomass across space and time. This should include finer scale sampling to understand seasonal variability in fish assemblages, including the distribution of prey and predator species across shallow and deeper habitats in the Coorong. Such information will inform the quantitative food web model development.

4 Current conceptual food web models for the Coorong

4.1 Background

Previous trophic investigations have provided a preliminary and/or qualitative understanding of the Coorong food web and the relationships between spatial variation, hydrology, key food sources and flow of energy through trophic pathways (e.g. Geddes and Francis 2008, Deegan et al. 2010, Giatas and Ye 2016). During low inflows in March 2005, Geddes and Francis (2008) conducted a trophic ecology pilot study at Pelican Point at the divide of the Murray Estuary and North Lagoon regions (Figure 1). They used invertebrate prey abundances and biomass, along with dietary information for four key fish species, to model a semi-quantitative food-web (Figure 38). This food-web model provided considerable insight into the contribution of prey to important fishes in the Coorong, but was spatially (conducted in a small area) and temporally (information from one sampling event) limited in resolution. The Coorong food web is likely to vary considerably across the salinity gradient of the system, and under different hydrological conditions.

During low inflows in March 2007, a trophic study of the Coorong undertaken by Deegan et al. (2010) used a combination of stable isotope–gut-content method approach to understand how the food web changes with increasing salinity, and to classify the trophic guilds of prey and predator species. This study focused on food-web interactions leading to fishes and was conducted over a much broader spatial scale compared to the previous pilot investigations in the system (Lamontagne et al. 2007, Geddes and Francis 2008), encompassing all the three geographical regions. Figure 39 shows a simplistic food-web model of the system by trophic guilds under different salinities derived from Deegan et al. (2010). Modelled food web structure changed considerably along the salinity gradient of the system (Murray Estuary to South Lagoon), reflecting a loss of prey diversity and specific trophic guilds (e.g. piscivorous fish) with increasing salinity.

Extensive ecological monitoring of key biota (Section 3) and dietary assessments (e.g. fish, summarised in Section 2.1) have been undertaken over the last decade and provided significant foundational knowledge to further inform our conceptual understanding of the food web (e.g. Brookes et al. 2009a, 2015, Giatas and Ye 2016, Giatas et al. 2018). Building on previous food web structure investigations (e.g. Geddes and Francis 2008, Deegan et al. 2010) and utilising available data, including those recently obtained during a high inflow period, Giatas and Ye (2016) developed basic (semi-quantitative) conceptual models to investigate how freshwater inflow may affect food web structure in the Coorong. Construction of the food web models allowed for the identification of key taxonomic groups or species facilitating transfer of energy to higher trophic levels during different hydrological periods. Food web complexity (number of trophic members and links) across the Murray Estuary and North Lagoon during high inflows to the Coorong was considered to be high – due to the presence of most functional guilds far into the North Lagoon and a relatively greater influence of pelagic production from allochthonous sources, i.e. nutrients or freshwater zooplankton input.

Knowledge gained from the decades of work and our resulting conceptual understanding of the food web dynamics in the Coorong is most recently summarised in Giatas et al. (2018) and presented below in Section 4.2. Refer to Giatas et al. (2018) for a more detailed description of the trophic components, food web types and the influence of flow on them.

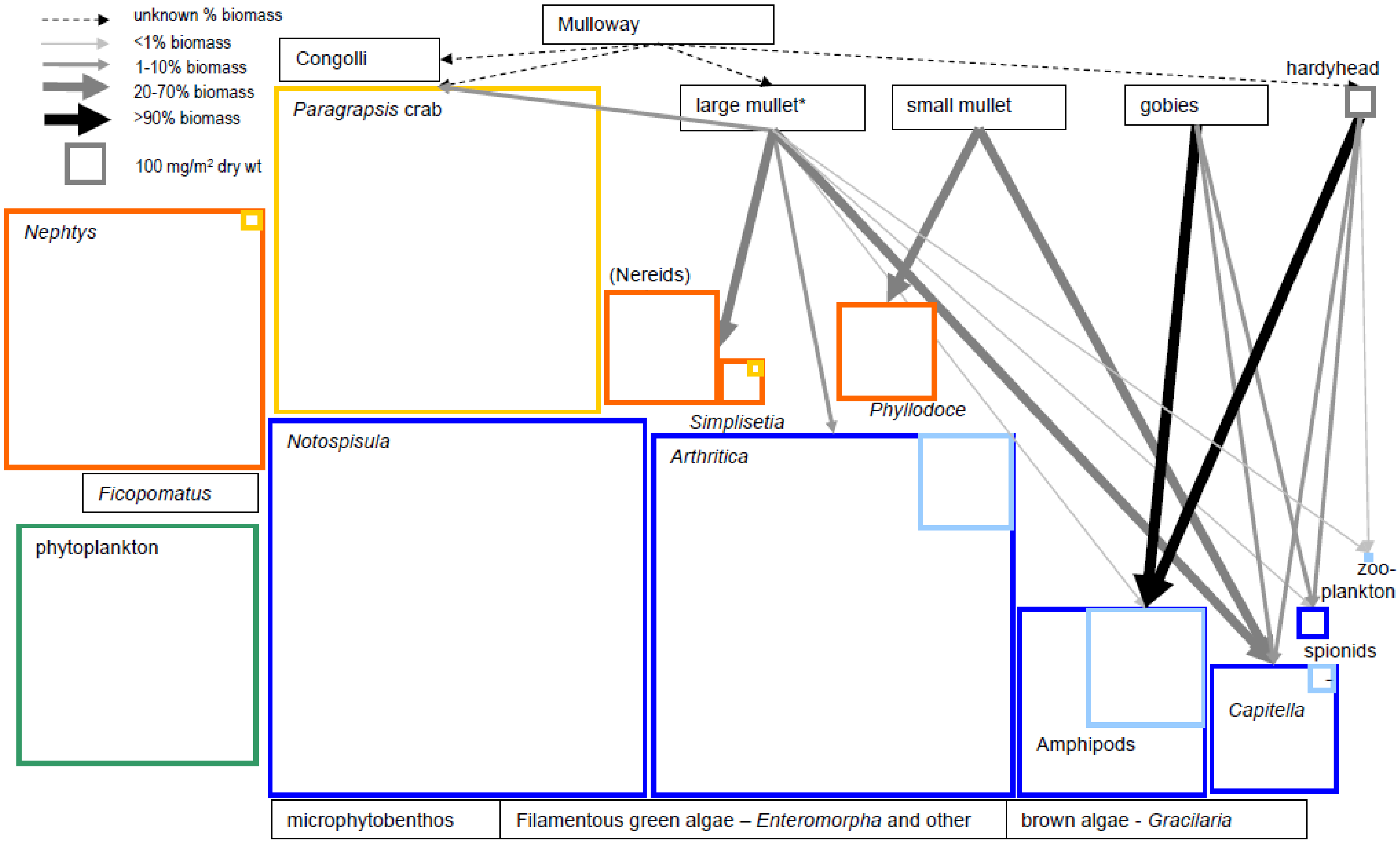


Figure 38. Semi-quantitative food-web structure for the Coorong at Pelican Point. Size of each box represents the biomass of the taxon (mg m^{-2}dry weight (wt)). Boxes in dark represent the total biomass and light coloured boxes are the proportion epibenthic, planktonic or nektonic. Source: Geddes and Francis (2008).

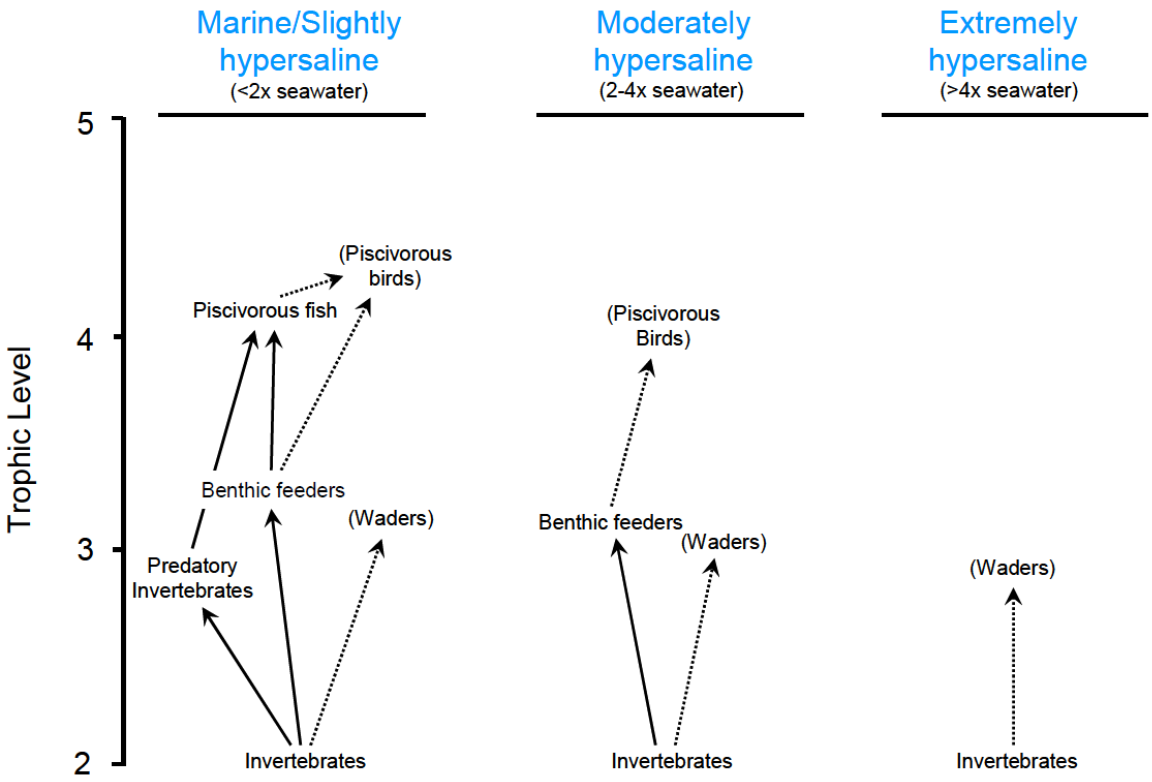


Figure 39. Guild-specific food-webs in the Coorong at different salinity levels Guilds are: "invertebrates" = primary consumers (grazers, filter feeder, etc); "predatory invertebrates" = larger omnivorous or predatory invertebrate species; "benthic feeders" = smaller fishes, or smaller size-classes of larger fishes; "piscivorous fish" = black bream and mulloway. Also included is the hypothesised trophic position and trophic relation (dashed lines) for "waders" (various species of shorebirds) and "piscivorous birds" (including terns, Australian pelican, etc.). Source: Deegan et al. (2010).

4.2 Conceptual understanding of the Coorong food web

4.2.1 Trophic components

The Coorong food web comprises four main trophic groups: primary producers, primary consumers, secondary consumers and higher order consumers (trophic level 4 or greater) (Figure 40). Each consumer group is made up of one or more feeding guilds, i.e. biota with similar feeding modes/diets and similar ecological function (Table 17). The key biota within these guilds and their contribution to the diet composition of key fish and waterbirds are discussed in Sections 3 and 2, respectively, of this report.

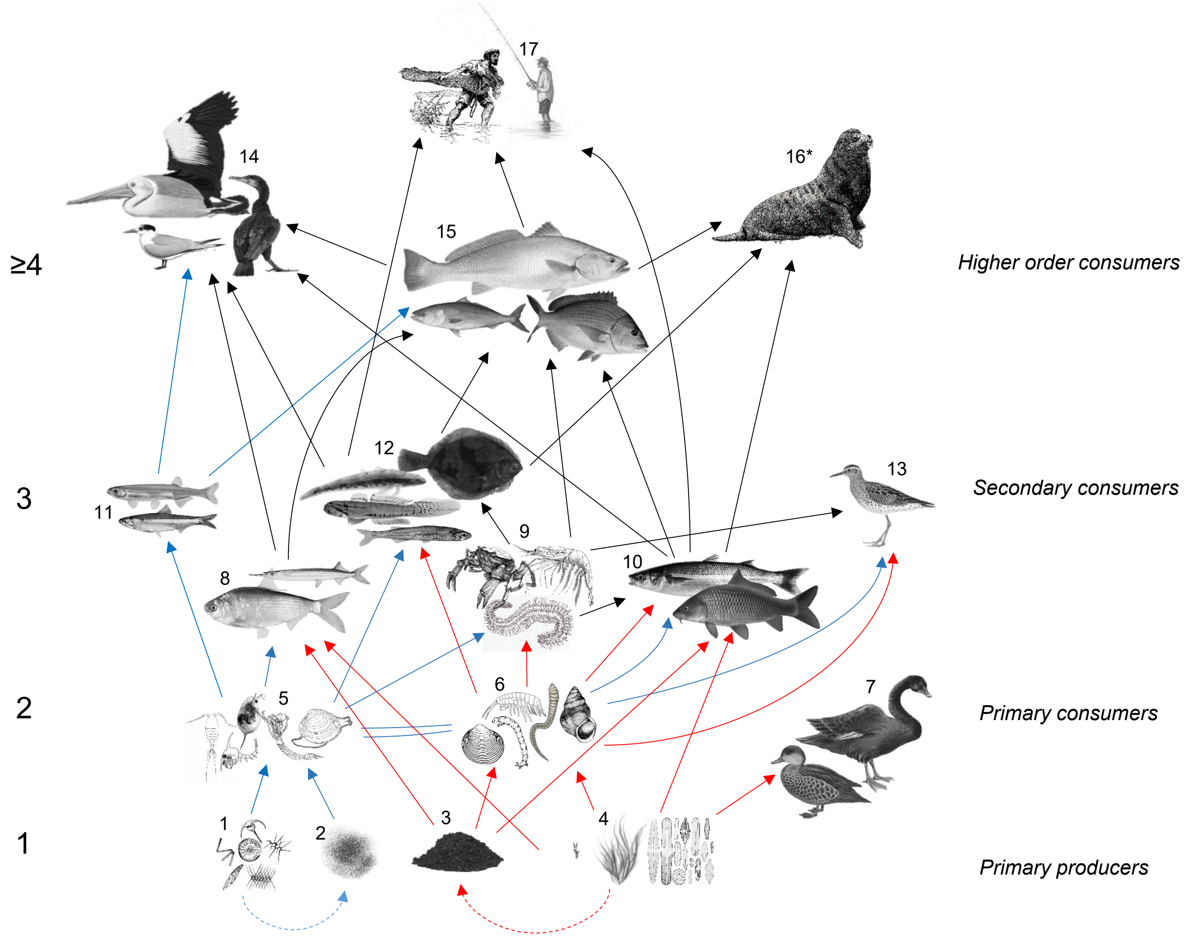


Figure 40. Conceptual food web of the Coorong using feeding functional guilds Red trophic links represent those supported by benthic production (benthic algae/plants), blue trophic links represent those supported by pelagic production (phytoplankton), while black trophic links may represent either or a combination. Primary producers and organic matter material are (1) phytoplankton, (2) suspended particulate organic matter, (3) benthic detritus and (4) benthic macrophytes, micro- and macro- algae. Feeding guilds are (5) suspension- feeding micro- and macro-invertebrates, (6) deposit-feeding and herbivorous macro- invertebrates, (7) herbivorous waterfowl, (8) omnivorous fishes Part 1, (9) carnivorous invertebrates, (10) omnivorous fishes Part 2, (11) zooplanktivorous fishes, (12) zoobenthivorous fishes, (13) zoobenthivorous shorebirds, (14) piscivorous birds, (15) piscivorous fishes, (16) piscivorous mammals*, and (17) humans. Refer to Table 17 for members within feeding guilds. Organic matter and benthic detritus are not primary producers and represent the microbial loop (dotted trophic links). *Long- nosed fur seals were largely undocumented in the Coorong prior to 2007. Source: Giatas et al. (2018).

Table 17. Coorong taxa allocated to feeding functional guilds. Refer to Giatas et al. (2018) for descriptions of feeding functional guilds. * indicates invertebrate taxa that also belong in another feeding mode. Note that some feeding guild allocations may have been updated during this review (e.g. black bream and Australian smelt) and some macroinvertebrates (e.g. scavengers). Source: Giatas et al. (2018).

FEEDING FUNCTIONAL GUILD	TAXA	TROPHIC GROUP
Suspension feeding invertebrates	Bivalvia – *Arthritica semen*, *Soletellina (Hiatula) alba**, *Spisula* (*Notospisula*) *trigonella*, Mytilidae; Polychaeta – *Ficopomatus enigmaticus*, *Boccardiella limnicola**, *Australonereis ehlersi**; Amphipoda* – *Paracorophium* sp.; Malacostraca – Mysidacea*.	Primary consumer
Deposit feeding and herbivorous macro-invertebrates	Deposit feeders: Bivalvia – *Soletellina (Hiatula) alba**; Oligochaeta; Polychaeta – *Capitella capitata*, *Boccardiella limnicola**, *Australonereis ehlersi**, *Simplisetia aequisetis**; Sipuncula; Malacostraca – Amphipoda*; Diptera – Ceratopogonidae*, Chironomidae*, Ephydridae*, Gastropoda – *Salinator fragilis**.	Primary consumer
	Herbivorous grazers and browsers: Gastropoda – Hydrobiidae, *Salinator fragilis**, *Coxiella striata*, Glacidorbidae; Malacostraca – Amphipoda*; *Macrobrachium intermedium**; Diptera – Chironomidae*, Ephydridae*.	Primary consumer
Herbivorous waterfowl[1]	e.g. black swan (*Cygnus atratus*), Australian shelduck (*Tadorna tadornoides*), grey teal (*Anas gracilis*), chestnut teal (*Anas castanea*).	Primary consumer
Carnivorous invertebrates	Omnivorous scavengers: Polychaeta – *Simplisetia aequisetis**; Malacostraca – Amphipoda*, *Macrobrachium**, *Paragrapsus gaimardii*, *Helograpsus haswellianus*, *Amarinus laevis.*	Omnivorous[2]
	Carnivores: Polychaeta – *Phyllodoce novaehollandiae*, *Aglaophamus australiensis*; Malacostraca – Mysidacea*, Diptera – Ceratopogonidae*.	Secondary consumer
Omnivorous fishes	Group 1, Zooplanktivore: bony herring (*Nematalosa erebi*), river garfish (*Hyporhamphus regularis*).	Omnivorous[2]
	Group 2, Zoobenthivore: yelloweye mullet (*Aldrichetta forsteri*), common carp (*Cyprinus carpio*), bridled goby (*Arenigobius bifrenatus*), bluespot goby (*Pseudogobius olorum*).	Omnivorous[2]
Zooplanktivorous fishes	Sandy sprat (*Hyperlophus vittatus*)[3], Australian smelt (*Retropinna semoni*).	Secondary consumer
Zoobenthivorous fishes	Greenback flounder (*Rhombosolea tapirina*), smallmouth hardyhead (*Atherinosoma microstoma*), Tamar goby (*Afurcagobius tamarensis*), congolli (*Pseudaphritis urvillii*), Australian herring (*Arripis georgianus*), flathead gudgeon (*Philypnodon grandiceps*).	Secondary consumer
Zoobenthivorous shorebirds[1]	e.g. red-neck stint (*Calidris ruficollis*), banded stilt (*Cladorhynchus leucocephalus*), sharp-tailed sandpiper (*Calidris acuminata*), black-winged stilt (*Himantopus himantopus*), red-capped plover (*Charadrius ruficapillus*), red-necked avocet (*Recurvirostra novahollandiae*), black tailed godwit (*Limosa limosa*), eastern curlew (*Numenius madagascariensis*).	Secondary consumer
Piscivorous fishes	Mulloway (*Argyrosomus japonicus*), Australian salmon (*Arripis trutta* and *A. truttaceus*), black bream (*Acanthopagrus butcheri*)[4].	Higher-order consumer
Piscivorous birds	e.g. Australian pelican (*Pelecanus conspicillatus*), cormorants (*Phalacrocorax* spp.), terns (*Sternula* spp.), hoary-headed grebe (*Poliocephalus poliocephalus*).	Higher-order consumer
Piscivorous mammals	Long-nosed fur seal (*Arctocephalus forsteri*).	Higher-order consumer

[1] Herbivorous waterfowl have been classified as such, but their diets (except for black swan) may also include animal material. Shorebirds have been classified as zoobenthivorous, but their diets may also include fish or plant material such as *Ruppia* seeds. Consequently, trophic levels for bird species within individual guilds may vary greatly, depending on their diets. [2] ‘Omnivorous’ refers to a group situated between primary consumers and secondary consumers. [3] Benthic microcrustaceans may be important in the diet of sandy sprat in the Coorong (Bice et al. 2016a). [4] While black bream could be classified as an omnivore because it may consume algae or macrophytes, the greatest proportion of its diet in the Coorong is made up of large benthic decapods (e.g. *Paragrapus gaimardii*) and fishes such as gobies. Stable isotope analysis has confirmed this species to be a higher-order consumer (≥ trophic level 4) (Deegan et al. 2010).

4.2.2 Influence of freshwater flow and salinity gradient on food web structure

Salinity gradient

At least four distinct food webs have been described for the Coorong along its salinity gradient (Deegan et al. 2010, Giatas and Ye 2016). As salinities increase from marine (~40 psu), there is a general decline in the diversity of species (Section 3) and feeding guilds, and food chain length (Figure 39), driven by species' salinity preferences and tolerances. Furthermore, as the salinity gradient is influenced by freshwater inflow, so too is the spatial positioning, presence and extent of the following distinct food webs (Table 18). For example, during high inflows, the extremely hypersaline food web is expected to be absent, and the spatial area where the hypersaline food web operates is likely restricted to the South Lagoon. The fresh-brackish and brackish-marine food webs cover a wide area spanning the Goolwa Barrage through the North Lagoon and seasonally into the South Lagoon (Figure 1). The wide spatial coverage of these two food webs is considered beneficial from a conservation, economic and ecological perspective because all feeding guilds are present (including piscivorous fishes), and these food webs support the greatest biomass and diversity of biota.

During prolonged periods of low freshwater inflow, the fresh-brackish food web is expected to be absent from the Coorong, and the brackish-marine food web is likely restricted to the Murray Estuary and northern end of the North Lagoon. Due to mostly marine salinities present in the Murray Estuary under low flows, freshwater species are absent or abundance is low and likely play a negligible role in food web function. Extended periods of little or no freshwater inflow may lead to prolonged mouth closure and disconnection between the estuary and freshwater environments, resulting in increased salinities. In turn, this can potentially lead to: 1) decreased species diversity and biomass, including fisheries production; 2) the loss of feeding guilds and simplification of food webs; and 3) extirpation of estuarine biota from the ecosystem.

Table 18. Characteristics of the distinct food webs at different salinity levels the Coorong. Aadapted from Giatas et al. (2018).

SALINITY	FOOD WEB CHARACTER DESCRIPTION
Fresh-brackish (<20 psu)	High relative abundances of freshwater zooplankton, benthic invertebrates (albeit at low diversity), zooplanktivorous and omnivorous freshwater fishes (bony herring, common carp, Australian smelt), and a zooplanktivorous marine forage fish (sandy sprat), and moderate abundances of omnivorous marine (yelloweye mullet) and piscivorous marine fishes (Australian salmon and mulloway). Sandy sprat is found in highest abundance during periods of freshwater discharge (Bice et al. 2016a) and likely transfers a significant amount of energy from primary producers and consumers (e.g. zooplankton) to higher-order consumers.
Brackish-marine (~30–50 psu)	Associated with the most diverse habitat for fish, with freshwater (bony herring), estuarine (smallmouth hardyhead) and marine (sandy sprat, yelloweye mullet, mulloway, Australian salmon) fishes from a variety of feeding guilds present. High diversities of benthic macro-invertebrates also occur at these salinities, characterised by polychaetes (*Capitella capitata* and *Simplisetia aequisetis*), bivalves (*Arthritica semen*) and crustaceans (amphipods).
Hypersaline (~70–120 psu)	Associated with seasonally inundated mudflats and historically characterised by extensive cover of *Ruppia* spp., high abundance of smallmouth hardyhead and diversity of bird species including waders (e.g. red-neck stint and banded stilt) and grazers (e.g. black swan). Chironomid larvae (*Tanytarsis barbitarsis*) and brine fly larvae (*Ephydrella* sp.) support the only fish prey species (smallmouth hardyhead) present for piscivorous birds. Piscivorous fishes are absent in this food web, and other zoobenthivorous species with quite high salinity tolerances (e.g. yelloweye mullet) occur occasionally.
Extremely hypersaline (>120 psu)	Characterised by an overall low species diversity, high densities of phytoplankton and ostracods, the presence of the Australian brine shrimp, and the absence of fish, including smallmouth hardyhead, and piscivorous birds.

Energy sources and pathways

Freshwater inflows to the Coorong are expected to increase inorganic nutrient input and stimulate primary production. They also directly transport riverine and terrestrial food resources (e.g. organic matter, phytoplankton and zooplankton) to the Coorong, potentially leading to enhanced secondary productivity (e.g. sandy sprat) which is propagated progressively up the food chain (e.g. Bice et al. 2016a). During high inflows, however, transported nutrients, organic matter and other food resources may have short residence times and be flushed out of the Coorong (Ye et al. 2018b), but may benefit nearshore marine communities (Auricht et al. 2017).

While both benthic and pelagic pathways support higher predators (e.g. large-bodied fish) during low inflows in the Coorong (Lamontagne et al. 2016), there is considered to be a greater contribution of pelagic components of the food web towards production in the Murray Estuary and North Lagoon during high freshwater inflows (Giatas and Ye 2016). This is the result of increased zooplankton abundance (dominated by freshwater species) during high inflows, presumably due to transportation from the Murray River and Lower Lakes to the Coorong or from increased local primary productivity of phytoplankton, stimulated by allochthonous nutrient input. Conversely, benthic production and energy propagation through benthic-based trophic pathways become relatively more important during lower inflows, particularly in the North and South lagoons.

5 Knowledge gaps for the Coorong food web and hypotheses

Ecological monitoring in the Coorong, particularly over the last two decades, has significantly advanced our foundational knowledge of the spatio-temporal dynamics of key biota and the primary environmental drivers (freshwater inflow and salinity) for these trophic components. Our conceptual understanding of the Coorong food web and how it operates spatially and temporally has also improved considerably during this period. However, knowledge gaps remain and are needed to develop quantitative food web models to inform and guide management for food web restoration in the Coorong. Here we summarise the knowledge gaps identified from the review and indicate those proposed for further research under the HCHB T&I Project, particularly *Component 3 Food web*. Hypotheses are also established with regard to restoring a productive and resilient food web in the South Lagoon, considering key environmental drivers, including those potentially affected by management interventions.

5.1.1 Knowledge gaps and development of quantitative food web models

While the conceptual understanding of the Coorong food web and its components has improved, food web models that have been developed in the past are semi-quantitative or qualitative (Geddes and Francis 2008, Deegan et al. 2010, Giatas and Ye 2016). These provide limited capacity to assess responses to environmental change, including responses to different management interventions. Integrated, quantitative food web models can assess food web responses to various management actions and interventions. They provide a key management toolkit to assess operational decisions in supporting the maintenance or restoration of systems. *Ecopath with Ecosim* software has been used to develop trophic mass-balance models of ecosystems across the world (e.g. Pauly et al. 2000, Christensen and Walters 2004), including southern Australia (e.g. Goldsworthy et al. 2013, 2017, 2019), predominantly to assess fisheries impact.

An integrated food web model is proposed to be developed under Activity 3.4 of *Component 3 Food web* of the HCHB T&I Project (Table 1). This model will integrate data from previous studies conducted in the Coorong and new data obtained from this study. It will provide a tool to assess how the Coorong food web may respond to different environmental conditions, and which environmental and/or management scenarios optimise conditions to restore the values for the South Lagoon ecosystem. The integrated food web model coupled with the hydrological and biogeochemical models, developed in the associated T&I Project *Component 7 Integration* and applied in the Water Resource Optimisation project of HCHB, will provide a key management ‘toolkit’. These ‘tools’ will be able to be used to assess operational decisions to support the availability and quality of habitat in the Coorong and in particular the South Lagoon to improve the viability of fish and waterbird populations.

The quantitative food web model and its effectiveness will depend on the availability and quality of the input data and the understanding of trophic links and environmental drivers. Knowledge and data gaps identified during this review, relating to the Coorong food web, are summarised below in Table 19.

In general, links between river flow, nutrient resources and salinity levels for productivity and ecosystem energetics is unknown (Brookes et al. 2015). Uncertainties remain regarding what food items actually support waterbirds and their relative importance, in the South Lagoon in particular, and what food resources are required to maintain viable waterbird populations. Additionally, key knowledge gaps remain in relation to critical food resources available, harvestable and bioenergetically valuable for key species across seasonal and spatial scales within the Coorong. Some of the key knowledge gaps will be addressed through the T&I Project (Table 19).

Table 19. Knowledge gaps relating to the Coorong food web and potential further research to be undertaken through the Healthy Coorong Healthy Basin Trials and Investigations (T&I) Project.

KNOWLEDGE GAP	PRIORITY	T&I PROJECT
Food sources		
The feeding mode or diet composition of lagoon goby (no diet information available from closely related species).	Medium	*Component 3 Activity 3.2*
Diets of other fish species (e.g. river garfish, bluespot goby, bridled goby, longsnout flounder, Australian herring, flathead gudgeon and Australian smelt) in the Coorong.	Low	
Diets of common freshwater species (e.g. bony herring) in the Coorong. Note: Diet literature available for these species in the Lower Lakes (freshwater habitat).	Medium	
Quantitative diet composition data for waterbirds in the Coorong.	High	*Component 3 Activity 3.2* Scat sample collection supported by *Component 4*
Contribution of particular food items to the diet of waterbirds, in particular: • *Ruppia tuberosa* seeds and turions by shorebirds • Filamentous algae by waterfowl • Animal prey in abundant omnivorous waterfowl (e.g. grey teal and chestnut teal).	High	*Component 3 Activity 3.2* Scat sample collection supported by *Component 4* (some questions)
Food sources of macroinvertebrates (difficult to assess)	Medium	
Ecology of biota and responses to environmental drivers*		
Zooplankton abundance, biomass, distribution, community composition and their responses to environmental drivers. Further data on spatio-temporal dynamics: • Longer-term data with variable and representative hydrological/climatic and environmental conditions • Data from the North and South lagoons • More frequent sampling (e.g. fortnightly).	High	*Component 3 Activity 3.3* Note: only seasonal sampling
Biotic effects for zooplankton with bottom up and top down controls on composition and abundance.	High	*Component 3 Activity 3.3* *(Partially)*
Flow source effect on the zooplankton composition in the Coorong (e.g. River/Lower Lakes, Salt Creek/Morella Basin).	Medium	
Macroinvertebrate abundance, biomass, distribution, community composition and responses to environmental drivers, including finer spatio-temporal dynamics (e.g. inter- and sub-tidal sampling, and monthly sampling to estimate productivity).	High	*Component 3 Activity 3.3*
Relevance of tubeworm reefs as foraging habitat for fish and crabs.	Medium	*Component 3*
Biomass, distribution and responses to environmental drivers (e.g. flow) of large epi-benthic crustaceans (i.e. the shorecrab *Paragrapsus gaimardii*). Note: This is a key food source for large predators in the Coorong, such as mulloway and black bream.	High	*Component 3 Activity 3.3*
Fish abundance, biomass, distribution, assemblage composition and responses to environmental drivers, including finer spatio-temporal dynamics (e.g. seasonal sampling, shallow and deeper habitat distribution).	High	*Component 3 Activity 3.3*

KNOWLEDGE GAP	PRIORITY	T&I PROJECT
The energetic and nutritional values of key food resources including plants, zooplankton, macroinvertebrates and fishes.	High	*Component 3 Activity 3.3* Sample collection for primary producers supported by *Component 2*
Food web dynamics/processes		
Pathways by which nutrients pass from primary producers to waterbirds.	High	*Component 1, 2, 3, 4 and 7*
Modelling of processes that are happening at the base of the food web such as • The introduction of freshwater-derived nutrients and organic matter, and • The decomposition of matter (e.g. microbes) and formation of detritus.	High	*Component 1* *Component 2 (partially)*
Top down impacts on biota (e.g. grazing pressure by swan on *Ruppia*, fish on invertebrates).	Medium	*Component 3 Activity 3.3 and Activity 3.4 Partially*
Incorporation of fishing mortality into models.	High	*Component 3 Activity 3.4*
Mass-balance food web models to predict changes by environmental drivers	High	*Component 3 Activity 3.4*

*Knowledge gaps relating to the ecology of other biota not covered in this review (e.g. primary producers and birds) will be discussed in the reviews as part of Components 2 and 4.

5.1.1 Food web restoration in the South Lagoon: hypotheses

Freshwater inflow from the Murray River, complemented by the inflow from the South East catchment (via Salt Creek), and seawater inflows (via Murray Mouth) are the primary drivers for physiochemical changes, ecological processes and biological responses in the Coorong, and thus the structure and functioning of the food webs (Mosley et al. 2018). Salinity, strongly influenced by freshwater inflow, is considered the major factor structuring assemblages of biota and the complexity of the food web in the Coorong. In addition, water levels are critical, affecting the availability of habitat (e.g. mudflat for shorebirds) and the life-history of some key biota (e.g. *Ruppia* spp.). Furthermore, nutrient cycling that maintains suitable water quality and improves ecological function is important for the ecosystem health (Brookes et al. 2009a, 2015).

With a general reduction in freshwater inflows over decades, the Coorong has experienced declining ecological health, particularly in the South Lagoon, likely due to the interactive effects of hypersalinity, changes in the water level regimes and more recent eutrophic conditions (Mosely et al. 2020). These environmental changes have interrupted nutrient cycling and key primary production processes, reduced habitat quality and the abundance and diversity of many biota, and impacted on the entire food web in the southern Coorong, which includes the South Lagoon and the North Lagoon from the Needles south (Brookes et al. 2018, DEW 2020).

Restoring a functioning and resilient food web is fundamental to improving the productivity and supply of energy to key biota, including fish and waterbirds. For the southern Coorong, a summary of the understanding of current ecological state, the trajectory of 'do-nothing', and the targeted desired state with proposed management strategies has been recently developed to guide the ecosystem restoration in this region (DEW 2020). The key aspects in relation to the environmental drivers and food web restoration are represented in Table 20.

Table 20. Food web restoration for the southern Coorong, adapted from DEW (2020).

DRIVERS/FOOD WEB RESPONSE	CURRENT STATE	DESIRED STATE	HOW TO GET THERE
Salinity	• Extremely hypersaline (>60 psu) • Long-term net accumulation of salt due to limited potential for increased inflow and flushing • Further evaporation leading to a concentration of salts	• A naturally variable salinity regime including: ○ Some periods of hypersalinity (>60 psu) ○ A range of lower maximum salinities between years	• Manage salinity to allow seasonal variation within years and between years; minimise the duration of peak salinities and frequency of peak salinity events • Assess options to improve long-term export of salt through inflow of low salinity water, flushing, and reducing salt load in flow sources
Nutrients / eutrophication	• The condition of the sediment is degraded, and is fueling the cycle of eutrophication: ○ Predominantly hypereutrophic (high levels of chlorophyll-a, nitrogen, and phosphorus). ○ High level of primary producers (phytoplankton and filamentous macro algae)	• Healthy sediment nutrient cycling and sediment-water fluxes • Mesotrophic conditions defined as moderate levels of primary productivity, chlorophyll-a, nitrogen, and phosphorus	• Assess options to remove nutrient pools and organic loads within the southern Coorong • Ongoing and long-term flushing and export of nutrients • Facilitating aquatic plant community and invertebrate restoration
Food webs (plants, invertebrates, fish and waterbirds)	• The entire food web of the southern Coorong has been affected by poor conditions • Nutrient cycling and key primary production processes have been disrupted, reducing the quality and availability of habitat and food sources for elements of the southern Coorong food web	• The southern Coorong supports functional food webs including: ○ Aquatic plant (*Ruppia*) communities, invertebrate, fish and waterbird populations ○ A more complex resilient food web with multiple trophic levels and productive and diverse biota	• Integrated management solutions addressing the needs of each key component of the southern Coorong food web • Strategies could include: ○ Improve water and sediment quality, and management of hypersaline and hypereutrophic conditions ○ Improve system connectivity to facilitate recolonisation of waterbirds, fish, plants and invertebrates ○ Direct restoration of habitat features and ecosystem processes

The prolonged hypersaline and hypereutrophic conditions in the southern Coorong currently constrain the reinstatement of key ecological attributes of a desired healthy state (Brookes et al. 2018, DEW 2020). We concur with the DEW (2020) assessment and support that to achieve the desired ecological state and restore a more complex and resilient food web in the South Lagoon, including multiple interconnecting trophic levels with aquatic plant (i.e. *Ruppia*), invertebrate, fish and waterbird populations, salinity and nutrients need to be managed. It is hypothesised that this requires establishing a more naturally variable salinity regime as described in Table 20. The approach of setting salinity targets linked to freshwater inflows for restoring a healthy food web in the South Lagoon is consistent with previous studies in the Coorong (Brookes et al. 2009a, Lester et al. 2009). Additionally, reinstating mesotrophic conditions with 'healthy' nutrient cycling and sediment-water flux is required, which could be assisted by increasing system flushing (frequency and magnitude) for the South Lagoon (Mosley et al. 2020). Furthermore, desired water level regimes for the South Lagoon are described in a recent review of the environmental water requirements for the CLLMM (Gehrig et al. 2020).

The current primary ecosystem management ‘levers’ available to managers of the Coorong include inflows from the Murray River and Salt Creek and seawater inflows (connection via Murray Mouth). A range of addition management interventions/options are being explored to help with South Lagoon restoration as part of the *Coorong Infrastructure Investigations Project* of the HCHB program. The ecological relationships and food web models that will be built through *Component 3 Food web* will provide an important decision support tool to assess the food web response to potential management scenarios (inflows, management interventions/options). The outcomes of these models will provide a basis for assessing and optimising different management options, and identify those that will maximise the ecological outcomes for the Coorong, particularly concerning the ecological restoration of the food web of the South Lagoon.

Glossary

Benthic	Of or associated with the sediment at the bottom of an estuarine or marine system
Bentho-pelagic	Living and feeding near the bottom, as well as mid-water or near the surface
Bioenergetics	The biological transfer and store of energy in food that is taken up by consumption in animals, measured in kilojoules and/or calories
Bioenergetic quality (or energy content)	A measure of energy (KJ/g dry mass) in a food item
Biomass	The total mass of living organisms (plants or animals) in a sampled area, measured as wet, dry or ash free dry mass
CLLMM	Coorong, Lower Lakes and Murray Mouth
Copepod	A microcrustacean that is typically pelagic in habit, but may be benthic
CPUE	‘Catch Per Unit Effort’, a measure of abundance
Decapod	An order of crustacean that includes crabs, prawns and shrimps
Detritivore	A consumer that that feeds predominantly on detritus
Fish, large-bodied	Fishes that have a maximum adult size typically >250 mm in total length
Fish, medium-bodied	Fishes that have a maximum adult size typically 150–250 mm in total length
Fish, small-bodied	Fishes that have a maximum adult size typically ≤150 mm in total length
Food web model, conceptual	Diagrammatic overview of the main concepts, current knowledge, and potential knowledge gaps of food webs
Food web model, quantitative	Data supported model based on multiple data sources to provide a plausible food web based upon different scenarios of ecosystem drivers (e.g. barrage flows)
Food web model, mass-balance	Models that include biomass, production (input and export), consumption, diet composition, and fisheries catch data to estimate flows throughout the food web by using linear equations and algebra to balance inputs and outputs
Foraging	The process of searching for food
Gizzard	A digestive organ, common in birds, used for breaking down food items such as vegetation
Haney trap	A box-like device used for sampling zooplankton in pelagic habitats
HCHB	Healthy Coorong Healthy Basin
Herbivore	A consumer that feeds predominantly on vegetation (plants and algae)
Hysteresis effect	Hysteresis is where the observed equilibrium of a system cannot be predicted solely based on environmental variables, but also requires knowledge of the system's past history
Hypersaline	High in salt concentration, i.e. salinity >60 psu

Intertidal	The area of the shore between the low and high water level that is regularly submerged and exposed by rising and falling tides
Insectivore	A consumer that that feeds predominantly on insects
Macroinvertebrate	Invertebrate fauna that are retained on sieve mesh size greater than 0.5 mm
MDB	Murray-Darling Basin
Microcrustacean	Crustacean that is small in size, typically less than 1 mm
Millennium Drought	The drought that affected southern Australia (e.g. Murray-Darling Basin) from 2001 to 2010
Obligate/obligatory (diet)	Obligatory is the reliance on a particular item or group of items, e.g. an obligate herbivore feeds exclusively on vegetation, while a facultative herbivore feeds predominantly on vegetation, but may also feed on other items, e.g. small animals
Omnivore	A consumer that that feeds on vegetation or detritus, and animal items
Opportunistic species	Species that can easily adapt to new habitats or environmental conditions. They usually produce many offspring and have high growth rates
Pelagic	Organisms that are mainly associated with the water column and do not interact as often with the bottom of an estuary
Piscivore	A consumer that feeds predominantly on fish
Planktivore	A consumer that primarily feeds upon the plankton
Plankton	Organisms that are found in the water column (pelagic) and are typically small in size (i.e. microscopic). This group includes phytoplankton and zooplankton
Productivity	Energy (e.g. calories) and its movement into, out of and within (e.g. across levels) food webs. The rate of secondary production which can be derived from annual production-to-biomass ratios
psu	Practical salinity unit
Region (geomorphic)	Spatial units, based on geomorphology, that divide the Coorong estuary. For the Coorong, moving from North to South, these are: the Murray Mouth and Estuary, North Lagoon and South Lagoon regions
Scat	Animal faeces
Shorebirds	A group of birds that often forage along the shoreline/intertidal zone of a waterbody. Shorebirds are often relatively small in size and may be migratory
Spatial	Refers to the dimension of space or area
Stable isotopes	Components of elements (e.g. carbon) that are not susceptible to radioactive decay, thus they are classified as stable
Subtidal	A spatial zone that describes an area of habitat that is always underwater, i.e. below the low water mark
T&I	Trials and Investigations
Taxa	Plural version of taxon. Group of organisms that are similar in structure and function, and characterised by common ancestors
Temporal	Refers to the dimension of time
TLM	The Living Murray

Trophic	Feeding and nutrition of plants and animals and where they fit into niches and levels of the food web
Waterbirds	A group of birds that are aquatic, i.e. live around the water. This group includes shorebirds
Waterfowl	A group of waterbirds that include ducks, geese and swans
Zooplankton	Animals (often microscopic) that either move by water currents or are weak swimmers in the water column and can spend partial or complete lives in the plankton
Zooplanktivore	A consumer that feeds predominantly on zooplankton
Zoobenthivore	A consumer that feeds predominantly on benthic invertebrates

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Appendix A – Fish catch summary 2007–2020

Figure A.1. Fish catch summary by seine net in the Coorong from 2007–2020. ME = Murray Estuary, NL = North Lagoon, SL= South Lagoon. Sampling occurred in March except for 2012 and 2013, which were in February. Data sources: Noell et al. (2009), Ye et al. (2016, 2020).

	2007				2008				2009				2010				2011				2012				2013				2014			
	ME	NL	SL	Total	ME	NL	SL	Total	ME	NL	SL	Total	ME	NL	SL	Total	ME	NL	SL	Total	ME	NL	SL	Total	ME	NL	SL	Total	ME	NL	SL	Total
Small-bodied species																																
Australian anchovy	1			1										1		1													3			3
Australian smelt																	700	321		1,021	146	8		154	47	36		83	5			5
Blue sprat														1		1																
Bluespot goby																										1		1		31		31
Bridled goby																	8			8	3	2		5	4	18	7	29	201	141		342
Common galaxias					1			1									7			7	3			3								
Dwarf flat-headed gudgeon																																
Flat-headed gudgeon																	107			107	5			5	5	1		6	1			1
Scary's Tasman goby	2	1		3														4		4	4	29		33	5	69		74	57	221		278
Sandy sprat	823	8		831										14		14	75			75	4,376	1,926	1,940	8,242	1,435	3,020	580	5,035	72,952	425		73,377
Smallmouth hardyhead	101	1,323	363	1,787	4	16,400	17	16,421		788		788		2,750		2,750	423	15,560	17,290	33,273	27	1,177	8,954	10,158	370	2,848	14,435	17,653	861	13,975	21,070	35,906
Tamar goby	14	32		46						1		1					68			68	10	1		11	22	96		118	176	190		366
Total	**941**	**1,364**	**363**	**2,668**	**5**	**16,400**	**17**	**16,422**		**789**		**789**		**2,766**		**2,766**	**1,388**	**15,885**	**17,290**	**34,563**	**4,574**	**3,143**	**10,894**	**18,611**	**1,888**	**6,089**	**15,022**	**22,999**	**74,256**	**14,983**	**21,070**	**110,309**
Number of species	5	4	1		2	1	1			2				4			7	3	1		8	6	2		7	8	3		8	6	1	
Medium and large-bodied species																																
Australian herring	1			1	1			1																								
Australian pilchard																																
Black bream	5			5																									1			1
Bony herring																	1,589	75		1,664	1,444	41	1	1,486	21	7	1	29	14	2		16
Carp																	96			96												
Congolli		3		3										1		1	18	6		24	2	24		26	17	115	29	161	5	328	2	335
Golden perch																	9			9												
Goldspot mullet																																
Greenback flounder	9	7		16	10	2		12		7		7		5		5		3		3	15	14		29	5	49		54	12	8		20
King George whiting																																
Little weed whiting																													1			1
Longsnout flounder					10			10													6	6		12		12		12	3			3
Red gurnard																																
Redfin perch																	191	1		192	8			8								
River garfish	66	13		79	115			115		2		2		30		30	58	1		59	3	29	1	33	34	9		43	62	36		98
Sea mullet																																
Soldier																													3			3
Southern crested weedfish																																
Southern garfish	1			1	8			8																								
Tetraodontidae*	55	1		56	11			11		1		1		2		2						4		4	58	18		76	15	3		18
Yelloweye mullet	120	8		128	208	21		229		1		1		6		6	28	78		106	63	23	3	89	458	40	25	523	666	27	3	696
Western Australian salmon	166			166	25	1		26		1		1		2		2					4	2		6	21			21	19			19
Total	**423**	**32**		**455**	**388**	**24**		**412**		**12**		**12**		**46**		**46**	**1,989**	**164**	**-**	**2,153**	**1,545**	**143**	**5**	**1,693**	**614**	**250**	**55**	**919**	**801**	**404**	**5**	**1,210**
Number of species	**8**	**5**			**8**	**3**				**5**		**5**		**6**			**7**	**6**	**-**		**8**	**8**	**3**		**7**	**7**	**3**		**11**	**6**	**2**	
Grand Total	**1,364**	**1,396**	**363**	**3,123**	**393**	**16,424**	**17**	**16,834**		**801**		**801**		**2,812**		**2,812**	**3,377**	**16,049**	**17,290**	**36,716**	**6,119**	**3,286**	**10,899**	**20,304**	**2,502**	**6,339**	**15,077**	**23,918**	**75,057**	**15,387**	**21,075**	**111,519**
Total Number of species	**13**	**9**	**1**		**10**	**4**	**1**			**7**		**5**		**10**			**14**	**9**	**1**		**16**	**14**	**5**		**14**	**15**	**6**		**19**	**12**	**3**	

Figure A.1. cont.

	2015				2016				2017				2018				2019				2020			
	ME	NL	SL	Total	ME	NL	SL	Total	ME	NL	SL	Total	ME	NL	SL	Total	ME	NL	SL	Total	ME	NL	SL	Total
Small-bodied species																								
Australian anchovy					24			24													18			18
Australian smelt	16			16	55			55	98			98												
Blue sprat					2			2					7			7	461	1		462				
Bluespot goby		4		4	15			15	3	4	16	23		53		53	2	14		16		36		36
Bridled goby	94	7		101	30	1		31					1	18		19	2	3		5	3	51		54
Common galaxias	12			12					21			21	4			4					1			1
Dwarf flat-headed gudgeon					1			1																
Flat-headed gudgeon	7			7					61			61	3			3	2			2	1			1
Scary's Tasman goby		5		5	1			1	5			5	2			2	3	102		105		154		154
Sandy sprat	152	354		506	16,183	949		17,132	2,698	90		2,788	4,237	47		4,284	2,263	3,678		5,941	14,712	7,597		22,309
Smallmouth hardyhead	663	2,186	9,135	11,984	2,601	7,350	24,735	34,686	8,130	8,780	20,290	37,200	4,823	2,056	9,950	16,829	3,283	8,885	20,010	32,178	364	26,710	17,060	44,134
Tamar goby	688	62		750	365	1,226		1,591	1,375	152		1,527	133	127		260	154	23		177	6	2		8
Total	**1,632**	**2,618**	**9,135**	**13,385**	**19,277**	**9,526**	**24,735**	**53,538**	**12,391**	**9,026**	**20,306**	**41,723**	**9,210**	**2,301**	**9,950**	**21,461**	**6,170**	**12,706**	**20,010**	**38,886**	**15,105**	**34,550**	**17,060**	**66,715**
Number of species	7	6	1		10	4	1		8	4	2		8	5	1		8	7	1		7	6	1	
Medium and large-bodied species																								
Australian herring																								
Australian pilchard					1			1																
Black bream													10	7		17	56			**56**		**2**		**2**
Bony herring	253	87	2	342	51	39		90	1,728	61		1,789		1		1	17			**17**	**187**			**187**
Carp																								
Congolli	48	43	2	93	29	7	1	37	6	144	24	174	16	69	18	103	14	154	1	169	21	127		148
Golden perch																								
Goldspot mullet					2			2													1			1
Greenback flounder	18	19		37	5	5		10					8	20		28	13	12		25	7	5		12
King George whiting													10			10	2			2				
Little weed whiting																								
Longsnout flounder	7			7									1			1					1			1
Red gurnard																					1			1
Redfin perch																								
River garfish	1	19	1	21	12	1		13	30	145		175	7	2		9	12	2		**14**	**8**	**21**		**29**
Sea mullet															1	1								
Soldier	1			1									1			1	1			**1**	**2**			**2**
Southern crested weedfish	1			1																				
Southern garfish																					5			5
Tetraodontidae*	86	4		90	4			4	7	2		9	15			15	29	6		35	45	1		46
Yelloweye mullet	177	37	13	227	179	6		185	1,871	122		1,993	73	47	59	179	428	75	17	520	797	15		812
Western Australian salmon	3			3										3		3					**132**			**132**
Total	**595**	**209**	**18**	**822**	**283**	**58**	**1**	**342**	**3,642**	**474**	**24**	**4,140**	**141**	**149**	**78**	**368**	**572**	**249**	**18**	**839**	**1,207**	**171**	**-**	**1,378**
Number of species	**10**	**6**	**4**		**8**	**5**	**1**		**5**	**5**	**1**		**9**	**7**	**3**		**9**	**5**	**2**		**12**	**6**	**-**	
Grand Total	**2,227**	**2,827**	**9,153**	**14,207**	**19,560**	**9,584**	**24,736**	**53,880**	**16,033**	**9,500**	**20,330**	**45,863**	**9,351**	**2,450**	**10,028**	**21,829**	**6,742**	**12,955**	**20,028**	**39,725**	**16,312**	**34,721**	**17,060**	**68,093**
Total Number of species	**17**	**12**	**5**		**18**	**9**	**2**		**13**	**9**	**3**		**17**	**12**	**4**		**17**	**12**	**3**		**19**	**12**	**1**	

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