Food resource availability, energy content and nutritional value of major food sources for key fish and waterbird species under varying environmental conditions in the Coorong

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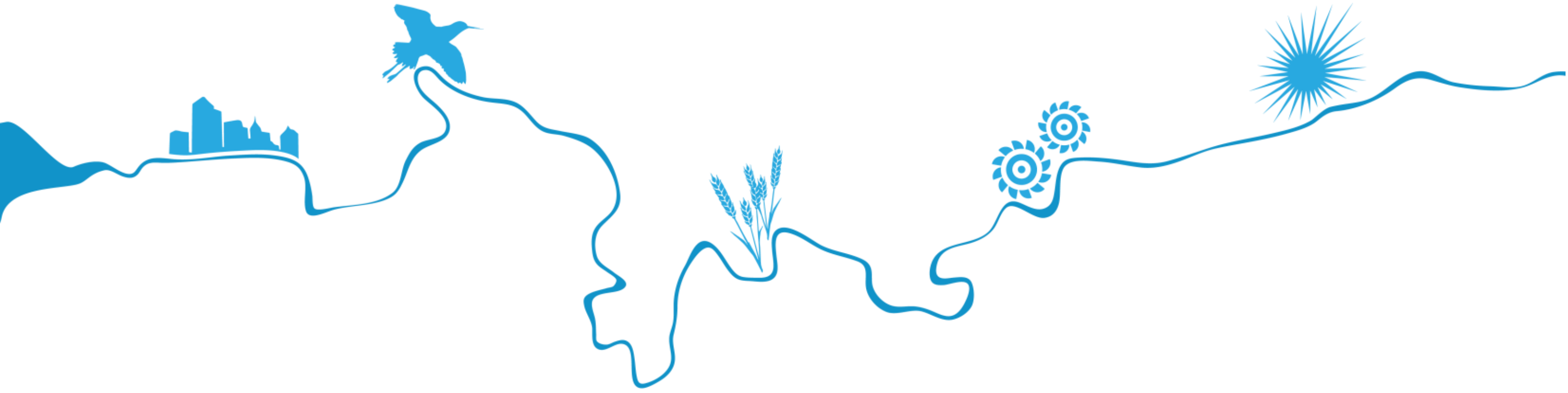

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WATER FOR CITIES AND PEOPLE

WATER FOR THE ENVIRONMENT

WATER FOR AGRICULTURE

WATER FOR MINING

CLIMATE RESILIENCE

Disclaimer

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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.

Executive summary

The Coorong is an internationally recognised estuary and lagoon wetland at the downstream end of the Murray-Darling Basin that has experienced declining ecological condition over several decades. The Healthy Coorong, Healthy Basin (HCHB) program aims to restore and maintain the ecological condition of the Coorong by providing evidence-based solutions to both immediate threats and future conditions anticipated under climate change. The Phase One Trials and Investigations (T&I) project of the Healthy Coorong, Healthy Basin (HCHB) program consists of a series of integrated components that collectively provide knowledge to inform the future management of the Coorong. *Component 3 – Restoring a functioning Coorong food web* forms part of the T&I project. It included four main activities: a review and synthesis of existing data and knowledge on the food web in the Coorong; investigations into the diet and food consumption of key waterbird and fish species; assessing bioenergetics and key drivers for food resource availability; and development of a quantitative food web model.

The aim of *Component 3* was to understand the food web dynamics in the Coorong, by analysing the environmental conditions required to increase the food resource availability, diversity of prey items and the energy supply for key biota (waterbirds and fish). Outcomes from the empirical investigations on food resources will inform an integrated quantitative food web model that can assess food web responses to various conditions (e.g. through management actions and interventions). This report presents findings which focussed on habitat requirements and key environmental drivers for spatial and temporal trends in food resource availability (i.e. abundance, biomass, distribution) and bioenergetics of key food resources.

Field investigations were carried out throughout the Coorong from the South Lagoon into the Murray Estuary from February 2020 to December 2021, with high frequency (monthly) sampling for macroinvertebrates and seasonal sampling for zooplankton and fish. The Coorong is characterised by a salinity gradient from brackish-marine at the Murray Estuary to hypersaline in the South Lagoon, and distinct communities characterised each region of the Coorong (Murray Estuary, North Lagoon and South Lagoon). Diversity and individual densities of zooplankton, macroinvertebrates and fish were generally higher in the Murray Estuary and North Lagoon than in the South Lagoon. For macroinvertebrates and fish, biomass densities for most species were also higher in the Murray Estuary and North Lagoon.

Size classes and trophic groups of macroinvertebrates and fish were differentiated. Macroinvertebrates of all size classes were abundant in the Murray Estuary and occurred at the sediment surface or in greater sediment depth. Macroinvertebrates in the South Lagoon were small and occurred only at the surface. Small-bodied fish in the South Lagoon were dominated by smallmouth hardyhead, while sandy sprat were the most abundant small-bodied species in the Murray Estuary, where large-bodied fish species occurred as well. Food availability for planktivorous and benthivorous fish contributed to explain some of the fish community pattern across the regions. There was less choice of prey types for benthivorous fish and shorebirds in the South Lagoon, which was characterised by a food web low in diversity, abundance, and biomass (except for the highly salt-tolerant fish species, smallmouth hardyhead), and with low energy density for higher trophic levels. A greater diversity of prey was available in the Murray Estuary, supporting predators that exhibit a range of foraging strategies.

The period of study coincided with good winter and spring inflows (>100 GL/month) from the River Murray in 2020, and stronger inflow (>400 GL/month) since winter 2021 following the onset of La Niña conditions. In addition to higher flow over the barrages into the Coorong, water release also occurred through Salt Creek into the South Lagoon in spring 2021 following the higher rainfall from La Niña. Environmental conditions throughout the Coorong changed as a result of the greater volumes of freshwater inflows, which reduced salinities and raised water levels. Yet, the inflows increased turbidity of the water, especially in the Murray Estuary.

Flow-related patterns in abundance explained most of the temporal variability within each region over the surveys for zooplankton, macroinvertebrates and fish. Higher flow, including higher water release from Salt Creek, was followed by increases in the diversity and individual densities of zooplankton, macroinvertebrates, and fish. The South Lagoon communities of zooplankton, macroinvertebrates and fish were more similar to those in the North Lagoon when higher water releases from Salt Creek occurred in spring 2021. Freshwater

influx from the River Murray through the barrages also brought additional freshwater fish into the Murray Estuary and further diversified prey availability to piscivorous predators.

Salinity emerged as the strongest environmental driver affecting the food web. Analyses linking the communities of macroinvertebrates and fish with environmental conditions revealed that salinities of >64-66 ppt (parts per thousand) defined the distinct differences between communities occurring in the South Lagoon from those in the North Lagoon and Murray Estuary. For individual species of macroinvertebrates and fish, a pronounced decrease in densities of individuals and biomass emerged when salinities exceeded 50-60 ppt, and highest densities recorded at salinities <40 ppt. Communities characterised by high diversity and density of individuals and biomass of macroinvertebrate prey were found at marine to brackish salinities <34 ppt.

The investigations provided not only critical data and understanding of the diversity, abundance and biomass and their environmental drivers for the Coorong food web, but also on Coorong-specific values for production, production to biomass (P:B) ratios and energy density determined by calorimetry. The equations to convert between individual counts, wet and dry mass for macroinvertebrates, and between wet and dry mass for fish, together with calorific content of species and trophic groups obtained by bioenergetic analyses, provide a tool kit for future food web analyses of the Coorong and beyond.

Production was highest for 'Benthic micro-molluscs' (including *Arthritica semen*) and benthic-pelagic crustacea (mainly amphipods). Production of 'Insect larvae/pupae' (mainly chironomids) was low while the P:B ratio was high relative to other Coorong macroinvertebrate taxa, but low compared to literature values for this group. Average calorific values were lowest for plankton (6.06 ± 1.12 kJ g^{-1} dry mass DM, mean ± standard error) and the seagrass *Ruppia* (10.09 ± 0.77 kJ g^{-1} DM), ranged from about 9–16 kJ g^{-1} DM for different macroinvertebrate species (averaged over all macroinvertebrates: 12.28 ± 0.56 kJ g^{-1} DM), and were highest for fish (averaged over all fish: 18.77 ± 0.21 kJ g^{-1} DM). Energy density of macroinvertebrate prey was low in the South Lagoon (mean 3.59 ± 0.40 kJ m^{-2}) and high (mean 355 ± 18.49 kJ m^{-2}) in the Murray Estuary, where 'Benthic micro-molluscs' provided the greatest contribution to energy density complemented by energy densities of other trophic groups, that were absent in the South Lagoon. Yet, crude lipid and protein contents were lower for taxa amongst the 'Benthic micro-molluscs' than for amphipods and benthic annelids.

The nutritional value of some fish varied with season and fish size, reflecting reproductive activities and ontogenetic diet shifts. Smallmouth hardyhead were important prey in the South Lagoon, but their nutritional quality (protein content) was low in summer. For fish, energy densities were more similar across the regions than for macroinvertebrates, due to high energy density by smallmouth hardyhead in the South Lagoon, and high energy densities by a range of other fish trophic groups in the Murray Estuary and North Lagoon.

Freshwater flow through the barrages and from Salt Creek were associated with a reduction in salinity that had a strong influence on prey availability and energy provision for planktivorous and benthivorous predators as well as piscivorous waterbirds in the Coorong. Higher freshwater flow through the barrages and from Salt Creek was associated with a reduction in salinity that had the strongest influence on the diversity and abundance of food availability and energy provision for planktivorous and benthivorous predators as well as piscivorous waterbirds in the Coorong. The higher complexity of the food web enabled by marine to brackish environmental conditions will make the food web more resilient than under hypersaline conditions. Lowering salinity in the South Lagoon (<60 or ideally <40 ppt) can increase food resources for key fish and waterbird species, as shown for the management of other hypersaline systems. The ecological improvements that emerged after higher flows during our study period are encouraging in that recovery can be supported by continuous and higher freshwater input to the Coorong.

Acknowledgments

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1 Introduction

1.1 Background

The Coorong is culturally, environmentally, and economically important at local, national, and international scales but has experienced a long-term decline in its ecological condition due to reductions of inflows (Brookes et al. 2018; Mosley et al. 2018). Whilst there has been recovery of some elements of the Coorong ecosystem associated with increased inflows since the Millennium Drought ended in 2010 (Dittmann et al. 2015; Hemraj et al. 2017; Brookes et al. 2022), the South Lagoon has not recovered to the levels expected. There has been a switch of the ecosystem from being dominated by aquatic plants to algae associated with eutrophication (nutrient enrichment), with subsequent impacts on macroinvertebrates, fish and waterbirds (Brookes et al. 2018). These changes in the ecosystem and the lack of recovery are likely caused by several complex, interacting factors, which are not well understood. 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 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* forms part of the T&I project. The aim was to understand food web dynamics in the Coorong, by analysing the environmental conditions required to increase the food resource availability, diversity of prey items and the energy supply for key biota (waterbirds and fish). Outcomes from the empirical investigations on food resources will inform an integrated quantitative food web model that can assess food web responses to various conditions (e.g. through management actions and interventions).

A part of food web dynamics is resilience, the capacity of an ecosystem to return to a reference state or dynamic after a disturbance (Rombouts et al. 2013). A functioning and resilient food web is critical to the ecological character of the Coorong through the production and supply of energy to key biota, including waterbirds and fish (Giatas et al. 2018; Ye et al. 2020). In particular, the South Lagoon food web has not recovered from decades of declining ecological conditions (Brookes et al. 2018). The key management questions relating to food webs in the Coorong, which informed this body of work were:

- How should barrage inflows, South East flows and the Murray Mouth dredging regime be managed in order to restore a functioning South Lagoon food web that supports diverse and abundant waterbirds and fish, including those species historically abundant or present?
- What are the implications of any proposed future management interventions on the food web that supports waterbirds and fish?

The *Component 3 – Restoring a functioning Coorong food web* included four main activities: a review and synthesis of existing data and knowledge on the food web in the Coorong (Ye et al. 2020); investigations into the diet and food consumption of key waterbird and fish species (Giatas et al. 2022); assessing bioenergetics and key drivers for food resource availability; and development of a quantitative food web model. This report presents outcomes of the investigations into the bioenergetics and key drivers for food resource availability.

1.2 Aims

To address key knowledge gaps and management questions about the Coorong food web described above, the investigations in this body of work aimed to:

- Determine food resource habitat requirements and key environmental factors influencing the spatial and temporal trends of abundance, biomass and distribution.
- Quantify food resource availability, productivity and bioenergetic quality.

This final technical report presents the results of work completed during the period from February 2020 to April 2022.

2 Methods

To determine key drivers for food resource availability and bioenergetics, our approach included investigating the variability in zooplankton, macroinvertebrate, and fish prey and determining the energy content and nutritional value of these major food resources. The sampling design and methods reported here were established during the food web investigation of Phase Zero of HCHB (Ye et al. 2019), and the early stage of Phase One (February and March 2020). Samples for bioenergetic analyses were obtained from field work for food resource availability.

2.1 Study sites

Field investigations were undertaken along the Coorong to assess the abundance and diversity of key food resources across the salinity gradient. This enabled the assessment of the influence of salinity, and other environmental conditions (e.g. water temperature, pH, dissolved oxygen DO, turbidity) on food abundance, diversity and quality, and to assess the changes in relation to management actions (e.g. freshwater inputs from the River Murray to the Coorong and from Salt Creek to the southern part of the South Lagoon).

The sampling sites for zooplankton, macroinvertebrate and fish surveys overlapped as much as feasibly possible (Figure 1; Appendix Table A.1). For seasonal fish sampling, twelve sites were surveyed in the Coorong, with four sites in each region (Murray Estuary, North Lagoon and South Lagoon). In the South Lagoon, the sites for fish sampling were Salt Creek, Jack Point, Villa de Yumpa and Hells Gate. Four sites were located in the North Lagoon: Mount Anderson, Noonameena, Long Point and Mark Point. In the Murray Estuary, sites were Pelican Point, Godfrey's Landing, Boundary Creek and Beacon 19). Seasonal zooplankton sampling was conducted at a subset of seven sites, three in the South Lagoon (Salt Creek, Jack Point and Hells Gate) and two each in the North Lagoon (Noonameena and Long Point) and Murray Estuary (Pelican Point and Beacon 19). Monthly macroinvertebrate surveys occurred at the same seven sites as for zooplankton sampling. Macroinvertebrates were also sampled at two additional sites where fish sampling occurred for some seasonal surveys: at Mount Anderson (December 2020, March and June 2021) and Mark Point (March and June 2021).

Macroinvertebrate samples were taken from three different zones per site: samples were taken at exposed mudflats on either side of the main Coorong Lagoon channel (referred to as 'Intertidal' (I), taken from the eastern side of the channel; and 'Peninsula' (P), taken from the western side of the channel); as well as samples of subtidal sediments within the channel ('Subtidal' (S)). Note that the terms 'intertidal' and 'subtidal were used for all regions, despite the tidal influence in the Murray Estuary being microtidal and tides not reaching beyond the North Lagoon. Figure 2 shows the bathymetry at the sampling locations across the zones for all surveys. This sampling design allowed assessment of the potential macroinvertebrate prey availability for birds and fish respectively. Exposed mudflat sediments were either intertidal (in the Murray Estuary) or wetted episodically subject to wind seiching and water level changes in the Coorong. In the Murray Estuary and North Lagoon, exposed mudflats were sampled on either side of the main channel (mainland shore, peninsula). In the South Lagoon, mudflats were sampled on foot on the north-eastern shoreline, while sampling of sediments in the channel occurred from a small boat in 1.5 to 2.5 m water depths at Hells Gate, or by wading into the water as deep as safely possible (knee to hip depth) at sites where the boat could not be launched. The peninsula zones were not sampled in the South Lagoon as the boat could not be safely launched or operated. The Noonameena peninsula site could not be accessed in June 2021 due to a boat engine failure.

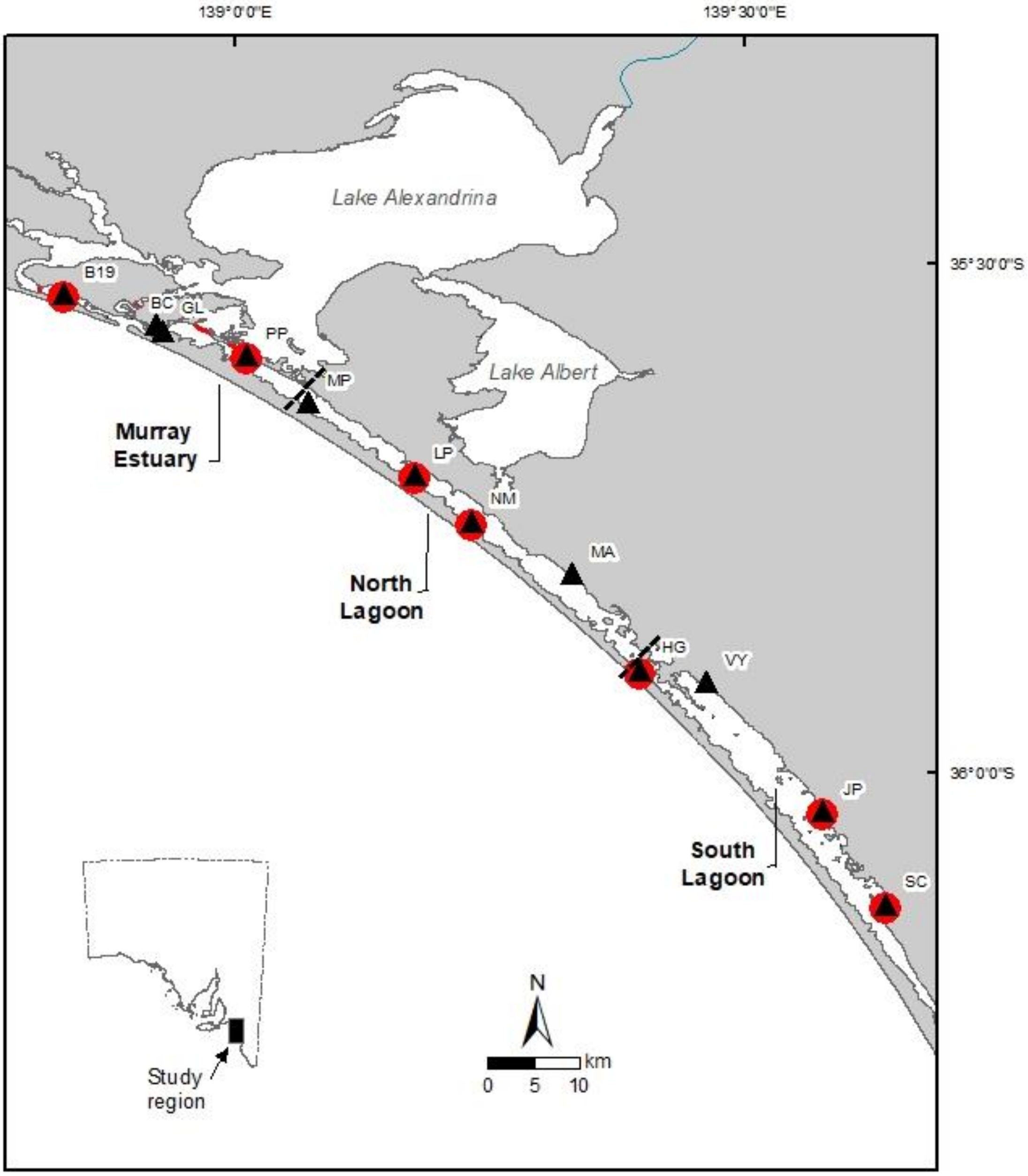

Figure 1. Macroinvertebrate/zooplankton (red circle) and fish (black triangle) sampling sites in the Coorong during 2020-2021. SC=Salt Creek, JP=Jack Point, VY=Villa de Yumpa, HG=Hells Gate, MA=Mt Anderson, NM=Noonameena, LP=Long Point, MP=Mark Point, PP=Pelican Point, GL=Godfrey's Landing, BC=Boundary Creek, B19=Beacon 19. Three regions (separated by black dashed lines) include South Lagoon, North Lagoon and Murray Estuary.

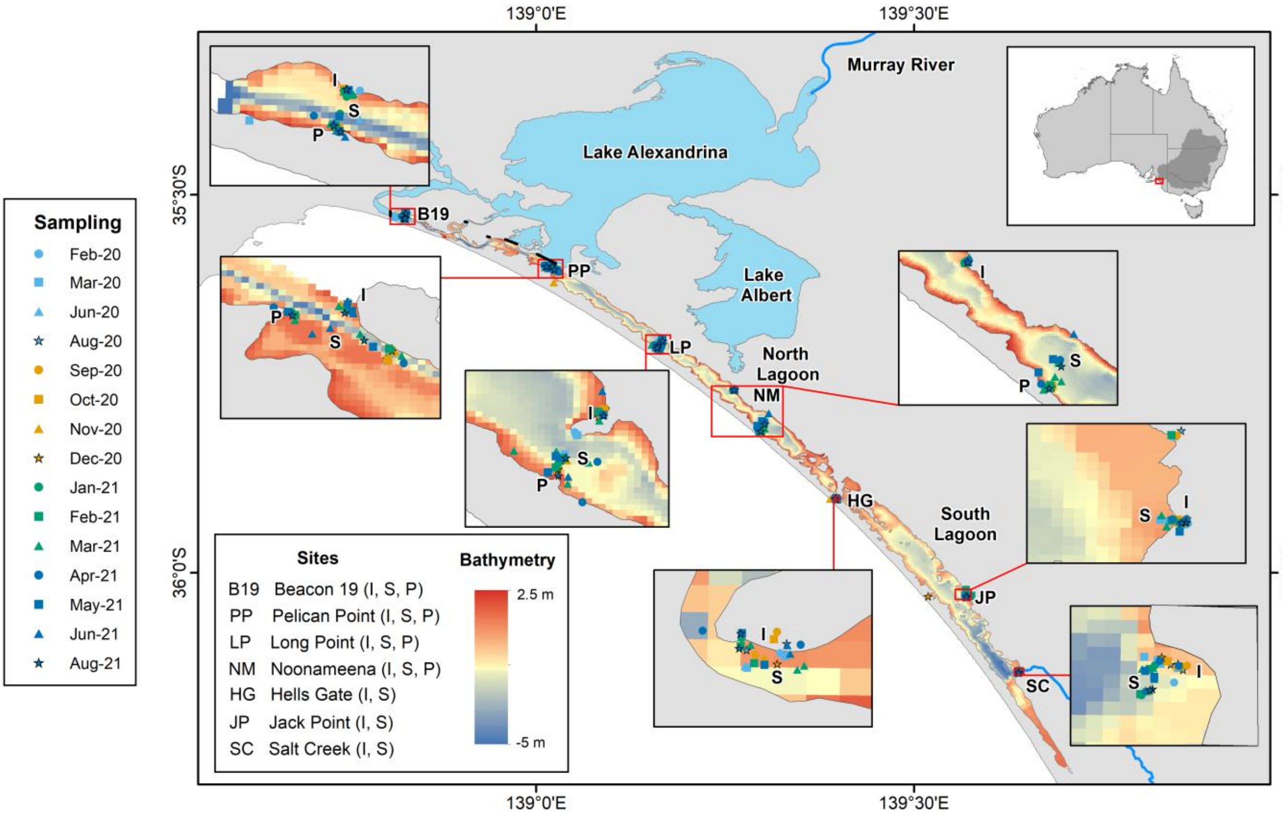

Figure 2. Macroinvertebrate sampling sites in the Coorong during 2020-2021 (see Table 2 for detail) with zones (I=Intertidal mudflat, S=Subtidal sediment, P=Peninsula mudflat) and underlying bathymetry metres in Australian Height Datum (m AHD) (Hobbs et al. 2019). SC=Salt Creek, JP=Jack Point, HG=Hells Gate, NM=Noonameena, LP=Long Point, PP=Pelican Point, B19=Beacon 19. MA=Mt Anderson (zone S) and MP=Mark Point (zones S and P) were sampled for seasonal surveys and are not included on the map.

2.2 Field investigations

2.2.1 Sampling dates

Sampling for food resource availability commenced in February 2020 for macroinvertebrates and occurred on a regular basis from mid-2020, with some interruptions from the COVID-19 pandemic. Sampling for zooplankton and fish was carried out seasonally from March 2020 (Table 1). Macroinvertebrates were surveyed in four-weekly intervals for calculation of production and production:biomass (P:B) ratios from August 2020 to August 2021, with additional seasonal surveys before and after this intensive sampling period (Table 2). The four-weekly intervals resulted in two surveys carried out in March 2021, indicated by Mar(1)-2021 and Mar(4)_2021. Macroinvertebrate sampling occurred within the same fortnight as the fish and zooplankton sampling and was conducted simultaneously at sites where possible. The sampling in December 2020 and 2021 was mostly carried out in conjunction with the macroinvertebrate and mudflat monitoring of The Living Murray (TLM), as the intertidal zone (zone 'I') of four sites overlapped. To align with the sites for fish sampling, samples were also taken at Mt Anderson in December 2020, and March, June, September and December 2021, and at Mark Point (peninsula) in March, June, September and December 2021.

For fish, eight seasonal sampling trips were conducted (March 2020 (autumn), June 2020 (winter), September 2020 (spring), December 2020 (summer), March 2021 (autumn), June (winter), September 2021 (spring) and December 2021 (summer)), noting the sampling during March 2020 and 2021 was carried out in conjunction with TLM fish condition monitoring.

Table 1. Sampling dates of all surveys for fish and zooplankton in each region of the Coorong, and number of samples taken (NF – for fish; NZ – for zooplankton).

SEASON	SOUTH LAGOON	NORTH LAGOON	MURRAY ESTUARY	NF	NZ
Autumn	13-14/03/2020	13-14/03/2020	16-19/03/2020	36	21
Winter	11-12/06/2020	11-12/06/2020	16-18/06/2020	30	21
Spring	15-16/09/2020	15-16/09/2020	22-24/09/2020	30	21
Summer	02-04/12/2020	02-04/12/2020	08-10/12/2020	36	21
Autumn	02-04/03/2021	02-04/03/2021	10-12/03/2021	36	21
Winter	21-22/06/2021	21-22/06/2021	15-18/06/2021	36	21
Spring	06-08/09/2021	06-08/09/2021	13-15/09/2021	36	21
Summer	07-09/09/2021	07-09/09/2021	13-16/09/2021	36	21

Table 2. Sampling dates of the surveys for macroinvertebrates for each region of the Coorong, and number of samples taken (N). Higher number of samples were taken for seasonal surveys where samples for calorimetry were taken, and additional sampling sites included to align with surveys for fish. On some occasions, not all sites could be reached due to boating/access issues. Because of four-weekly intervals, two surveys were carried out in March 2021.

SURVEY	SOUTH LAGOON	NORTH LAGOON	MURRAY ESTUARY	N
Feb-20	4/02/2020	5/02/2020	4-5/02/2020	75
Mar-20	11/03/2020	11-12/03/2020	10/03/2020	100
Jun-20	16/06/2020	16-17/06/2020	15/06/2020	90
Aug-20	25/08/2020	25-26/08/2020	24/08/2020	84
Sep-20	22-23/09/2020	23/09/2020	24, 28/09/2020	105
Oct-20	15, 19/10/2020	15-16/20/20	15-16/10/2020	84
Nov-20	10/11/2020	9-10/11/20	9/11/2020	84
Dec-20	3/12/2020	3-4, 8/12/2020	4, 8/12/2020	124
Jan-21	4-5/01/2021	4,5/01/21	6/01/2021	84
Feb-21	3/02/2021	3/02/2021	1/02/2021	84
Mar(1)-21	1/03/2021	2-3, 10/03/2021	3, 10/03/21	144
Mar(4)-21	30/03/2021	29-30/03/2021	29/03/2021	84
Apr-21	28/04/2021	27-28/04/2021	27/04/2021	84
May-21	27/05/2021	27-28/05/21	24/05/2021	84
Jun-21	23/06/2021	21-22/06/2021	21, 29/06/2021	139
Aug-21	5/08/2021	5-6/08/2021	6/08/2021	84
Sep-21	7/09/2021	6-8/09/2021	8, 14/09/2021	84
Dec-21	7-8/12/2021	7-9/12/2021	6-7/12/2021	144

2.2.2 Field methods

Environmental conditions

Water quality variables were measured in the field during sampling events. At each sampling site for fish and zooplankton, water quality parameters (i.e. salinity, temperature, pH and dissolved oxygen (DO)) were recorded using a TPS water quality meter and water transparency was measured with the aid of a Secchi disc at each site on each fish sampling occasion. The macroinvertebrate survey team measured water quality (salinity, temperature, pH and DO with a Hannah Multiparameter probe, and salinity additionally with a handheld refractometer for hypersaline waters. From August 2021, salinity was also recorded with a digital seawater refractometer (Hanna Instruments HI96822). DO and water temperature were also measured with an OxyGuard probe, and after August 2021 using a Hanna DO meter. The salinity and DO measurements by the macroinvertebrate and fish survey teams aligned well (Appendix Figure A.1), with some deviations possibly due to changing salinity with water releases during the seasonal survey, or for DO due to different times of day for sampling at field sites. Salinity was measured as unitless practical salinity (UNESCO 1985) but for reader clarity, values are presented throughout the report in parts per thousand (ppt). DO was recorded as concentration and saturation. Additional data on flow over barrages, salinity and water level were obtained from DEW or downloaded from 'Water Data SA' (https://water.data.sa.gov.au) to relate food availability to environmental conditions.

Samples for sediment grain size composition and organic matter content were taken at the macroinvertebrate sampling sites during seasonal surveys. Three replicate samples were taken per site and zone for grain size, using a cut off plastic syringe as corer with 6.6 cm^2 surface area to 4-5 cm sediment depths, and for organic matter using a smaller cut-off syringe with 1.8 cm^2 surface area, also to 4-5 cm depths. All samples for sediment characteristics were stored frozen (-20 °C) until further analysis.

Zooplankton

Zooplankton samples were collected using a 4.5 L Haney trap and a 37 µm plankton net. At each site, three replicate composite trap samples were collected, with each ~18 L composite sample comprising two surface traps and two bottom traps where possible. The total volume of each replicate sample was concentrated to approximately 50 mL by filtering through a 37 µm net. Concentrated samples were transferred to a 200 mL PET jar, preserved with ~ 70% ethanol, and returned to the laboratory for identification. To aid species identification in the laboratory, a more concentrated sample was also collected at each site by towing the net close to the surface for approximately 50 m.

Macroinvertebrates

Samples for macroinvertebrates were taken using either a handheld PVC corer (83.32 cm^2 surface area) or an Ekman grab (225 cm^2 surface area), subject to water depth at the time of sampling and access by foot or boat respectively. Subsamples (6.6 cm^2 surface area to 5 cm depth) were taken from each corer or grab sample taken at sampling sites in the Murray Estuary and North Lagoon to quantify the highly abundant amphipods, polychaetes of the genus *Capitella*, and the micro-molluscs *Arthritica semen*. All samples were sieved through 500 µm mesh and rinsed using seawater into zip-lock bags. Samples for monthly productivity assessments were preserved in ethanol, and samples for seasonal bioenergetic analyses (see Section 2.3.3) were frozen (-20˚C) in a portable freezer before being stored in freezers (-20˚C) at Flinders University.

For monthly productivity sampling, 12 replicate samples were taken per site across the zones, with six replicates each for the exposed and subtidal sediments at the South Lagoon sites, and four replicates each across the exposed sediments of the mainland shore and peninsula, and subtidal sediments from the channel for the sites in the Murray Estuary and North Lagoon. For the seasonal sampling events, further (21-60) replicate samples were taken per site and frozen for calorimetric analyses (Table 2). In June and December 2021, additional live specimens of key macroinvertebrates were collected and freeze dried for analysis of lipid and protein contents.

Fish

At each site, sampling was conducted during the day using a standard seine net (61 m net length, 29 m wing length, 22 mm mesh, three m bund length (eight mm mesh); *n* = three hauls). The seine net was deployed in a semi-circle, which sampled to a maximum depth of two m and swept an area of ~592 m^2. All fish collected in each haul were identified to species, and the total number of individuals of each species recorded. In addition, the number of shore crabs (*Paragrapsus gaimardii*) caught in seine nets were recorded. A random subsample of 'key species', i.e. those likely to occur in the South Lagoon after ecosystem restoration (e.g. lower salinities) and known to be important food resource for higher level predators in other regions of the Coorong, were retained from each site. These key species were smallmouth hardyhead (*Atherinosoma microstoma*), yelloweye mullet (*Aldrichetta forsteri*), congolli (*Pseudaphritis urvillii*), sandy sprat (*Hyperlophus vittatus*), Tamar goby (*Afurcagobius tamarensis*), lagoon goby (*Tasmanogobius lasti*) and shore crab. Opportunistic samples were also collected for the following fish species: black bream (*Acanthopagrus butcheri*), mulloway (*Argyrosomus japonicus*), Western Australian salmon (*Arripis truttaceus*), greenback flounder (*Rhombosolea tapirina*), longsnout flounder (*Ammotretis rostratus*) and river garfish (*Hyporhamphus regularis*). All samples were kept frozen for later laboratory processing and analysis of nutritional values (energy content).

2.3 Laboratory analyses

2.3.1 Environmental conditions

Laboratory processes for sediment characteristics included determining grain size composition by laser diffraction using a particle size analyser (Malvern Mastersizer Model: 2000). Samples were defrosted and the fraction >1 mm sieved off manually to avoid blockage in the machine and weighed. To correct for this procedure, the weight of this fraction and of the remaining sediment were determined and normalised (emulated) in the dataset. Median (D_{50}) and sorting (σ_G) as well as the sorting coefficient (geometric (modified) Folk and Ward graphical measures) were determined and classified using the *Gradistat* program v8 (Blott and Pye 2001, 2012). The sediment organic matter content was determined as a bulk parameter in % dry weight (DW), after drying samples to constant weight on an Ohaus MB45 Moisture Balance before burning in a muffle furnace at 450 °C for five hrs. Sediment grain size and organic matter for December 2020 and June 2021 are presented in this report.

2.3.2 Abundance and biomass

Zooplankton

In the laboratory, the 200 ml quantitative samples were inverted three times and a 1 ml sub-sample transferred into a Pyrex gridded Sedgewick-Rafter cell. The entire sub-sample was counted, and zooplankton identified to the finest taxonomic level possible using a Leica compound microscope. The average number of zooplankton was calculated and expressed as numbers of individuals per cubic metre (individuals m^{-3}). Total densities and taxonomic richness include all rotifers, copepods, cladocerans and macroinvertebrates and microcrustacean densities include all copepods, cladocerans and ostracods present in the zooplankton samples.

Macroinvertebrates

In the laboratory, macroinvertebrates were sorted into species to the finest possible taxonomic level and counted using dissecting microscopes. Biomass was determined as wet and dry mass for each macroinvertebrate species and for each replicate sample from all sites. Wet mass was determined after blotting the organisms on Kimwipes to remove excess moisture before weighing (to within 0.0001 g). Samples for analysis of nutritional values (energy content) were then dried in an oven at 60 °C to constant weight. Samples for analysis of productivity were dried in a OHAUS moisture balance at 80 °C to constant weight. For small molluscs (e.g. *Arthritica semen*, Hydrobiidae, *Salinator fragilis*), biomass was determined with the shell, while the shell was removed for determining the biomass of larger bivalves (> 5 mm in size, e.g. *Hiatula alba, Spisula trigonella*). For *S. fragilis*, wet and dry weights were determined separately for shell and flesh for ten snails to obtain a correction factor for later calculations of energy density. Abundance was calculated as individuals per m^2, and biomass data as mass per m^2. Dried organisms were ground with a mortar and pestle and stored in plastic vials for calorimetry (see Section 2.3.3).

A total of 1,761 macroinvertebrate samples were collected between February 2020 and December 2021, and macroinvertebrate data up to August 2021 are presented in this report. Once sample processing for spring and summer surveys from 2021 is completed, the data will be presented in publications.

Macroinvertebrate species were grouped into prey type categories according to their habitat and size, as a possible indicator for their availability to predators. Species living mostly on top of the sediment or demersal (e.g. mysid shrimp) were classified as 'Epifauna'. Species living on the sediment surface or within the top 1–2 cm of the sediment were classified as 'Surface'; and those living deeper in the sediments to a depth of 2–20 cm as 'Deep'. The size (length) of organisms was also considered, with 'Small' = <1 cm, 'Medium' = ~ 1–2 cm, and 'Large' = >2 cm.

Fish

The samples of key species of fish collected at the seasonal surveys were defrosted in the laboratory. Each individual was measured for total length (TL) to the nearest millimetre (mm) and weighed to the nearest gram (g). The length and weight relationships were developed for key species. The individual species biomass (wet weight) was calculated using catch-per-unit-effort (CPUE) data (individuals per 1000 m^2) and mean fish weights, which were calculated based on the mean lengths and length-weight relationships. Dry biomass density was calculated based on wet biomass and percentage of weight left following oven drying. Both dry and wet biomass density (per 1000 m^2) were calculated using the area of water sampled via seine net (~592 m^2 per shot) and standardised to 1000 m^2.

2.3.3 Calorimetry

To determine the energy content (kJ/g mass per species) of food resources in the Coorong, calorimetry was used based on heat production of samples burned in a bomb-calorimeter (Glover et al. 2010; Van der Meer et al. 2013). Energy content was determined for zooplankton, the seagrass *Ruppia* and filamentous algae, detritus, macroinvertebrates, and fish. All zooplankton, macroinvertebrate, and fish samples were frozen in the field and stored at -20 °C until further processing to reduce any risk of energy density changes with dissolving of lipid in ethanol (Bertoli et al. 2018).

Sample material for calorimetry of macroinvertebrates was collected at seasonal surveys, where additional samples were taken (see Section 2.2.2). Opportunistic collection of some species occurred to get enough material for analyses. For meiofauna, subsamples had been taken from some of the macroinvertebrate samples and sorted live before freezing, but not enough material could be compiled for calorimetry. From some of the meiofauna samples, detrital material (Appendix Figure C.1) was separated under the microscope and frozen for obtaining a calorific value for detritus.

Ruppia and filamentous algae samples for calorimetry were taken in October 2020, and October and December 2021 from three sites in the South Lagoon (Salt Creek, Policeman Point and Parnka Point) and Noonameena in the North Lagoon. Additional filamentous algae samples were taken from Parnka Point in November 2021.

Plankton was obtained from plankton net samples (75 µm mesh size of cod end) taken in conjunction with macroinvertebrate monthly and seasonal surveys from September 2020 to December 2021 to obtain bulk material for plankton calorimetry.

Energy content is measured in the calorimeter based on dry mass (DM) and for macroinvertebrates, energy contents are mostly presented as kilojoules (kJ) per dry mass (DM), shell-free dry mass or ash-free dry mass (Brey et al. 2010; van der Meer et al. 2013). However, for the T&I Component 3 food web model, values were needed in relation to wet mass (WM). To convert the kJ g^{-1} DM to kJ g^{-1} WM, a ratio of DM/WM was calculated based on the respective mass determined during sample preparation for calorimetry.

Sample preparation

Frozen samples for macroinvertebrates were thawed just before sorting. All specimens were identified to the lowest possible taxonomic level and their individual abundance recorded. Specimens of each species per replicate sample were weighed for wet mass (e.g. to within 0.0001 g) after blotting dry for one minute to remove excess moisture (Bertoli et al. 2018). All samples were dried in an oven at 60˚C for up to 136 h, or until constant weight was recorded, and then stored in a desiccator. Dry mass was weighed on a micro balance (to 0.0001 g). In preparation for calorimetric analyses, each sample of dried material was ground to a powder consistency using mortar and pestle and then sealed in a plastic vial until processing in a bomb-calorimeter.

Fish samples were thawed, identified, and measured for lengths and weight. Subsamples were taken from larger fish while small fish were processed whole. On average, five g of wet fish tissue or whole organisms were used. Biomass was weighed for wet mass (0.001g) and dried in an OHAUS moisture balance at 80 °C to constant weight. Dried samples were pulverised and homogenised using a mortar and pestle. For samples of larger individuals of fish, biomass subsamples were pulverised in an electric food grinder. Homogenised dried samples were sealed and stored in plastic vials until processing in a bomb calorimeter. Following these sample preparation steps, the material available for replicate samples which could be analysed with the calorimeter varied across the species and regions (Table 3).

Calorimetry measurements

The calorimeter used was a PARR 6220 Isoperibol Calorimeter with both a semi-micro and standard bomb capability for different sample sizes, installed at the Flinders University Analytical Laboratory (Figure 3). The standard bomb was used for samples of fish and larger macroinvertebrates (e.g. larger bivalves), whereas the semi-micro bomb was used for most macroinvertebrates, some fish, and other prey items.

Figure 3. Parr Calorimeter used to determine the energetic value of aquatic organisms in the Coorong. The inset images show the semi-micro and standard vessel, and the pellet press is shown on the right.

Table 3. Sample size of aquatic organisms for which energy content values could be determined. The total number of replicate measurements is shown as well as the number of samples for each region, SL = South Lagoon, NL = North Lagoon, ME = Murray Estuary.

			NUMBER OF REPLICATES FOR CALORIMETRY			
FOOD CATEGORY	SPECIES	COMMON NAME	TOTAL	SL	NL	ME
Detritus			1			
Plankton						
Plants	*Ruppia*		10	6	4	
	Filamentous algae		8	8		
Macroinvertebrates	*Amarinus laevis*		8			8
	Amphipoda		46		20	26
	Arenicolidae	Lugworm	5		3	2
	Australonereis ehlersi		2		2	
	Capitella capitata		15		13	2
	Ceratopogonidae	Biting midge larvae	1	1		
	Chironomidae	Non-biting midge larvae	27	15	8	4
	Ficopomatus enigmaticus	Australian tubeworm	8		4	4
	Mysidae	Opossum shrimp	2		2	
	Aglaophamus (Nepthys) australiensis		22		1	21
	Paragrapsus gaimardii	Spotted shore crab	24		11	13
	Phyllodoce novaehollandiae	Green paddle worm	6		1	5
	Salinator fragilis		6			6
	Simplisetia aequisetis		58		28	30
	Hiatula (Soletellina) alba		28		9	19
	Spisula trigonella		30		15	15
	Stratiomyidae	Soldier fly larvae	10	10		
Fish	*Acanthopagrus butcheri*	Black bream	4			
	Afurcagobius tamarensis	Tamar goby	17	1	2	14
	Aldrichetta forsteri	Yelloweye mullet	60		27	33
	Ammotretis rostratus	Longsnout flounder	1			1
	Argyrosomus japonicus	Mulloway	5		1	4
	Arripis truttaceaus	Western Australian salmon	28		12	16
	Atherinosoma microstoma	Smallmouth hardyhead	48	16	16	16
	Hyperlophus vittatus	Sandy sprat	26		11	15
	Hyporhamphus regularis	River garfish	14		8	6
	Pseudaphritis urvillii	Congolli	46	8	19	19
	Rhombosolea tapirina	Greenback flounder	23		12	11
	Tasmanogobius lasti	Lagoon goby	11		7	4

Benzoic acid standard was used at the beginning of each day prior to sample analyses. About 15-25 samples could be analysed per day. The calculation included corrections for the fuse wire, which had burned off for each sample. No corrections were made for nitric acid, following Schaafsma et al. (2018). The procedures and calculations followed the manuals (492M, 585M) of the manufacturer for the calorimeter (Parr Instrument Company).

Energy density calculations

The energy content was calculated from gross heat (H) in Cal/g, based on equation (1)

$$Gross\ heat\ (H) = ((EE * T) - e_f) / m \qquad (1)$$

where EE is the Energy Equivalent of the calorimeter, T the observed temperature rise, e_f the fuse correction for the heat produced by the heating wire, and m the mass of the sample. Values were multiplied by 4.184 to converted energy values from calories (Cal) to Joules (J).

Calorimetry gave the energy content of macroinvertebrates, fish, and other prey items which could be analysed. For energy densities in kJ m^{-2} or kJ 1000 m^{-2}, the calorific contents were multiplied with the mass (wet as well as dry mass) of the prey items from field surveys.

Samples of the small molluscs, *Arthritica semen* and *Hydrobia* spp., did not combust in the calorimeter, likely due to a high proportion of calcium carbonate ($CaCO_3$) from their shells. Due to their small size, it was not feasible to remove the flesh material from the shells of enough individuals to obtain a sufficient sample mass for calorimetry. Trials were undertaken to implement an acid digestion stage for these species, where 1M hydrochloric acid was added drop-by-drop to dried and ground samples until bubbling ceased, before drying and grinding again; however, these were unsuccessful. Spiking the samples with mineral oil was also trialled but did not result in consistent combustion.

For species where we could not obtain our own calorific content, we used literature values from related species (Appendix Table C.3), or approximated the calorific content. For insect larvae (unidentified Diptera), we used the average of the calorific content we obtained for three taxa of Diptera. For *A. semen*, ash-free dry mass (AFDM) was calculated using data from TLM Icon Site Condition Monitoring for 2019 and 2020 (Dittmann et al. 2021). The AFDM for *A. semen* was calculated from dry mass (DM) using a conversion factor which is the mean AFDM/DM ratio across all samples with DM >0.01 g from TLM monitoring in 2019 and 2020 (N = 113): AFDM = 0.35*DM. Shell-free dry mass (SFDM) was then calculated using the mean AFDM/SFDM ratio across all Bivalvia (N = 167) from a global data bank of body composition in aquatic organisms (Brey et al. 2010): SFDM = AFDM/0.825. Finally, energy density was calculated by multiplying SFDM density (g m^{-2}) by the mean energy content of the other bivalve species in this study, *Spisula trigonella* and *Hiatula alba*, for which energy content was directly measured by bomb calorimetry (11.56 KJ/g SFDM).

Energy densities were not calculated for those macroinvertebrate taxa for which a cumulative dry mass of <1 g m^{-2} DM was recorded over the entire study (>1500 samples). Only ostracods, where the total dry mass over the entire study was 0.92 g m^{-2}, were included due to their occurrence in the South Lagoon. Average energy densities were analysed per region. Not enough material could be obtained for an even design of sample sizes across regions and seasons, and therefore, analyses focussed on regional differences.

2.3.4 Lipid and protein analyses

To explore the lipid and protein content of macroinvertebrate and fish prey items, additional specimens of key species were collected in the field during winter and summer 2021 (December 2021 for macroinvertebrates and March 2022 for fish) and frozen immediately. Samples were transported and stored frozen at -20 °C. Macroinvertebrates were freeze-dried within several days after return to the laboratory from the field trip, and fish were freeze-dried prior to the lipid and protein analyses. Material from filamentous algae and *Ruppia* was also analysed although not all had been kept frozen until analysis.

Prior to analyses, the freeze-dried samples were homogenised using either a ball mill grinder, mortar and pestle or a blender, depending on sample size and sample substance. Crude lipid (% Dry mass) was measured gravimetrically using the Folch technique (Folch et al. 1957). Crude protein (% Dry mass) was analysed from the total nitrogen concentrations determined using a Leco TruSpec CNS analyser, which had a quantification limit for total nitrogen of 0.2871 mg. A multiplier of 6.25 was used to calculate crude protein from the total nitrogen value. The analyses for crude lid and protein were carried out at the SARDI Aquatic Sciences

Environment and Analytical Laboratories. For macroinvertebrates, the quantity of material required for replicate samples could only be obtained for some species from the winter and summer sampling, and material for further species was used to obtain at least a single value (Table 4). Obtaining values for lipid content was prioritised over protein analysis when material was scarce. For fish, enough material was obtained in each of the two seasons for four replicate samples per region (Murray Estuary and North Lagoon for yelloweye mullet and sandy sprat, three regions for smallmouth hardyhead) (Table 4). For yelloweye mullet, size was differentiated in summer samples and an additional eight samples of larger mullet analysed.

Table 4. Sample size of aquatic organisms for which lipid and/or protein content could be determined. Samples were obtained where possible from the winter (W) and summer (S) season in 2021. A * indicates that the sample amount was minimal and values are to be interpretated with caution (this may have applied to one or several of the replicates only). Size for yelloweye mullet (*Aldrichetta fosteri*) is given in mm Total Length (TL).

FOOD CATEGORY	SPECIES	SIZE mm TL	SEASON	LIPID ANALYSES	PROTEIN ANALYSES
Plants	*Ruppia*				3
	Filamentous algae				5
Macroinvertebrates	*Amarinus laevis*		S	1	1
	Amphipoda		S	4	1
			W	4	1
	Anemone		S	1*	
	Arenicolidae		S	3*	1
	Arthritica semen		S	4	1
			W	4	1
	Australonereis ehlersi		S	4*	1
	Capitella capitata		S	3*	
	Chironomidae		S	1*	
	Ficopomatus enigmaticus		S	1	1
	Hydrobiidae		S	3*	
			W	4	1
	Aglaophamus (Nepthys) australiensis		S	1*	
			W	1	
	Salinator fragilis		S	4	1
			W	4	1
	Simplisetia aequisetis		S	4	1
			W	4	1
	Hiatula (Soletellina) alba		W	4	1
	Spisula trigonella		S	1	1
			W	4	
Fish	*Aldrichetta forsteri*	<120	S		8
		≥120	S		8
		<120	W		8
	Atherinosoma microstoma		S		12
			W		12
	Hyperlophus vittatus		S		8
			W		8

2.4 Data analyses

Water quality variables measured by the macroinvertebrate and fish team were combined for the seasonal surveys and the average and standard error plotted. For December 2020, a Principal Component Analysis (PCA) of environmental data for water quality and sediment characteristics was carried out using average values for site and zone from the macroinvertebrate survey, and square root transformation prior to normalisation of data for the PCA. Similarly, PCA analysis was done with the averaged environmental parameters, including water flow (average per quarter to match with seasonal sampling). Vector overlays were applied to indicate the patterns of correlation in the specific dataset. The PCA was carried out in PRIMERv7 (Clarke et al. 2014).

2.4.1 Design and factors used for statistical testing

For zooplankton, diversity is reported as taxonomic richness (number of taxa identified within the samples processed as described above where copepod nauplii and copepodites were counted as individual taxa) and density is reported as the number of individuals per cubic metre (ind.m^{-3}). All results are reported as the mean value to two significant figures ±1 standard error. For macroinvertebrates, species diversity was based on the number of taxa identified, and by trophic group or prey type. Abundance, biomass, and energy content and energy density are also presented based on taxa, prey type and trophic group. Macroinvertebrate data are reported per m^{2}. For fish, diversity is reported as species richness (number of species identified within the samples) and density is reported as the number of individuals per 1,000 square metre netting area (ind. 1,000 m^{-2}), and biomass as grams per 1,000 square metre netting area (wet and dry mass, g. 1000 m^{-2}).

Because of the extreme salinity gradient in the Coorong, most data were not normally distributed, and a non-parametric approach was followed. This included presenting data in box plots, which are showing the median and quartile ranges (25 and 75 percentiles) in the box, with outliers as whiskers (1.5 interquartile range IQR or minimum and maximum values). Permutational Analysis of Variance (PERMANOVA) was applied for statistical tests, as PERMANOVA is not violating assumptions of normality and homogeneity of variance (Anderson et al. 2008).

Taxonomic richness, individual densities, biomass (for macroinvertebrates and fish) and multivariate assemblage patterns were analysed using permutational Analysis of Variance (PERMANOVA). Analyses were carried out using PRIMER Version 7 with PERMANOVA+ add-on. The design for analyses presented in this report included two fixed factors: region and survey date (month-year for macroinvertebrates and season-year for fish and zooplankton). This statistical analysis design was used for testing for differences in diversity, individual densities, biomass (wet and dry mass) densities and communities for zooplankton, macroinvertebrates, and fish, and to test for energy densities of macroinvertebrates and fish. For macroinvertebrates, zone was a further fixed factor for some tests on differences between habitats. For calorific contents, no testing could be done for differences between regions or seasons as the number of replicate samples which could be analysed was too unbalanced (Table 3).

For univariate analyses, Euclidean distance was used as resemblance matrix. For tests of differences in abundance and biomass as well as multivariate community analyses, data were transformed (for zooplankton: square root transformation, for macroinvertebrates fourth-root transformation, for fish: no data transformation) before calculating the Bray-Curtis similarity with a dummy value of 1 added because of the large number of 0 values. All PERMANOVA were run with 9,999 permutations. Pairwise tests were carried out when interaction terms were significant. Significant (P<0.05) values are set in bold in tables throughout the report.

The zooplankton and fish assemblage pattern was visualised using multi-dimensional scaling (MDS) plots with trajectory overlay (survey date and split by region), and for zooplankton, with taxa densities and environmental data as overlay vectors. Principal coordinates analysis for the ordination (PCO) of fish samples in multivariate space was performed with vector overlays to indicate fish species that were correlated (Spearman rank correlation, r > 0.6) with the ordination axes. The macroinvertebrate community analyses are displayed in a dendrogram from cluster analyses with SIMPROF (similarity profile) test (Clarke et al. 2014) for *a posteriori* testing of significant differences between surveys. The analysis of sample similarities was combined with an analysis of species associations, for which coherence plots were created to obtain indicator species groups. A shade plot of the data matrix of all samples, averaged over surveys and regions, was then constrained by the indicator groups for variables and by the SIMPROF for samples (Somerfield & Clarke 2013; Clarke et al. 2014).

Analyses of correlations between salinity and diversity for macroinvertebrates were performed in Origin Pro v2020, including ANOVA to test whether the slope was significantly different from zero. To develop equations to convert between individual counts, wet and dry mass, respective correlations were run in Origin Pro for samples from seasonal surveys which had been frozen for calorimetry. For linear fits, the correlations were forced through zero.

To explore relationships with potential environmental drivers and the availability of prey (plankton, macroinvertebrates, fish), distance-based linear models (DISTLM) were carried out with the forward selection procedure and displayed using distance-based redundancy analysis (dbRDA) plots (Anderson et al. 2008). BEST test was used to determine the best combination of environmental variables driving the spatio-temporal variations in fish assemblage structure. Distance-based redundancy analysis (dbRDA) ordination of the fitted model of individual fish species density data from different regions were plotted against selected predictor variables from BEST results. LINKTREE analysis, which is a multivariate regression, was performed using a using a decision tree to identify subsets of samples from the biological dataset that were explained by the thresholds of selected environmental variables. For macroinvertebrate communities, the environmental variables were DO, salinity, average flow (monthly total in gigalitres GL), Salt Creek flow (monthly total) and average water level by region for each survey month. Flow and water level data as environmental predictor variables were downloaded from ‘Water Data SA’ (https://water.data.sa.gov.au). For fish, data were grouped by season-year and region and the four environmental variables selected to best predict fish assemblage variations were salinity, water temperature, DO and transparency. DISTLM was also applied to link the fish community pattern across the regions and seasonal surveys with the prey abundance of zooplankton and macroinvertebrates.

Box plots, bar and scatter plots for zooplankton and fish were generated using the software package SigmaPlot 14.0. For macroinvertebrate data presentation, Origin Pro v2020 was used. PERMANOVA, multivariate analyses, LINKTREE and DISTLM analyses and plots were carried out using PRIMER Version 7 with PERMANOVA+ add-on.

2.4.2 Production estimations

Production (µg AFDM/individual/day) of macroinvertebrates was estimated using the empirical equation (2) developed by Edgar (1990), relating macrobenthic production P (µg.day^{-1}) to biomass B (µg AFDM) and water temperature T (°C):

$$P = 0.0049 * B^{0.80} T^{0.89} \qquad (2)$$

This model is applicable to marine and estuarine species living in waters of 5–30 °C (Edgar 1990). Edgar’s (1990) methods involved separating the macrobenthic community into different size-classes, and therefore, when not separating into size-classes, the model may be less reliable for species which display greater variation in individual size (Wong 2018). Many of the dominant invertebrate taxa in the Coorong such as amphipods, *Arthritica semen*, Chironomidae, and *Capitella* do not display significant variation in size, except for the polychaete *Simplisetia aequisetis*.

Firstly, AFDM was calculated from dry mass using a species-specific conversion factor which was the mean ratio of AFDM to DM in data from the TLM macroinvertebrate monitoring in 2019 and 2020, as well as HCHB (i.e. for Oligochaeta and Stratiomyidae, only samples with DM >0.005 g were included when calculating conversion factors, for all other species, only samples with DM >0.01 g were included). Mean AFDM per individual was calculated by dividing the total AFDM by the total number of individuals (raw count). Mean biomass density was calculated by multiplying the mean abundance (ind. m^{-2}) by the mean AFDM per individual. The total dry mass and individual counts included all sites as they were only used to calculate mean mass per individual, whereas mean abundance (ind. m^{-2}) only included sites which were sampled consistently, i.e. B19, PP, LP, NM, HG, JP, and SC. Water temperature was obtained from measurements taken directly in the field. The mean water temperature across all sites and zones for each month/region was used in the production calculation.

Production in g AFDM m^{-2} day^{-1} was calculated by multiplying Production in µg AFDM $individual^{-1}$ day^{-1} by abundance (ind. m^{-2}) and dividing by 10^6. Production for each month was then calculated by multiplying with the number of days in the respective month. Annual production, P (g AFDM m^{-2} $year^{-1}$), was taken as the sum of monthly production across the twelve sampling events from August 2020 to June 2021. Finally, the overall mean biomass density, B, was calculated as the mean of the monthly mean biomass densities across this period and used to calculate Production – Biomass (P:B) values.

3 Results

3.1 Environmental conditions

Key results:

- The study period was characterised different flow conditions, with high (>400 GL/month) in 2021 following the onset of La Niña conditions.
- The flow characteristics over the study period shaped the water quality conditions and rising water levels, especially during spring and summer. Water transparency was reduced in autumn and winter.
- Despite the freshening effect of the flows, the extreme salinity gradient from brackish-marine salinity in the Murray Estuary to hypersalinity in the South Lagoon prevailed.
- Sediments throughout the Coorong were predominantly fine to medium sands, with coarser sediments at the South Lagoon sampling sites.
- The distinct environmental conditions in each of the regions create different habitats for plankton, macroinvertebrates and fish occurring in the Coorong.

3.1.1 Flow characteristics over the study period

The two study years were characterised by different flow conditions (Figure 4). Both years started with low flow over summer and autumn. Good winter and spring flows (>100 GL/month) were observed in 2020; while in 2021, the onset of La Niña conditions brought high flows (>400 GL/month) in winter which continued into spring 2021, and summer and autumn of 2022. The total flow over barrages in the flow year 2019-2020 was about 705 GL, in 2020-2021 the total flow was 1,330 GL, and the 2021-2022 flow year (up to February 2022) had 4,404 GL of water flow over the barrages.

3.1.2 Water quality

The flow characteristics shaped the water quality conditions during the study period (February 2020 to December 2021) (Figure 5). In the South Lagoon, average salinities over seasonal surveys ranged from 58 to 108 ppt and were >70 ppt for most of the time. The lower salinity of 58 ppt was recorded after the Salt Creek flow release in spring 2021, which had a freshening effect in the southern South Lagoon. The average dissolved oxygen (DO) concentration in this region during seasonal surveys ranged from 6.5 to 10.8 mg/L, with lower values in autumn and higher DO concentrations in spring. Water level varied with season, being lower in autumn and higher over the winter months and spring, but continued to be high with the high flows over summer 2021-2022. The water in the South Lagoon was consistently turbid and the Secchi depth was low, mostly <0.5 m (Figure 5).

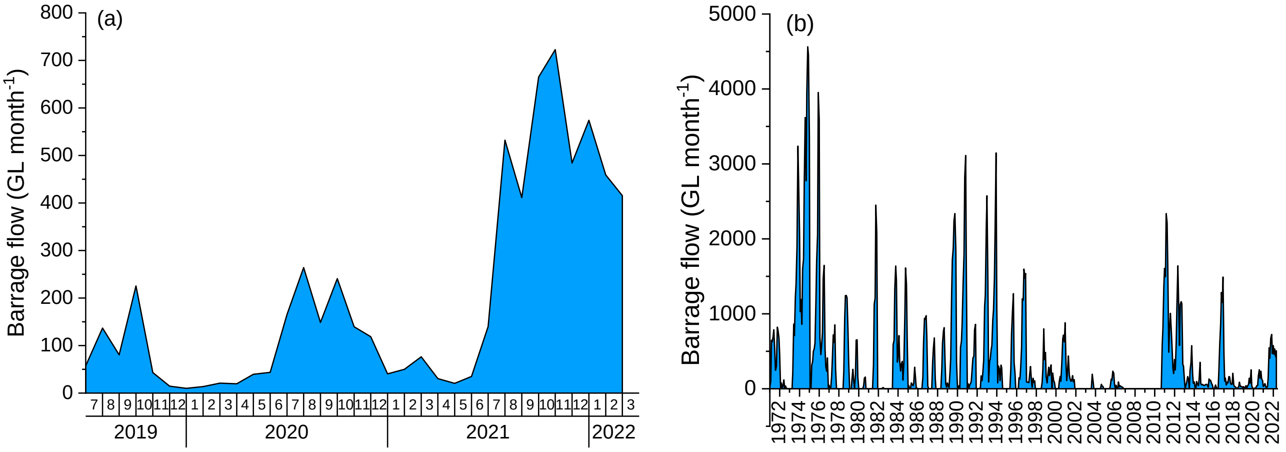

Figure 4. Monthly flow over the barrages into the Coorong (a) since the start of the flow year 2019-20, covering the study period from early 2020 to the end of 2021, and (b) since 1971. Data supplied by the Department for Environment and Water (DEW).

The North Lagoon was characterised by marine salinities around 41 ppt, and the Murray Estuary by brackish to marine salinities, which became increasingly fresh as high flows commenced in spring 2021 (Figure 5). The DO concentration was about nine mg/L on average in the North Lagoon and Murray Estuary and lower after high flows in the estuary. Water levels increased with higher flows, which led to less exposure of mudflats in the North Lagoon and Murray Estuary. Secchi depths were typically between 1-1.5 m in the North Lagoon and Murray Estuary but more variable, particularly in the Murray Estuary, with Secchi depths dropping to only 0.2–0.3 m indicating more turbid conditions during higher flows in late 2021 (Figure 5).

The water temperatures recorded in the winter surveys were about 12 °C, and around 22 °C in summer and autumn in both years, and followed a similar seasonal pattern in each region (Figure 5). Water temperatures were within the range recorded for the Coorong over longer-term periods (see https://water.data.sa.gov.au).

3.1.3 Sediment characteristics

The sediments throughout the Coorong were predominantly fine to medium sands, with higher mud contents in the North Lagoon and Murray Estuary (Figure 6). In the South Lagoon, sediments had higher contributions of coarse and very coarse particles, and were poorly to moderately sorted and similar between zones (Table 5; Appendix Figure A.2). Based on samples from the intertidal and subtidal zone at Salt Creek and Jack Point, sediments in the South Lagoon had a relatively low organic matter content (Table 5). Note that no sediments were sampled for grain size analysis at Hells Gate in December 2020, but the sediments were muddy based on field observations, particularly in the subtidal zone. In June 2021, sediment organic matter content was higher, as subtidal sediments at Hells Gate had high organic matter (mean 11.39 ± 4.45 % DW).

In the North Lagoon, sediments were fine to medium sand. Sediments on the peninsula side had a high mud content and were very poorly sorted in December 2020, but medium sand and moderately sorted in June 2021 (Table 5; Appendix Figure A.2). The muddy sediments on the peninsula side in December 2020 also had high organic matter content, due to the peninsula mudflat at Noonameena (mean 19.63 ± 2.00 % DW) (Table 5). As the peninsula side could not be reached in June 2021, the low value for organic matter for the North Lagoon Peninsula reflects only the Long Point site. Sediments in the Murray Estuary were mostly fine to medium sand, and poorly (December 2020) or moderately (June 2021) sorted (Table 5; Appendix Figure A.2). In June 2021, subtidal sediments in the Murray Estuary were very fine sand and had a higher silt content, especially at Beacon 19. The organic matter content was lower on the intertidal and peninsula mudflats than in the subtidal sediments (Table 5). This was more pronounced in June 2021 due to very high organic matter content in subtidal sediments at Beacon 19 (mean 44.76 ± 9.92 % DW).

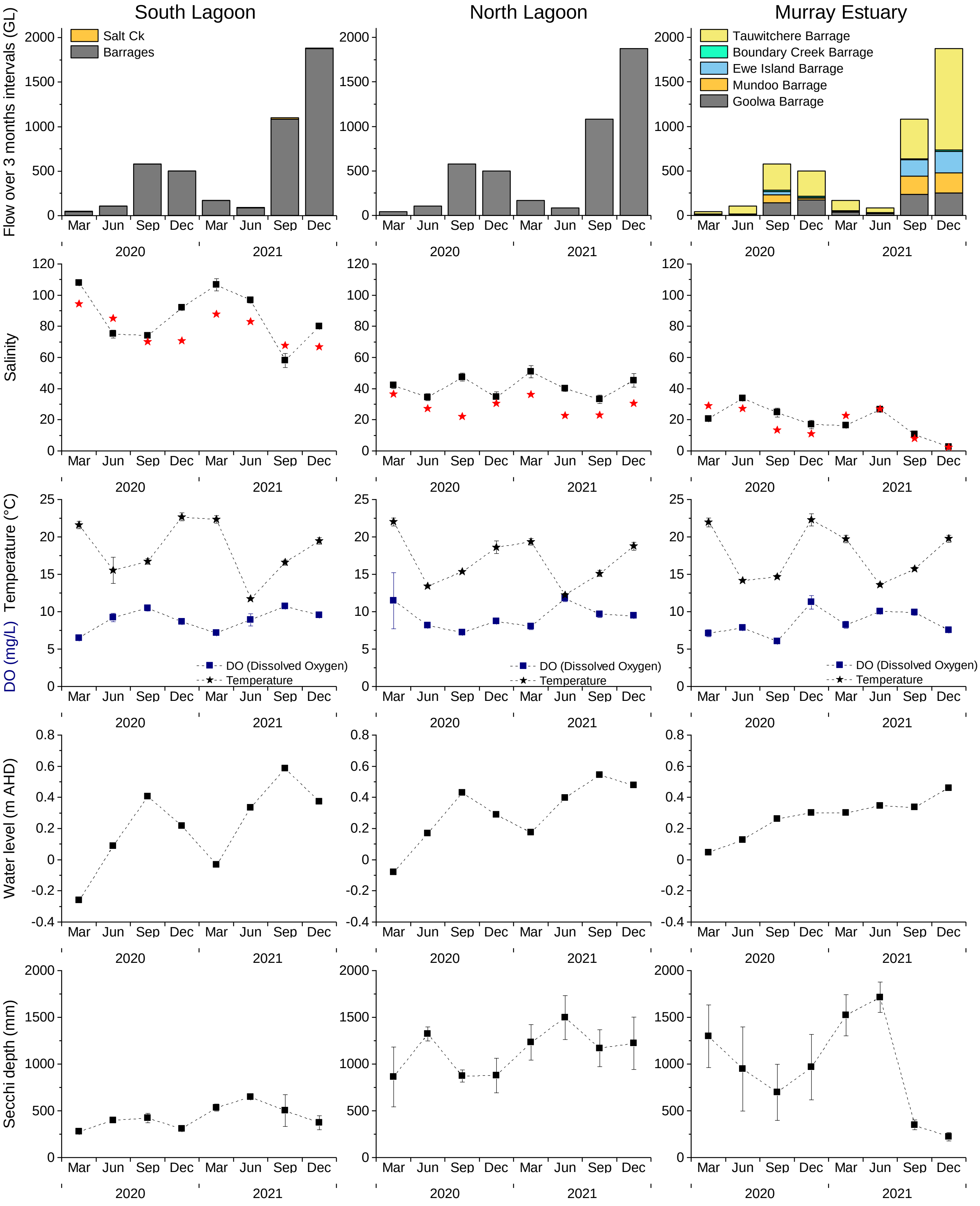

Figure 5. Environmental conditions over the seasonal surveys for the South Lagoon, North Lagoon and Murray Estuary. The total flow over each of the three months leading up to and including the seasonal survey is presented in bar graphs, with Salt Creek flow included in stacked bar graphs for the South Lagoon, and flow by barrage for the Murray Estuary. Salinity (ppt), dissolved oxygen, water temperature and Secchi depths are mean ± standard error based on field measurements. For salinity, the red stars indicate the average salinity over the quaterly intervals based on data from DEW. Water level data were averaged for each quaterly period. Flow and water level data were obtained from DEW.

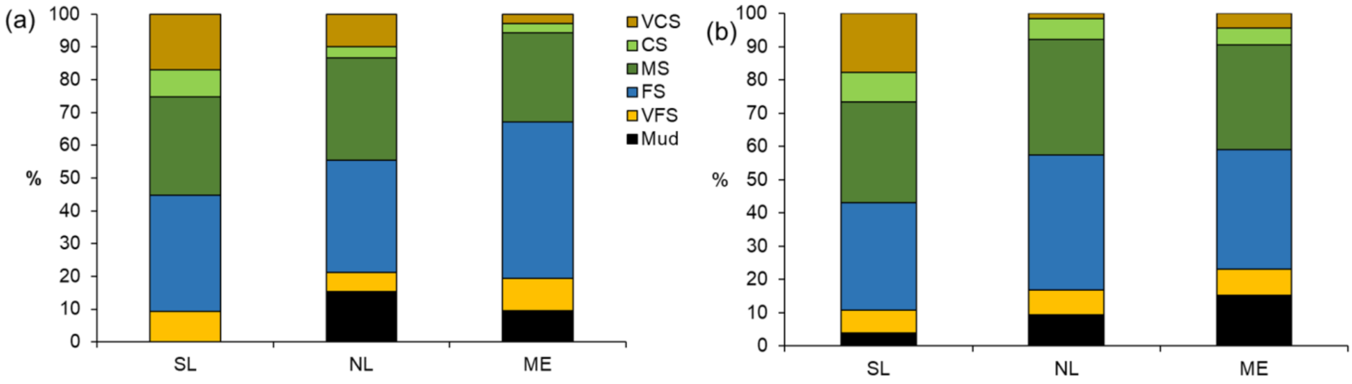

Figure 6. Grain size composition (%) of sediments in the South Lagoon (SL), North Lagoon (NL) and Murray Estuary from (a) December 2020, based on two sites per region (no sediment sampled at Hells Gate), and (b) June 2021 (all sites). The grain size fractions are: Mud <63 µm, VFS (very fine sand) 63-125 µm, FS (fine sand) 125-250 µm, MS (medium sand) 250-500 µm, CS (coarse sand) 500-1000 µm, VCS (very coarse sand) >1000 µm.

Table 5. Sediment characteristics for the three study regions and zones from the seasonal survey in (a) December 2020 and (b) June 2021, with the mean and standard error for median grain size, sorting coefficient and sediment organic matter. Verbal descriptions for grain size and sorting follow the geometric Folk and Ward measures.

REGION AND ZONE	MEDIAN GRAIN SIZE (µm)				SORTING COEFFICIENT				ORGANIC MATTER (%DW)		
	MEAN	±	SE		MEAN	±	SE		MEAN	±	SE
(a) December 2020											
South Lagoon	312	±	36.84	medium sand	2.04	±	0.04	poorly sorted	2.74	±	0.25
Intertidal	361	±	67.01	medium sand	1.98	±	0.05	moderately sorted	2.63	±	0.30
Subtidal	262	±	22.23	medium sand	2.10	±	0.07	poorly sorted	2.84	±	0.43
North Lagoon	225	±	22.55	fine sand	3.10	±	0.36	poorly sorted	5.41	±	1.63
Intertidal	295	±	38.16	medium sand	2.06	±	0.09	poorly sorted	1.07	±	0.14
Subtidal	232	±	7.26	fine sand	3.21	±	0.36	poorly sorted	4.10	±	1.07
Peninsula	149	±	39.11	fine sand	4.04	±	0.90	very poorly sorted	11.06	±	3.94
Murray Estuary	205	±	13.33	fine sand	2.37	±	0.15	poorly sorted	2.59	±	0.42
Intertidal	265	±	26.28	medium sand	2.03	±	0.07	poorly sorted	1.56	±	0.22
Subtidal	167	±	2.54	fine sand	3.03	±	0.25	poorly sorted	4.06	±	1.00
Peninsula	184	±	3.23	fine sand	2.05	±	0.18	poorly sorted	2.15	±	0.29
(b) June 2021											
South Lagoon	332	±	34.47	medium sand	2.29	±	0.14	poorly sorted	4.91	±	1.01
Intertidal	389	±	59.14	medium sand	2.04	±	0.12	poorly sorted	3.40	±	0.33
Subtidal	276	±	27.57	medium sand	2.53	±	0.23	poorly sorted	6.42	±	1.90
North Lagoon	218	±	20.40	fine sand	2.72	±	0.53	poorly sorted	2.41	±	0.60
Intertidal	198	±	5.09	fine sand	1.94	±	0.17	moderately sorted	1.48	±	0.22
Subtidal	180	±	33.34	fine sand	4.03	±	1.18	very poorly sorted	4.06	±	1.23
Peninsula	336	±	8.98	medium sand	1.65	±	0.01	moderately sorted	0.96	±	0.17
Murray Estuary	207	±	23.07	fine sand	2.81	±	0.41	poorly sorted	10.65	±	4.24
Intertidal	294	±	36.92	medium sand	1.64	±	0.03	moderately sorted	1.25	±	0.38
Subtidal	115	±	28.50	very fine sand	4.79	±	0.73	very poorly sorted	29.04	±	9.02
Peninsula	211	±	4.75	fine sand	1.99	±	0.13	moderately sorted	1.66	±	0.23

3.1.4 Environmental differentiation of sites/regions

A combined perspective of water quality and sediment characteristics for December 2020 and June 2021, based on measurements and samples collected in combination with the macroinvertebrate survey, shows that the environmental conditions that characterise macroinvertebrate habitat throughout the Coorong are salinity, grain size composition and organic matter load of sediments, and dissolved oxygen in the water column (Figure 7a). The South Lagoon sites were characterised by high salinity and coarser sediments, and the North Lagoon sites had environmental characteristics which were intermediary between those in the South Lagoon and Murray Estuary. The distinction of zones in the PCA plot indicates that finer scale differentiation of environmental conditions occurs (Figure 7a). Note that no sediment characteristics were available for Hells Gate in December 2020. The two axes of the PCA plot explained 82.7% of the variation.

A combined water quality and flow analysis shows that flow characterised the spring and summer surveys in 2020 and in 2021, salinity and dissolved oxygen (DO) in autumn 2020, and the water transparency during the autumn 2021 and winter surveys in both years (Figure 7b).

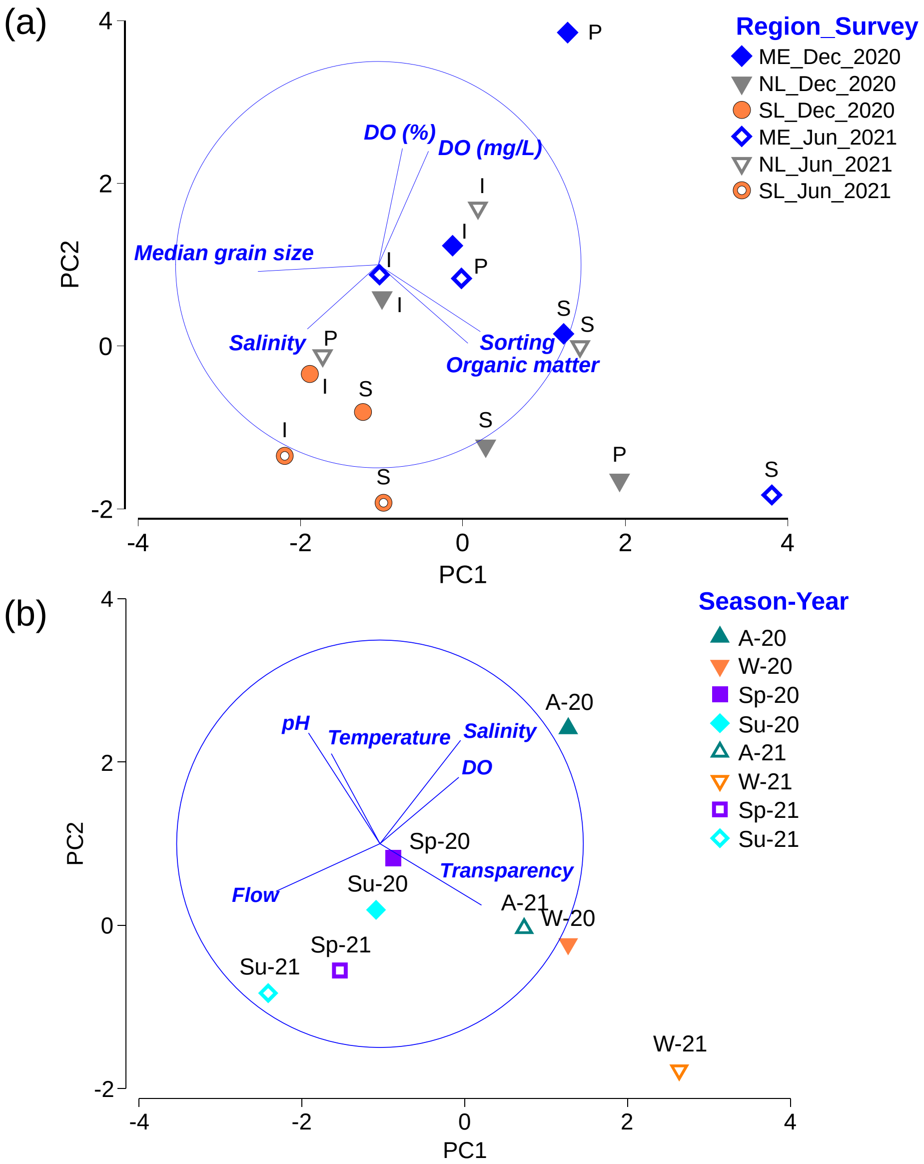

Figure 7. PCA (Principal Component Analysis) plots of environmental conditions. (a) PCA across the regions and zones for two macroinvertebrate surveys, December 2020 (no sediment was sampled at Hells Gate for grain size and organic matter) and June 2021 (all sites). The zones were I = Intertidal mudflat, S = Subtidal sediment, P = Peninsula mudflat. (b) PCA of water quality and flow from seasonal fish and zooplankton surveys, whereby A-20 = Autumn 2020, W-20 = Winter 2020, Sp-20 = Spring 2020, Su-20 = Summer 2020, A-21 = Autumn 2021, W-21 = Winter 2021, Sp-21 = Spring 2021, Su-21 = Summer 2021.

3.2 Food resource availability and associated habitat requirements, including environmental influences

3.2.1 Zooplankton

Key results:

- Taxonomic richness of zooplankton was low throughout the Coorong, but similar to that found by other studies conducted throughout the Coorong during periods of low discharge.
- Taxonomic richness of zooplankton was lowest in the South Lagoon and highest in Murray Estuary.
- Across the entire study period and all three regions, taxonomic richness of zooplankton was the highest in the Murray Estuary in September 2021, when discharge to the Coorong was also the highest for the study period.
- In the South Lagoon, total zooplankton density was generally lower than the other two regions. Total and microcrustacean densities increased significantly in September 2021 when discharge via Salt Creek was the highest for the study.
- In the North Lagoon, total zooplankton density was generally higher than the other two regions. Total, microcrustacean and rotifer densities did not appear to be closely associated with freshwater discharge, varying from what was seen in the South Lagoon and the Murray Estuary.
- In the Murray Estuary, total zooplankton density was generally very low. Total and rotifer density were slightly higher in December 2020, when discharge increased, than previously during the study, but still low compared to other regions. Total, microcrustacean and rotifer density were highest for the Murray Estuary in September 2021 when freshwater discharge was also highest.

Zooplankton diversity

Throughout the study, between one and 12 taxa were identified in the zooplankton samples at each site, with the mean taxonomic richness being 4.46 ± 0.54 taxa (mean ± standard error). This taxonomic diversity is low in comparison to higher discharge periods in the Coorong but similar to that in low discharge periods (Tables 6 and 7). In the South Lagoon, taxonomic richness ranged from one to seven taxa with a mean of 4.25 ± 1.38 in 2020 and 5.25 ± 0.63 taxa in 2021 (Table 6). In the North Lagoon, taxonomic richness ranged from two to seven taxa with a mean of 3.5 ± 1.19 in 2020 and 4.5 ± 0.50 taxa in 2021 (Table 6). In the Murray

Table 6. Taxa richness (estimated taxa per litre) recorded during months of March, June, September and December across three regions of the Coorong in the zooplankton surveys from March 2020 to December 2021.

		MAR	JUN	SEP	DEC	MEAN	SE
South Lagoon	**2020**	1	7	3	6	**4.25**	**1.38**
	2021	4	5	7	5	**5.25**	**0.63**
North Lagoon	**2020**	2	2	3	7	**3.50**	**1.19**
	2021	5	5	3	5	**4.50**	**0.50**
Murray Estuary	**2020**	11	6	8	8	**8.25**	**1.03**
	2021	5	5	12	6	**7.00**	**1.68**
Mean		**4.13**	**4.63**	**6.50**	**6.13**		
SE		**1.43**	**0.68**	**1.51**	**0.48**		

Estuary, taxonomic richness ranged from five to 12 taxa with a mean of 8.25 ± 1.03 in 2020 and 7 ± 1.68 taxa in 2021 (Table 6). Taxonomic richness was the highest for the study, with 12 taxa identified, in the Murray Estuary when flow was highest in September 2021.

Table 7. List of taxa recorded in the zooplankton surveys from (A) March 2020 to December 2020, and (B) March 2021 to December 2021. The occurrence of species across the three regions SL = South Lagoon, NL = North Lagoon and ME = Murray Estuary.

(A) 2020	MARCH			JUNE			SEPTEMBER			DECEMBER		
	SL	NL	ME	SL	NL	ME	SL	NL	ME	SL	NL	ME
Rotifers												
Asplanchna sp.											●	
Trichocerca species				●								
Filinia longiseta												●
Keratella cochlearis						●						
Keratella australis									●			●
Lecane cf (M) *lunaris*												●
Polyarthra species											●	
Synchaeta oblonga												●
undescribed *Synchaeta* species				●	●	●		●	●		●	
unidentified *Floscularieaceae* sp		●		●								●
Unknown <100 µm										●		
Cladocerans												
Bosmina meridionalis				●								●
Ceriodaphnia cf. *quadrangula*									●			
Copepods												
Cyclopoid copepod			●							●		
Gladioferens pectinatus			●									
Calanoid copepodite									●		●	●
unidentified harpacticoid copepodite			●			●						
Mesochra baylyi							●	●		●		
cf. *Mesochra* species									●			
unidentified harpacticoid 1		●	●									
unidentified harpacticoid 2			●									
unidentified harpacticoid 3												
Nauplii			●		●	●	●	●	●	●	●	●
Ostracods												
Ostracod	●		●	●					●	●		
Juvenile ostracod			●									
Macroinvertebrates												
unidentified Amphipod			●									
unidentified cf. *Hydrachnidia*			●									
cf. *Polychaete* larvae				●							●	
Chironomidae larvae						●				●		
unidentified Mollusc			●	●		●			●		●	

cont.

(B) 2021	March			June			September			December		
	SL	NL	ME	SL	NL	ME	SL	NL	ME	SL	NL	ME
Rotifers												
unidentified Bdelloid rotifer				●		●						
Filinia australiensis									●			
Keratella tropica			●						●			
Keratella australis			●						●			●
Synchaeta cf. *vorax*					●	●						
undescribed *Synchaeta* species		●		●		●		●	●	●	●	
Synchaeta neapolitana							●					
unidentifed cf. *Epiphanidae*	●											●
Conochilus unicornis												●
unidentified *Flosculariaceae* sp										●		
Cladocerans												
Daphnia glaeata									●			
Bosmina meridionalis									●			●
Ceriodaphnia cf. *quadrangula*									●			
Copepods												
Cyclopoid copepod										●		
Boeckella triarticulata									●			
Calamoecia ampulla									●			
Gladioferens pectinatus					●							
Acartia fancetti				●								
Calanoid copepodite		●				●	●		●			
unidentified harpacticoid copepodite								●	●			
Mesochra baylyi				●			●					
unidentified harpacticoid 3											●	
Nauplii	●	●	●	●	●	●	●	●	●	●	●	●
Ostracods												
Ostracod	●			●			●			●		
Macroinvertebrates												
unidentified Nematode					●						●	
Crab nauplii	●					●						
cf. *Polychaete* larvae		●										
unidentified Mollusc		●	●				●				●	●

Zooplankton individual densities

Total density varied greatly, with the average ranging from 4.34 x 10^3 (± 1.76 x 10^3) ind. m^{-3} (mean ± standard error) in the South Lagoon to 4.47 x 10^5 (± 3.45 x 10^4) ind. m^{-3} in the North Lagoon, however, across all three regions, total density was often below ~2 x 10^5 ind. m^{-3} (Figure 8). PERMANOVA tests on total density, microcrustacean density and rotifer density indicated that there was a significant interaction between region and month (*P*=0.0001 for all comparisons), signifying that temporal variability was not consistent among regions (Table 8).

In the South Lagoon, total zooplankton density was commonly lowest where salinity was highest (4.34 x 10^3 ± 1.76 x 10^3 to 1.14 x 10^5 ± 2.57 x 10^4 ind. m^{-3}), with total densities being significantly lower than both other regions in September 2020, December 2020 and March 2020 (*P*=0.0002-0.024) (Figure 8a and Appendix Table B.1). Total density was especially low from March 2020 until March 2021 (4.34 x 10^3 ± 1.76 x 10^3 – 1.70 x 10^4 ± 6.69 x 10^3) (Figures 8a and 9a). During this period, rotifers were almost completely absent and microcrustaceans including copepod nauplii and ostracods were present in very low densities (Figures 8a Figure 9a). Total and microcrustacean densities were significantly greater in September 2021 than all other sampling occasions as flow into the South Lagoon increased via Salt Creek (*P*=0.0001-0.0128 and 0.0002-0.0037, respectively) (Figures 8a and 9a; Appendix Table B.1). These higher densities of microcrustaceans were primarily driven by copepod nauplii and ostracods. In the North Lagoon, total density was generally higher than the other regions (5.56 x 10^3 ± 5.56 x 10^3 to 4.47 x 10^5 ± 3.45 x 10^4 ind. m^{-3}) with total densities being significantly higher than both other regions in June 2020, September 2020, December 2020, March 2021 and June 2021 (*P*=0.0003-0.0078) (Figure 8b and Appendix Table B.1). Unlike the Murray Estuary and the South Lagoon, total densities in June 2020 were significantly greater than March and September 2020 (*P*=0.0025 and 0.0091, respectively) (Table Appendix B.1). These higher densities were largely driven by significantly higher densities of rotifers (*P*=0.0034 and 0.0074, respectively), primarily an undescribed *Synchaeta* species (Figures 8b and 9b). This undescribed *Synchaeta* species continued to be prevalent in the North Lagoon throughout September, December, and March 2021. As seen in the Murray Estuary, this undescribed *Synchaeta* species also contributed to an increase in rotifer densities in September 2021 during high flow and lower salinities (Figure 9b). Total and microcrustacean densities peaked in December 2020 (4.44 x 10^5 ± 3.29 x 10^4 ind. m^{-3} and 3.39 x 10^5 ± 1.92 x 10^4 ind. m^{-3}, respectively), primarily due to high densities of copepod nauplii (Figures 8b, 9a, and 9b). After December 2020, total and microcrustacean densities gradually decreased before returning to relatively low densities in December 2021 (Figure 8b).

Table 8. Test results from permutational ANOVA (PERMANOVA) on differences in zooplankton density, microcrustacean density, rotifer density and assemblage over the surveys from March 2020 to December 2021. Significant P-values are shown in bold.

		TOTAL DENSITY	MICROCRUSTACEAN DENSITY	ROTIFER DENSITY	ZOOPLANKTON ASSEMBLAGE
MAIN TEST	DF	$P_{(PERM)}$	$P_{(PERM)}$	$P_{(PERM)}$	$P_{(PERM)}$
Region (Re)	2	**0.0001**	**0.0001**	**0.0001**	**0.0001**
Date (Da)	7	**0.0001**	**0.0001**	**0.0001**	**0.0001**
RexDa	14	**0.0001**	**0.0001**	**0.0001**	**0.0001**
Residual	144				

Total densities were low in the Murray Estuary in March, June and September 2020 (2.27 x 10^4 ± 4.80 x 10^3 to 6.36 x 10^4 ± 1.82 x 10^4 ind. m^{-3}), a period of very low flow (Figure 8c). In March 2020, the community was primarily comprised of microcrustaceans (4.95 x 10^4 ± 1.95 x 10^4 ind. m^{-3}), including adult and nauplii harpacticoid copepods and the calanoid copepod *Gladioferens pectinata* (Table 7 and Figure 9). There were considerable numbers of amphipods detected at Pelican Point (1.98 x 10^4 ± 7.38 x 10^3 ind. m^{-3}) (Table 8). Following higher flow from July through to December 2020, total densities were higher in December 2020 (1.27 x 10^5 ± 3.11 x 10^4 ind. m^{-3}) than those recorded earlier in the year (i.e. significantly higher than June and September 2020 where *P*=0.0131 and 0.0064, respectively) (Figure 8c; Appendix Table B.1). These higher densities were primarily driven by freshwater rotifers, including *Synchaeta oblonga, Keratella australis* and *Filinia longiseta* as well as copepod nauplii (Table 7; Figures 8c, 9a, and 9b). Total density was low in the Murray Estuary in March and June 2021 (5.88 x 10^4 ± 7.10 x 10^3 and 3.99 x 10^4 ± 1.52 x 10^4 ind. m^{-3}, respectively), again during a period of low flow (Figure 8c). During this period the only microcrustaceans present were copepod nauplii. Despite the low flow, most of the rotifer community was comprised of freshwater taxa such as *Filinia pejleri, Keratella tropica* and *Keratella australis* (Table 7). After significant increases in flow through July and August total densities were significantly higher in September 2021 than on any other sampling occasion in the Murray Estuary ($4.11 \times 10^5 \pm 8.97 \times 10^4$ ind. m^{-3}) (P=0.0018-0.007) (Appendix Table B.1 and Figure 8c). These greater densities were driven by a combination of microcrustaceans, including freshwater calanoid copepods (*Boeckella triarticulata* and *Calamoecia ampulla*), cladocerans (*Ceriodaphnia* cf. *quadrangula*), and rotifers (*Keratella tropica*, *Keratella australis, Filinia australiensis* and an undescribed *Synchaeta* species) (Table 7 and Figure 9b). Total densities were significantly lower in December 2021 than September 2021 (P=0.0018). This was due to significantly lower densities of microcrustaceans (P=0.0021) and lower, however not significantly (P=0.796), densities of rotifers, despite flow remaining high (Appendix Table B.1).

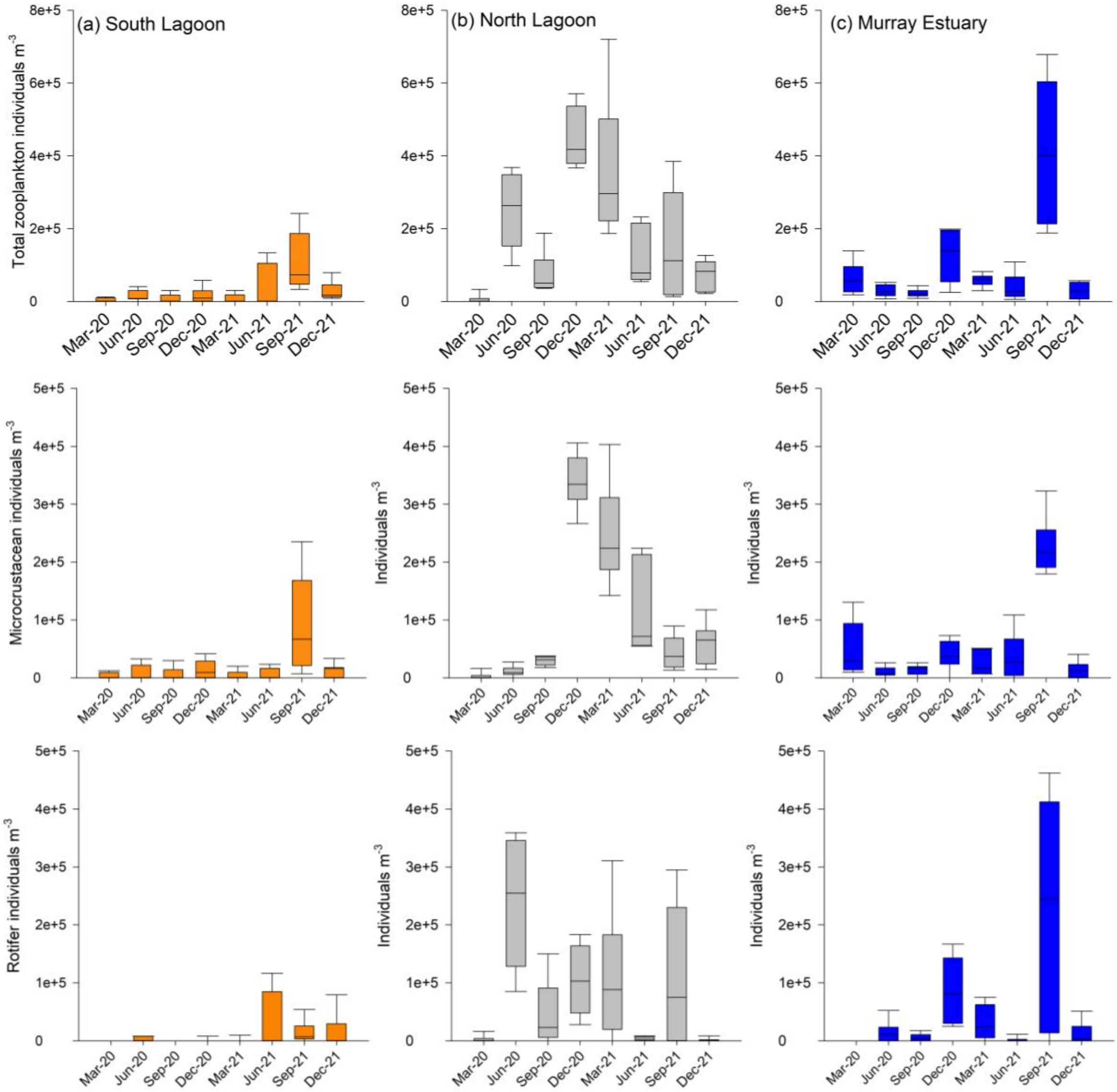

Figure 8. Density (average ± standard error) of total zooplankton (rotifers, cladocerans, copepods and ostracods), microcrustaceans (cladocerans, copepods and ostracods) and rotifers across regions and surveys from March 2020 to December 2021.

Zooplankton community

The zooplankton communities across all three regions were dominated by calanoid and harpacticoid copepods, and rotifers from the genus *Synchaeta* (Figures 8, and 9; Table 8). There did not appear to be any clear trends in assemblages in relation to month (i.e. season), however flow and the associated changes in water quality appeared to have some influence on total, microcrustacean and rotifer density in the South Lagoon and Murray Estuary (Figure 9). PERMANOVAs on zooplankton assemblage indicated that there was a significant interaction between region and month (P=0.0001), signifying that temporal variability was not consistent among regions (Table 8).

Figure 9. Multi-dimensional scaling (MDS) ordinations showing grouping of zooplankton assemblage by region and date in the Coorong between March 2020 and December 2021 with trajectory overlay (survey date split by region) and (a) taxa densities, (b) environmental data as overlay vectors and (c) with temporal trajectory (split by region). Correlation value = 0.4.

3.2.2 Macroinvertebrates

Key results:

- The 42 different macroinvertebrate taxa recorded in this study represented several types of prey, with more species, prey types and trophic groups in the Murray Estuary and North Lagoon than in the South Lagoon.
- Macroinvertebrate communities were diverse in the Murray Estuary with high individual densities and biomass of several prey types and trophic groups offering abundant food for benthivorous predators with a range of foraging strategies.
- The few macroinvertebrate species occurring in the South Lagoon were mostly small size organisms living at the sediment surface in very low individual densities and biomass, offering little choice and low abundance of prey for benthivorous predators.
- At salinities >50 ppt, the number of macroinvertebrate species, their individual densities and biomass decreased sharply, reflecting less prey choice and a lower amount of prey available for benthivorous fish and shorebirds in the high salinities of the South Lagoon Only chironomid larvae were found at all salinities.
- Seasonal increase in macroinvertebrate abundances coincided with higher flows over the barrages.
- Salinity explained most of the pattern seen in macroinvertebrate communities and prey availability throughout the Coorong. The macroinvertebrate communities with highest food availability in the Murray Estuary occurred at salinities <34 ppt. Water level, barrage flow, dissolved oxygen and sediment grain size explained some of the further variation.
- To convert from individual counts or wet mass to dry mass for energy density calculations, equations were developed for most macroinvertebrate species, which will facilitate future bioenergetic assessments
- Benthic micro-molluscs and benthic-pelagic crustaceans had the highest annual production due to high production of a small bivalve (*Arthritica semen*) and amphipods respectively, which were both also the most abundant prey in the Murray Estuary and North Lagoon.

Macroinvertebrate diversity

Across all surveys since February 2020, 42 macroinvertebrate taxa were recorded at the study sites throughout the Coorong (Table 9). This includes several species that had not been found in previous Coorong studies, for example, a marine leech (Rhynchobdellidae), a lugworm (Arenicolidae), a seaslug (*Liloa brevis*), the venerid bivalve *Irus carditoides*, and two species of spionid polychaetes. The higher flows during the study period also brought some freshwater macroinvertebrates into the Murray Estuary, such as the snail *Physella acuta,* aquatic insects Notonectidae (backswimmers) and freshwater isopods (Janiridae). Taxonomically, Annelida accounted for most (15) of the macroinvertebrate taxa. Mollusca were represented with 10 taxa (five taxa each of bivalve and gastropods), followed by eight taxa of Crustacea and seven types of insects (Hexapoda), which were present as larvae, apart from the adult Notonectidae found.

The South Lagoon was species poor, with only 12 of the 42 macroinvertebrate taxa found, compared to 29 taxa recorded from the North Lagoon and 35 from the Murray Estuary (Table 10). On average, only one taxon was found per replicate sample in the South Lagoon, and five taxa per survey at the South Lagoon sites (Figure 10). The mean number of species was significantly different across the regions and surveys (Table 11). For each of the surveys, the mean number of species in the South Lagoon was significantly lower compared to the North Lagoon, which had an average of four taxa per replicate sample and 14 taxa per survey, and the Murray Estuary with an average of seven taxa per replicate sample and 16 taxa per survey (Figure 10; Tables 10, 11, and B.2). The mean number of species was significantly higher in the Murray Estuary than the North Lagoon, apart from May 2021 (Appendix Table B.2). Between the surveys, the mean number of species based on taxa were significantly different for each region (Table 11), whereby pairwise differences between surveys varied for each region (Appendix Table B.3).

Macroinvertebrate species were grouped into five different prey types based on their habitat and size (Table 9). Of these five prey types, three were recorded from the South Lagoon, whereas all five were present in the North Lagoon and Murray Estuary (Table 10). In the South Lagoon, macroinvertebrates were mostly of the prey type ‘Surface-Small’. In the Murray Estuary and North Lagoon, macroinvertebrate prey types were of all sizes and occurred as epifauna, in surface or deeper sediment layers. A greater diversity of prey was thus available in the Murray Estuary for a higher diversity of predators with a range of foraging strategies. The mean number of prey types had similar trends between regions and surveys as the mean number of species based on taxa (Table 11), but pairwise comparisons showed greater similarity between the North Lagoon and Murray Estuary (Tables B.2 and B.3).

Macroinvertebrates were also grouped into trophic groups used in the T&I Component 3 food web model (Table 9). Several macroinvertebrates which were rarely encountered and did not fit into the main trophic groups were assigned to a group ‘other’. Nine trophic groups were thus differentiated for macroinvertebrates, whereby ‘Benthic annelids’ were represented by ten taxa, ‘Insect larvae/pupae’ by six, and ‘Benthic micro-molluscs’ by five taxa (Table 9). All trophic groups were present in the Murray Estuary and North Lagoon (‘Benthic decapods’ were not present in the North Lagoon based on corer and grab sampling methods used, but were caught in seine nets for fish), while only six trophic groups occurred in the South Lagoon (Table 10). The mean number of species based on trophic groups was also significantly different across the regions and surveys (Table 11), but more similar between the North Lagoon and Murray Estuary for several surveys based on pairwise comparisons (Tables B.2 and B.3).

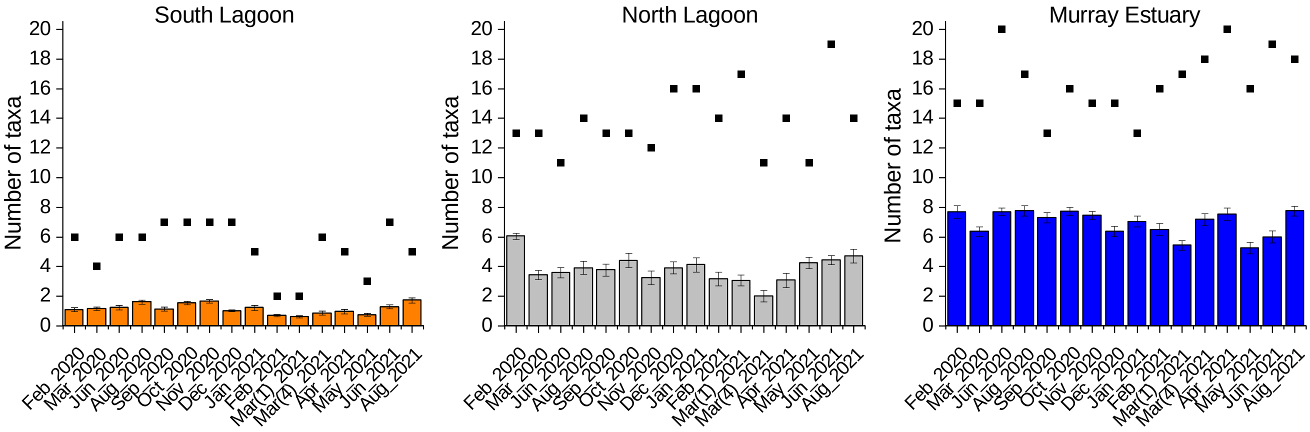

Figure 10. Bar graphs of species density (mean ± standard error) of macroinvertebrates based on taxa, for each of the surveys and by region. The black squares indicate the total number of taxa found per survey in the region.

Table 9. List of macroinvertebrate species recorded in the surveys from February 2020 to August 2021, grouped taxonomically by phyla and class/order and assigned per trophic group. * indicates new record for the Coorong. Their occurrence in each of the three regions (SL = South Lagoon, NL = North Lagoon, ME = Murray Estuary) is indicated by a tick √. Prey access type is assigned based on their living habitat and size, whereby the first letter indicates habitat, and the second the macroinvertebrate size. D-L = Deep-Large, E-L = Epifauna-Large, S-L = Surface-Large, S-M = Surface-Medium, S-S = Surface-Small.

			REGION			PREY TYPE	
PHYLA	CLASS/ORDER	TAXON	SL	NL	ME	(HABITAT-SIZE)	TROPHIC GROUP
Cnidaria	Anthozoa	Anemone		√	√	S-S	Other
Plathyhelminthes	Polycladida	Polycladida sp. indet.*			√	S-M	Other
Annelida	Clitellata	Rhynchobdellida sp. indet.*			√	S-L	Other
	Oligochaeta	Oligochaeta sp. indet.		√	√	S-S	Benthic deposit-feeding annelids
	Polychaeta	*Aglaophamus (Nephtys) australiensis*		√	√	D-L	Benthic annelids
	Polychaeta	Arenicolidae sp. indet.*		√	√	D-L	Benthic annelids
	Polychaeta	*Australonereis ehlersi*		√	√	D-L	Benthic annelids
	Polychaeta	*Boccordiella limnicola*		√	√	S-S	Benthic annelids
	Polychaeta	*Capitella* sp. indet.	√	√	√	S-M	Benthic deposit-feeding annelids
	Polychaeta	*Euchone variabilis*		√	√	S-S	Benthic annelids
	Polychaeta	*Ficopomatus enigmaticus*		√	√	E-L	Ficopomatus
	Polychaeta	*Minospio* sp. indet.*		√	√	S-S	Benthic annelids
	Polychaeta	*Phyllodoce novaehollandiae*		√	√	S-L	Benthic annelids
	Polychaeta	*Prionospio* sp. indet.*			√	S-S	Benthic annelids
	Polychaeta	*Simplisetia aequisetis*	√	√	√	D-L	Benthic annelids
	Polychaeta	Spionidae sp. indet.			√	S-S	Benthic annelids
Nemertea		Nemertinea sp. indet.		√		S-L	Other
Mollusca	Bivalvia	*Arthritica semen*		√	√	S-S	Benthic micro-molluscs
	Bivalvia	*Hiatula (Soletellina) alba*		√	√	D-L	Subtidal benthic molluscs
	Bivalvia	*Irus carditoides**			√	S-M	Subtidal benthic molluscs
	Bivalvia	*Spisula trigonella*		√	√	D-L	Subtidal benthic molluscs
	Bivalvia	*Macomona (Tellina) deltoidalis*		√	√	D-L	Subtidal benthic molluscs
	Gastropoda	*Coxiella striatula*	√			S-S	Benthic micro-molluscs
	Gastropoda	Hydrobiidae/Tateidae spp. indet.		√	√	S-S	Benthic micro-molluscs
	Gastropoda	*Liloa brevis**		√	√	S-S	Benthic micro-molluscs
	Gastropoda	*Physella acuta*			√	S-S	Other
	Gastropoda	*Salinator fragilis*		√	√	S-S	Benthic micro-molluscs
Crustacea	Amphipoda	Amphipoda spp. indet.	√	√	√	S-S	Bentho-pelagic crustaceans
	Decapoda	*Amarinus laevis*			√	S-M	Benthic decapods
	Decapoda	*Halicarcinus ovatus*			√	S-M	Benthic decapods
	Decapoda	*Paragrapsus gaimardii*			√	E-L	Benthic decapods
	Isopoda	*Haloniscus searlei*	√			S-S	Other
	Isopoda	Janiridae sp. indet.*			√	S-S	Bentho-pelagic crustaceans

cont.

PHYLA	CLASS/ORDER	TAXON	SL	NL	ME	(HABITAT-SIZE)	TROPHIC GROUP
	Mysidae	Mysidae sp. indet.		√	√	E-L	Bentho-pelagic crustaceans
	Ostracoda	Ostracoda sp. indet.	√	√	√	S-S	Bentho-pelagic crustaceans
Hexapoda	Diptera	Ceratopogonidae sp. indet.	√	√		S-S	Insect larvae/pupae
	Diptera	Chironomidae sp. indet.	√	√	√	S-S	Insect larvae/pupae
	Diptera	Diptera sp. indet.	√	√		S-S	Insect larvae/pupae
	Diptera	Dolichopodidae sp. indet.	√	√	√	S-S	Insect larvae/pupae
	Diptera	Empididae sp. indet.	√	√		S-S	Insect larvae/pupae
	Diptera	Stratiomyidae sp. indet.	√	√		S-S	Insect larvae/pupae
	Hemiptera	Notonectidae sp. indet.			√	S-S	Other

Table 10. Total number of species (S) and mean number of species (± standard error SE) in each region and all regions of the Coorong over all investigations from February 2020 to August 2021, based on taxa, prey types and trophic groups.

	TAXA		PREY TYPES		TROPHIC GROUPS	
REGION	S	MEAN ± SE	S	MEAN ± SE	S	MEAN ± SE
South Lagoon	12	5.31 ± 0.44	3	1.44 ± 0.13	6	2.75 ± 0.23
North Lagoon	29	13.81 ± 0.56	5	4.31 ± 0.12	8	6.50 ± 0.18
Murray Estuary	35	16.44 ± 0.54	5	4.56 ± 0.13	9	7.00 ± 0.20
All regions	42	11.85 ± 0.75	5	3.44 ± 0.22	9	5.42 ± 0.30

Table 11. Test results from permutational ANOVA (PERMANOVA) on differences in macroinvertebrate species density, by taxa, prey type categories and by trophic groups, across the three regions (Re) of the Coorong and over the surveys (Su) from February 2020 to August 2021. Significant P-values are shown in bold.

		TAXA			PREY TYPES			TROPHIC GROUPS		
MAIN TEST	df	MS	PSEUDO-F	$P_{(PERM)}$	MS	PSEUDO-F	$P_{(PERM)}$	MS	PSEUDO-F	$P_{(PERM)}$
Region (Re)	2	4123.40	1631.40	**0.0001**	576.00	952.26	**0.0001**	1600.70	1428.90	**0.0001**
Survey (Su)	15	27.49	10.88	**0.0001**	5.07	8.39	**0.0001**	8.83	7.88	**0.0001**
Re x Su	30	10.47	4.14	**0.0001**	2.88	4.77	**0.0001**	3.95	3.53	**0.0001**
Residual	1485	2.53			0.60			1.12		

The overall number of species recorded was higher in sediments that were permanently submerged than in sediments that were periodically exposed sediments at intertidal mudflats and on the peninsula (Figure 11), with significant differences across regions and zones, Tables 12 and 13). In the Murray Estuary, the total number of species found in subtidal sediments was higher than in sediments in the intertidal or peninsula mudflats, but the mean number of species was not significantly different (Tables 12 and B.4). In the North and South Lagoon, less difference occurred in the number of taxa across the zones (Tables 12, 13, and Appendix B.4).

There was no difference in species density by prey type between zones, but there was a difference between regions. Species density based on trophic groups was, however, significantly different between both zones and regions (Table 13). The diversity of prey options for higher trophic levels (fish, shorebirds) was similar across the zones, but differed between regions.

Table 12. Total number of species in each region of the Coorong for the three sampling zones, based on all investigations from February 2020 to August 2021, and shown separate for taxa, prey types and trophic groups. The zones were: I = Intertidal mudflat, S = Subtidal sediment, and P = Peninsula mudflat. The peninsula zone could not be sampled in the South Lagoon.

	TAXA			PREY TYPES			TROPHIC GROUPS		
REGION	I	S	P	I	S	P	I	S	P
South Lagoon	11	10		3	2		5	5	
North Lagoon	23	23	21	4	5	5	7	8	7
Murray Estuary	18	31	24	5	5	5	7	9	8
All regions	28	38	29	5	5	5	9	9	8

Table 13. Test results from permutational ANOVA (PERMANOVA) on differences in macroinvertebrate species density, by taxa, prey type categories and by trophic groups, across the regions (Re) and zones (intertidal mudflat, peninsula mudflat, subtidal sediment) over the entire survey period from February 2020 to August 2021. Significant P-values are shown in bold.

		TAXA			PREY TYPES			TROPHIC GROUPS		
MAIN TEST	df	MS	PSEUDO-F	$P_{(PERM)}$	MS	PSEUDO-F	$P_{(PERM)}$	MS	PSEUDO-F	$P_{(PERM)}$
Region (Re)	2	3590.30	1250.30	**0.0001**	478.38	699.58	**0.0001**	1377.90	1131.00	**0.0001**
Zone (Zo)	2	10.58	3.68	**0.0253**	1.66	2.43	0.0929	9.77	8.02	**0.0001**
Re x Zo	3	15.39	5.36	**0.0010**	3.25	4.76	**0.0019**	14.21	11.67	**0.0001**
Residual	1525	2.87			0.68			1.22		

The number of taxa, prey types and trophic groups decreased significantly with increasing salinities, and over 60% of the variability in species richness could be explained by salinity (Figure 12). The slopes of linear fits were significantly different from zero (P <0.05) in all cases. Consequently, at the higher salinities in the South Lagoon, there is less choice of accessible prey types for benthivorous fish and shorebirds with different foraging strategies.

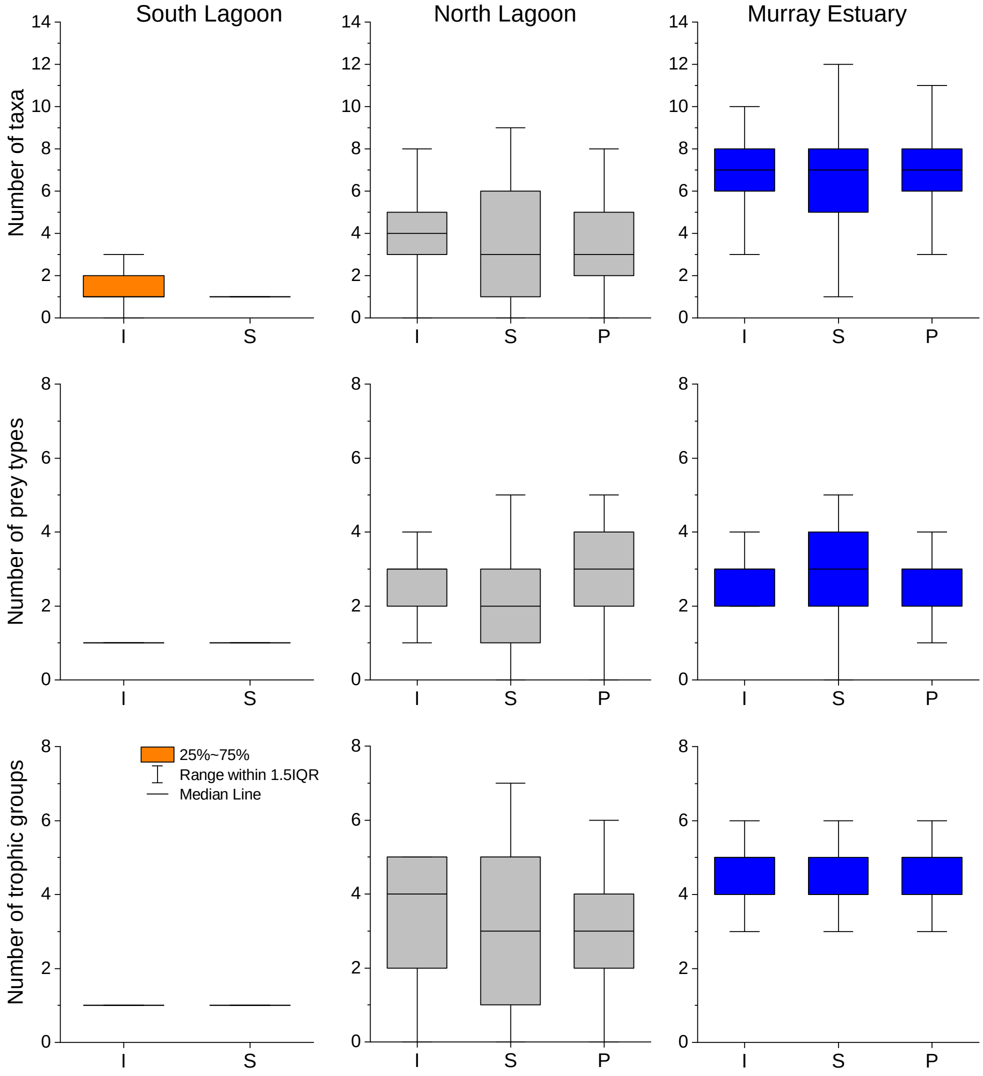

Figure 11. Boxplot of macroinvertebrate species density based on taxa, prey type categories and trophic groups per region and zone in the Coorong, based on all surveys between February 2020 and August 2021. The zones were: I = Intertidal mudflat, S = Subtidal sediment, and P = Peninsula mudflat. The peninsula zone could not be sampled in the South Lagoon. The whiskers display the 1.5 interquartile range IQR.

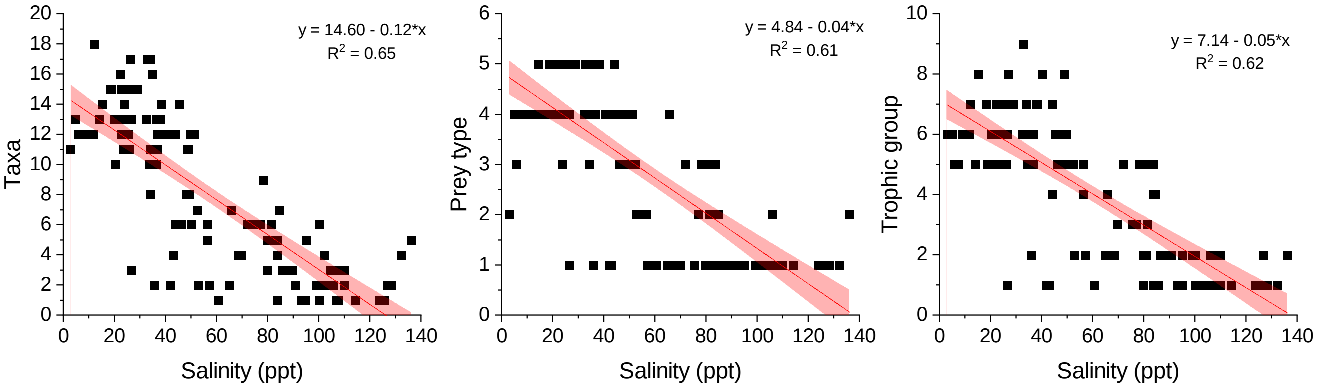

Figure 12. Correlations between taxonomic richness, the number of prey types and trophic groups of macroinvertebrates found during all surveys from February 2020 and August 2021 (n = 117). Linear fits are shown with 95% confidence bands.

Macroinvertebrate individual densities

The individual densities of macroinvertebrates were significantly lower in the South Lagoon than in the North Lagoon and Murray Estuary, over the entire study period and in each survey (Figure 13, Table 14, and for pairwise tests Appendix Table B.5). The median over all surveys from February 2020 to August 2021 was 480 individuals m^{-2} for the South Lagoon compared to median densities of 32,524 individuals m^{-2} for the North Lagoon and 77,559 individuals m^{-2} for the Murray Estuary respectively. In most of the surveys, individual densities were not significantly different between the North Lagoon and Murray Estuary (Appendix Table B.5).

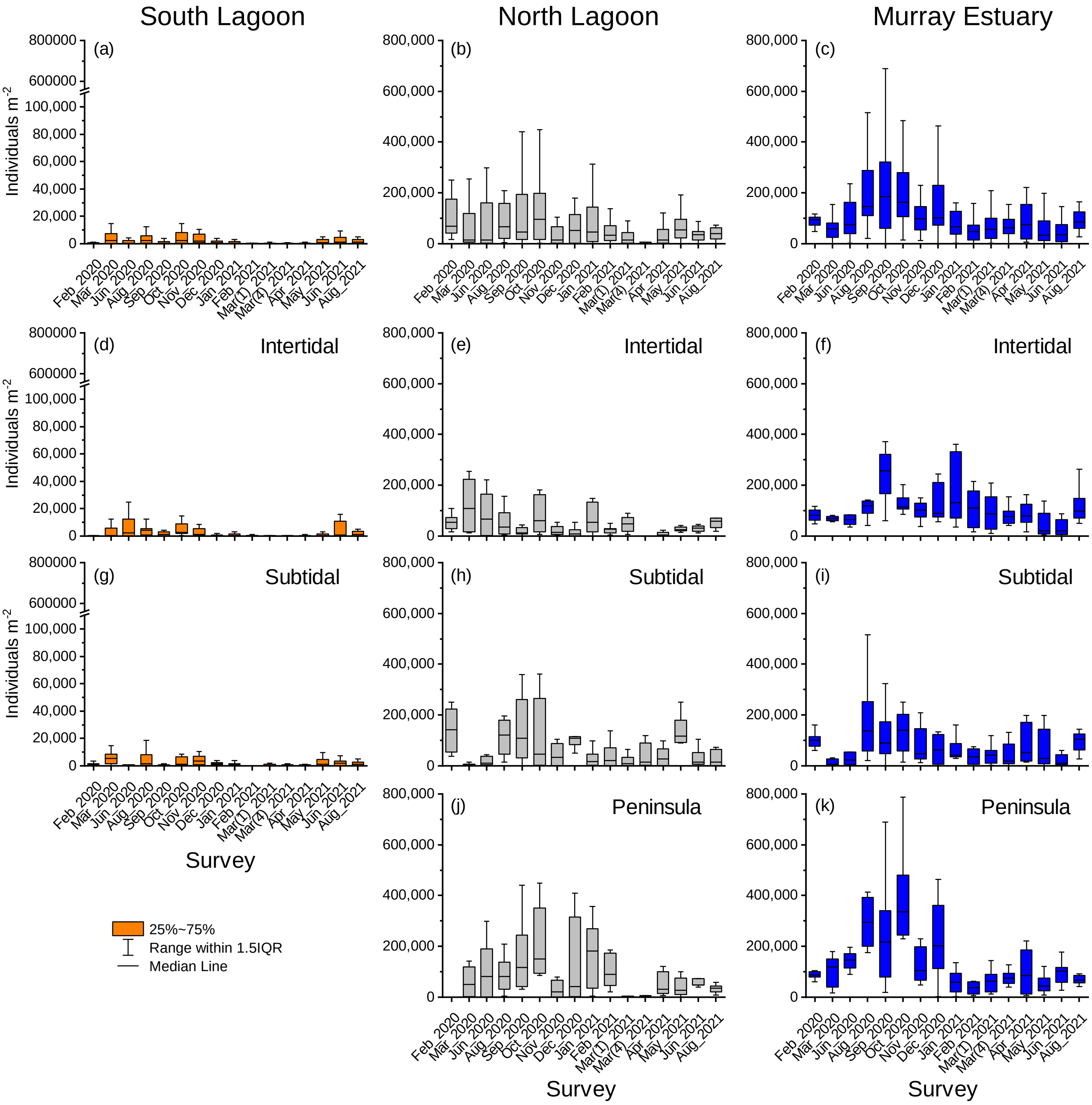

Figure 13. Box plots of macroinvertebrate abundances (individuals m^{-2}) per region and survey, and for the zones, with (d), (e) and (f) for intertidal mudflats, (g), (h) and (i) for subtidal sediments, and (j) and (k) for mudflats on the peninsula side. Graphs (a), (d) and (g) are for the South Lagoon, graphs (b), (e), (h) and (j) for the North Lagoon, and (c), (f), (i) and (k) for the Murray Estuary. Note the break in the y-axis scale for the South Lagoon graphs. The whiskers display the 1.5 interquartile range IQR.

In seasonal surveys from December 2020 onwards, two additional sites were sampled for macroinvertebrates in the North Lagoon for further comparison with fish data. For the median macroinvertebrate individual density per region, including or excluding the data from these two sites gave similar box plots (Appendix

Figure A.3). Data from these two sites were therefore not included in analyses across all surveys to keep a more balanced design.

Individual densities were variable across the surveys for each of the zones, with macroinvertebrates in mudflats on the peninsula side contributing most to the pattern over the months (Figure 13). In both the North Lagoon and Murray Estuary, densities increased over the spring and summer months and were lower in late summer and autumn (Figure 13, Appendix Table B.6). The seasonal increase in densities coincided with higher flows over the barrages (Figure 14).

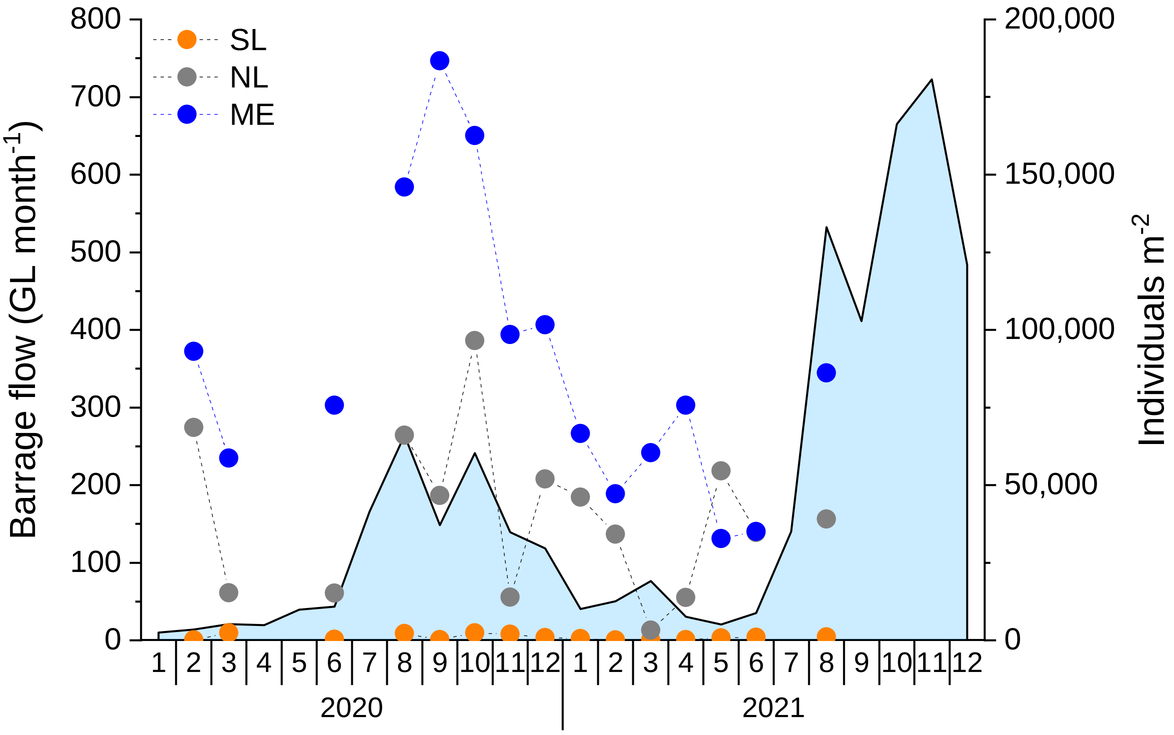

Figure 14. Median abundances of macroinvertebrates (coloured circles) for each region and survey month with underlying monthly flow over the barrages (flow data from DEW). The regions were SL = South Lagoon, NL = North Lagoon, ME = Murray Estuary.

Macroinvertebrates occurring in the South Lagoon were predominantly of the 'Surface-small' prey type, with few individuals of other prey types found. The density of 'Surface-small' prey for benthivorous predators was higher in the North Lagoon and Murray Estuary than in the South Lagoon (Figure 15). The 'Surface-small' prey type was the most abundant of all prey types, with the 'Surface-medium' prey type also abundant in the North Lagoon, and the 'Deep-large' prey type in the Murray Estuary (Figure 15). Individual densities of all prey types varied significantly between regions and surveys (Table 14). The prey type 'Epifauna-large', which included mysid shrimps, was more abundant during periods of higher flow (Figure 14 and 15).

Table 14. Test results from permutational ANOVA (PERMANOVA) on differences in macroinvertebrate densities, by total individual density and prey type categories (based on habitat and size, see Table 9), across the three regions (Re) of the Coorong and over the surveys (Su) from February 2020 to August 2021. S-M = Surface-Medium, S-S = Surface-Small, S-L = Surface-Large, E-L = Epifauna-Large, D-L = Deep-Large. Significant P-values are shown in bold.

		TOTAL INDIVIDUAL DENSITY			PREY TYPES				
					S-M	S-S	S-L	E-L	D-L
MAIN TEST	df	MS	PSEUDO-F	P(PERM)	P(PERM)	P(PERM)	P(PERM)	P(PERM)	P(PERM)
Region (Re)	2	18714.00	1017.50	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**
Survey (Su)	15	253.26	13.77	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0003**
Re x Su	30	84.36	4.59	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0274**
Residual	1410	18.39							

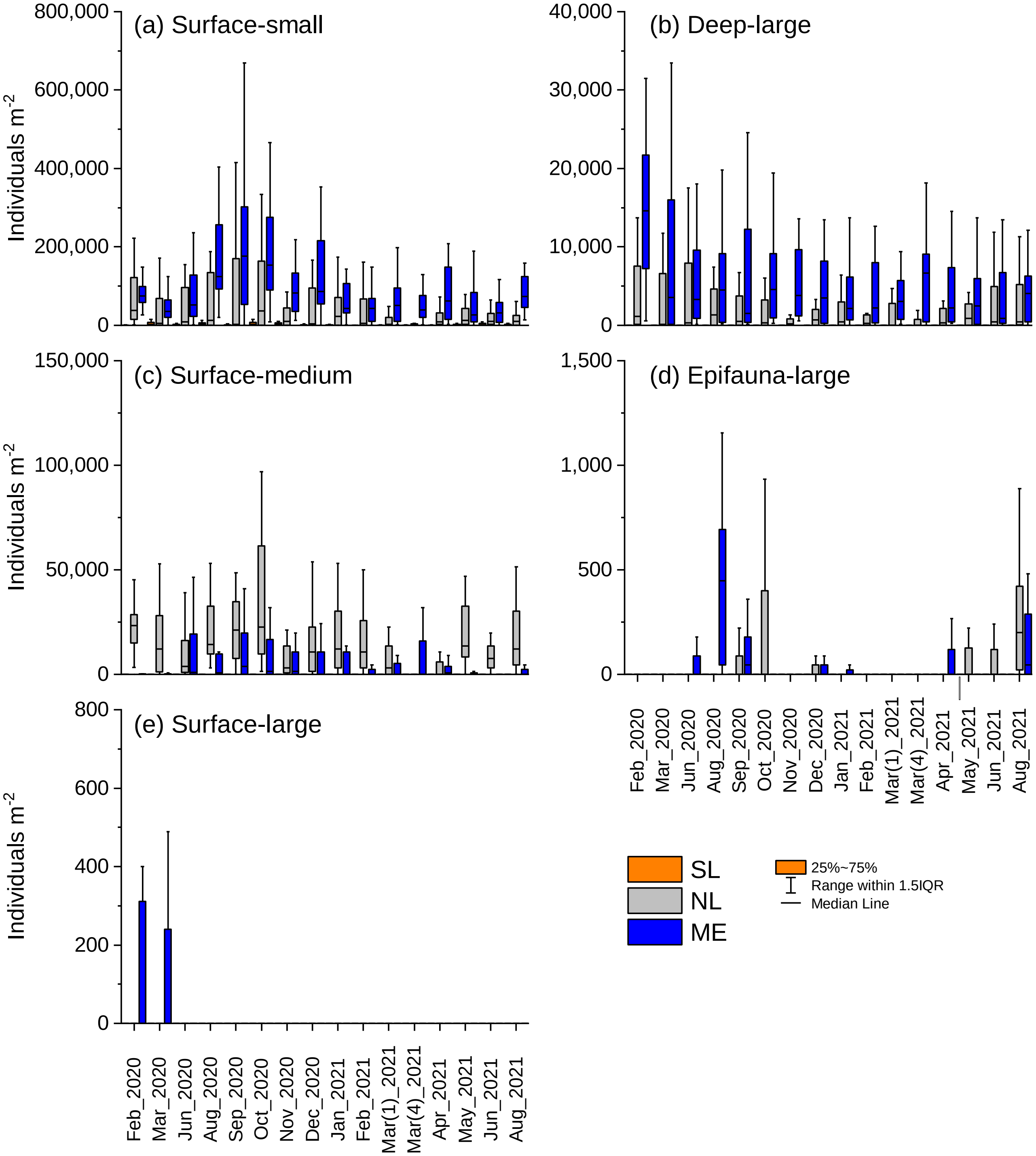

Figure 15. Box plot of macroinvertebrate individual densities, grouped into prey access types based on their habitat and size, across regions and surveys from February 2020 to August 2021. See Table 9 for species allocated to each prey type. The regions are ME – Murray Estuary, NL – North Lagoon and SL – South Lagoon of the Coorong. Note the differences in y-axis scales. The whiskers display the 1.5 interquartile range IQR.

Chironomids and other insect larvae accounted for the abundance of the 'Surface-small' prey type in the South Lagoon (Figures 15a and 16b). By trophic group, only 'Insect larvae/pupae' and occasionally a few individuals of 'Benthic-pelagic crustaceans' were found in the South Lagoon (Figure 16). The higher density of the 'Surface-small' prey type in the North Lagoon and Murray Estuary came from individual densities of key species such as amphipods, *Arthritica semen*, *Boccardiella limnicola*, hydrobiid snails and *Salinator* fragilis. Under trophic group classification, these key species were 'Benthic-pelagic crustaceans', 'Benthic micro-molluscs' and 'Benthic annelids' (Figure 16a, c, d). The seasonal variability seen in the total individual density of macroinvertebrates, mainly in the Murray Estuary (Figure 13b), and of the 'Surface-small' prey type (Figure 15a) came from 'Benthic-pelagic crustaceans' and 'Benthic micro-molluscs' (Figure 16a, c). The similar abundance pattern over the surveys for the ‘Deep-large’ (Figure 15b) and ‘Benthic annelids’ (Figure 16e) came mostly from the high density of the polychaete *Simplisetia aequisetis*. The larger bivalves *Spisula trigonella* and *Hiatula alba* were also classed as ‘Deep-large’ prey, but occurred with low individual densities in the Murray Estuary and North Lagoon, as seen when they were grouped as ‘Subtidal benthic-molluscs’ (Figure 16d). The polychaete *Capitella* accounted for most of the relatively high individual densities of the ‘Surface-medium’ prey type and the ‘Benthic deposit-feeding annelids (Figure 16f). Crabs (Benthic Decapoda) were rarely captured with the corer and grab sampling method, and their density was low and not significantly different between surveys (Table 15). For all other trophic groups, individual densities were significantly different between surveys and regions (Table 15).

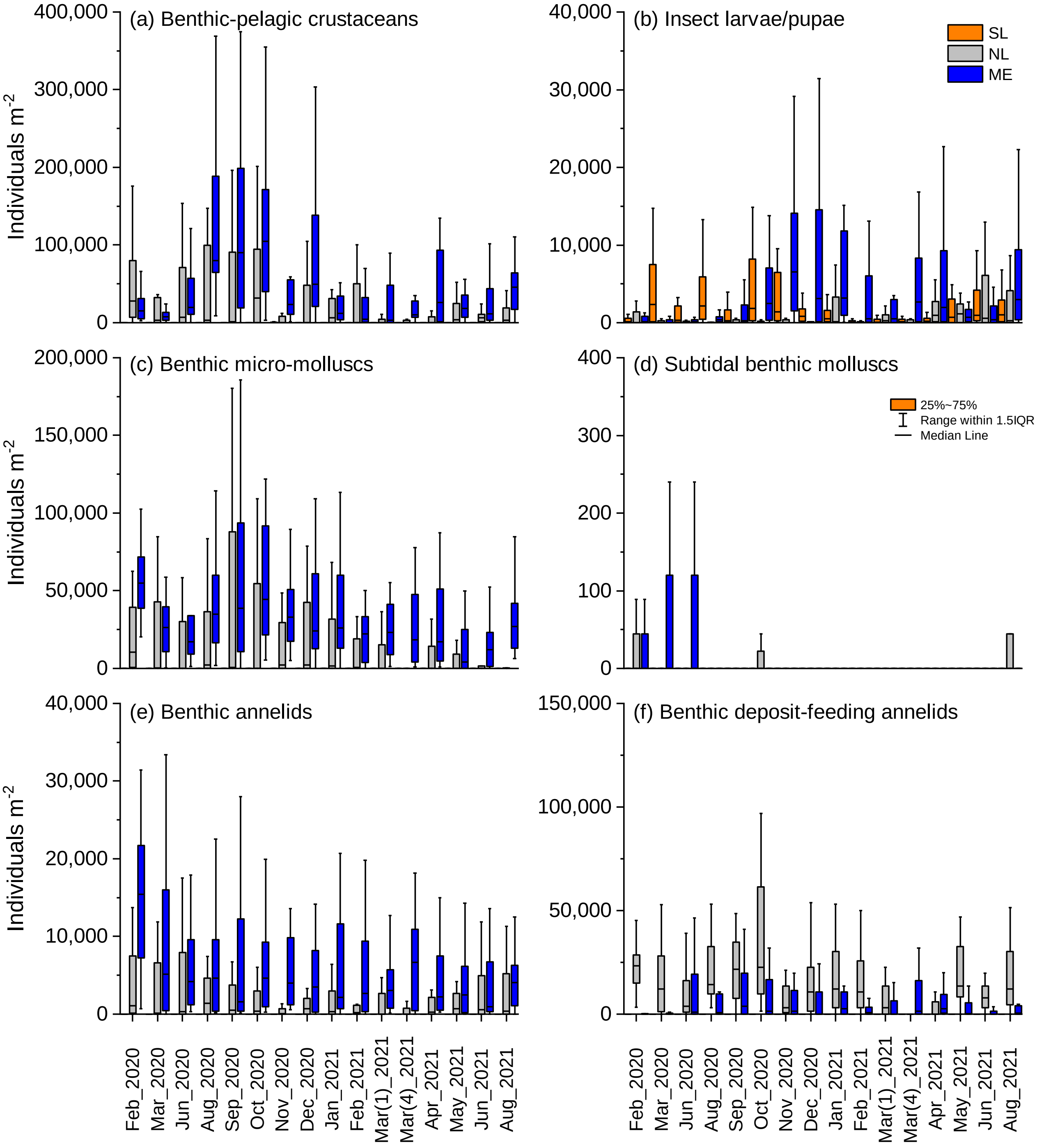

Figure 16. Box plot of macroinvertebrate individual density, grouped into trophic groups, across regions and surveys from February 2020 to August 2021. See Table 9 for species allocated to each trophic group. The regions are ME – Murray Estuary, NL – North Lagoon and SL – South Lagoon of the Coorong. Note the differences in y-axis scales. The whiskers display the 1.5 interquartile range IQR.

Table 15. Test results (permutation p-values) from permutational ANOVA (PERMANOVA) on differences in macroinvertebrate individual densities, by trophic groups, across the three regions (Re) of the Coorong and over the surveys (Su) from February 2020 to August 2021. The trophic groups are B-p-C for Benthic-pelagic Crustacea, B-A for Benthic Annelida, B-df-A for Benthic deposit feeding Annelida, B-m-M for Benthic micro-Mollusca, S-M for Subtidal benthic molluscs, I-lp for Insect larvae/pupae, B-D for Benthic Decapoda. Ficopomatus and 'other' trophic groups were rarely encountered in the surveys and not tested. Significant P-values are shown in bold.

		B-p-C	B-A	B-df-A	B-m-M	S-M	I-LP	B-D
MAIN TEST	df	$P_{(PERM)}$	$P_{(PERM)}$	$P_{(PERM)}$	$P_{(PERM)}$	$P_{(PERM)}$	$P_{(PERM)}$	$P_{(PERM)}$
Region (Re)	2	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**
Survey (Su)	15	**0.0001**	**0.0007**	**0.0001**	**0.0001**	**0.0015**	**0.0001**	0.0674
Re x Su	30	**0.0001**	**0.0264**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**
Residual	1410							

Salinity was a main driver of macroinvertebrate individual densities, as high densities were only recorded when salinity was <50 ppt (Figure 17a). This pattern of high individual densities at brackish to marine salinities was also apparent for individual macroinvertebrate species and taxa (Figure 18). The polychaete *Capitella* was found in salinities up to 80 ppt (Figure 18e). Only chironomid larvae were found in high densities along the entire salinity range, but the highest densities were also found under fresh to brackish conditions (Figure 18c). Ostracods are salt tolerant species and occurred in higher salinities, but their overall density was low (Figure 18i).

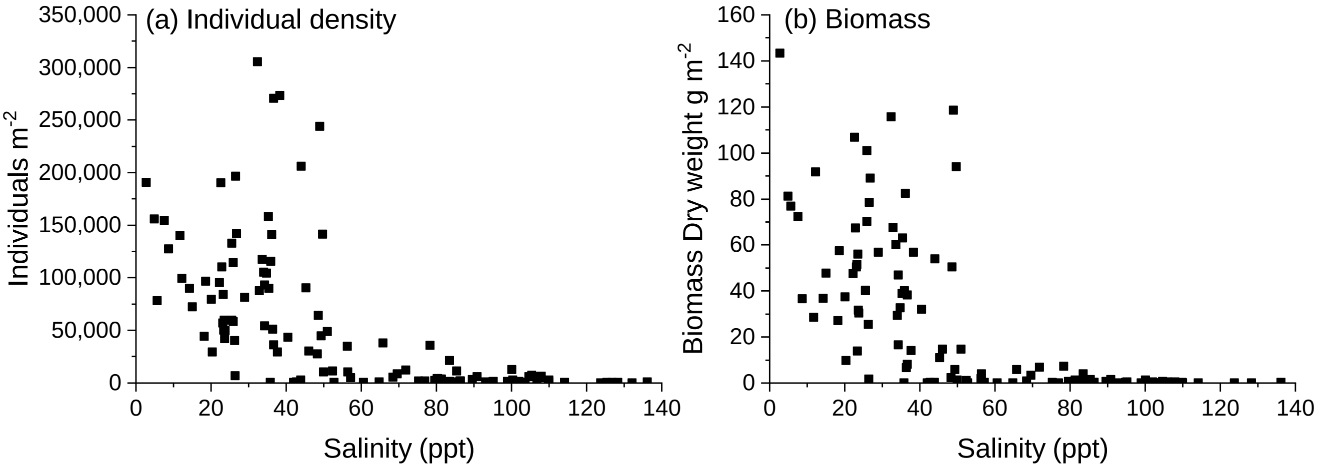

Figure 17. Scatterplot with (a) individual densities and (b) biomass of macroinvertebrates against salinities recorded in the field for all surveys and sites from February 2020 to August 2021. Zero values for densities and biomass were not included.

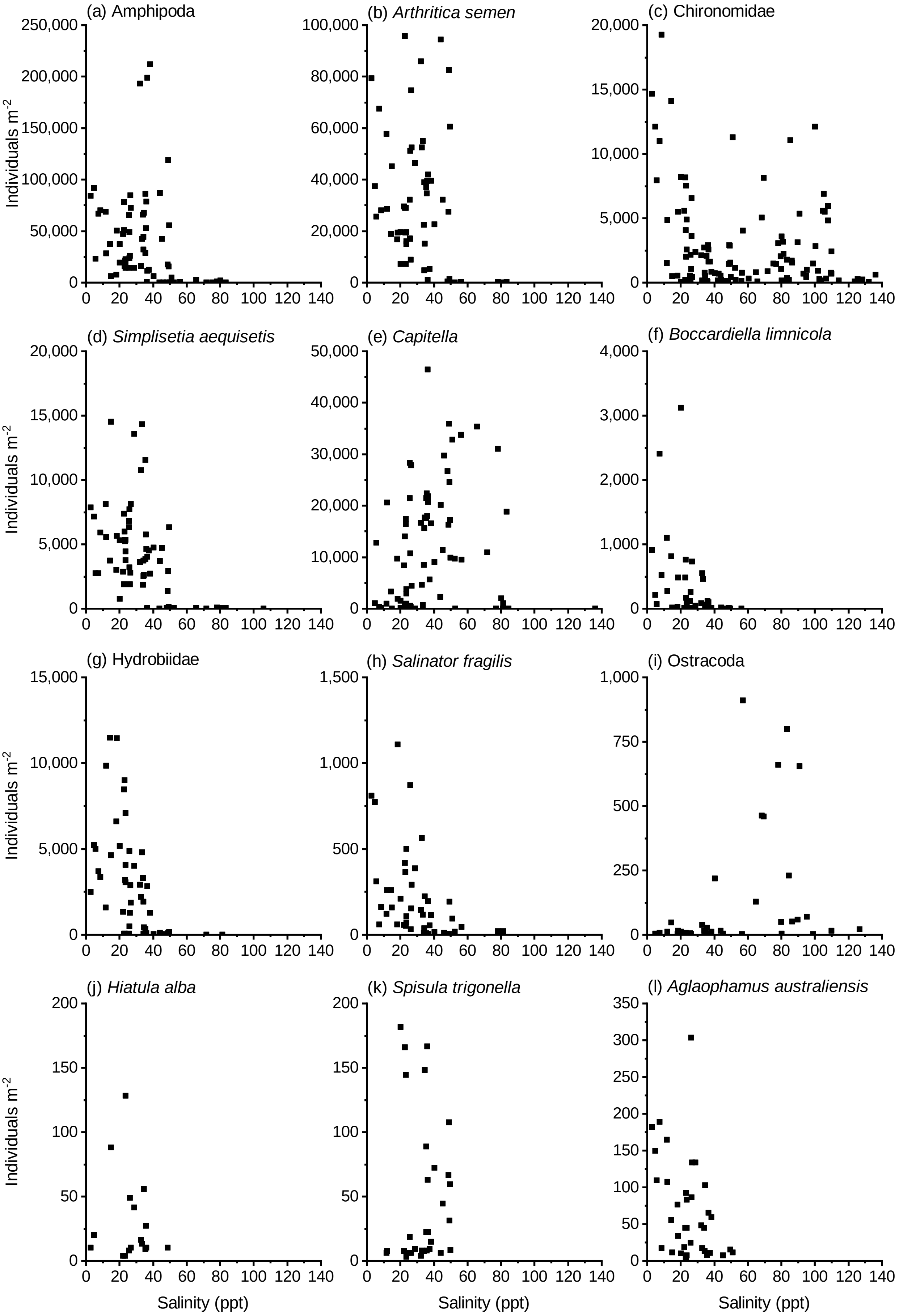

Figure 18. Scatterplot of individual densities of key macroinvertebrate species and taxa against salinities recorded in the field for all surveys and sites from February 2020 to August 2021. Note the different y-axis scales. Zero values for densities were not included.

Macroinvertebrate biomass

Similar to the patterns across regions for individual densities, biomass of macroinvertebrates was significantly lower in the South Lagoon (median wet mass 0.13 g m^{-2} across surveys from February 2020 to August 2021) than in the North Lagoon (median wet mass 24.70 g m^{-2}) and Murray Estuary (median wet mass 106.84 g m^{-2}) (Figure 19, Table 16). In dry mass (DM), the median for the South Lagoon was 0 g m^{-2}, for the North Lagoon 5.64 g m^{-2} and for the Murray Estuary 40.65 g m^{-2} (Figure 19). The dry to wet mass ratio over all macroinvertebrate taxa was 0.32 (see Section 3.3.1, Table 29 for species specific ratios). Biomass was significantly different between the regions for every survey, apart from several surveys (September and December 2020, May and June 2021) when biomass was similar between the North Lagoon and Murray Estuary (Tables B.5 and B6). The high variability in macroinvertebrate biomass within each region and survey was due to fine scale differences between sites within regions and across the zones within sites.

Macroinvertebrate biomass did not align with individual densities for all taxa, for example amphipods were recorded in very high densities (Figure 18a) but did not have the highest biomass values (Figure 20a). Some of the highest biomass values in g dry mass m^{-2} were recorded for *Arthritica semen*, which was also very abundant (Figures 18b and 20b).

Some of the higher biomass values in each region were recorded in surveys which occurred in periods of higher flow (Figure 19 and 4). Biomass of macroinvertebrates was negligible at salinities >50 ppt (Figure 17b). For single taxa, highest biomass was recorded at brackish to marine salinities (Figure 20). For some key species like amphipods (Figure 20a), *Simplisetia aequisetis* (Figure 20d) and hydrobiid snails (Figure 20g), biomass was highest at salinities of about 20 to 40 ppt. For chironomid larvae, no pattern between biomass and salinity was apparent. Biomass of chironomid larvae was low (mostly ≤1 g m^{-2} dry mass) but greater than zero across all salinities (Figure 20c).

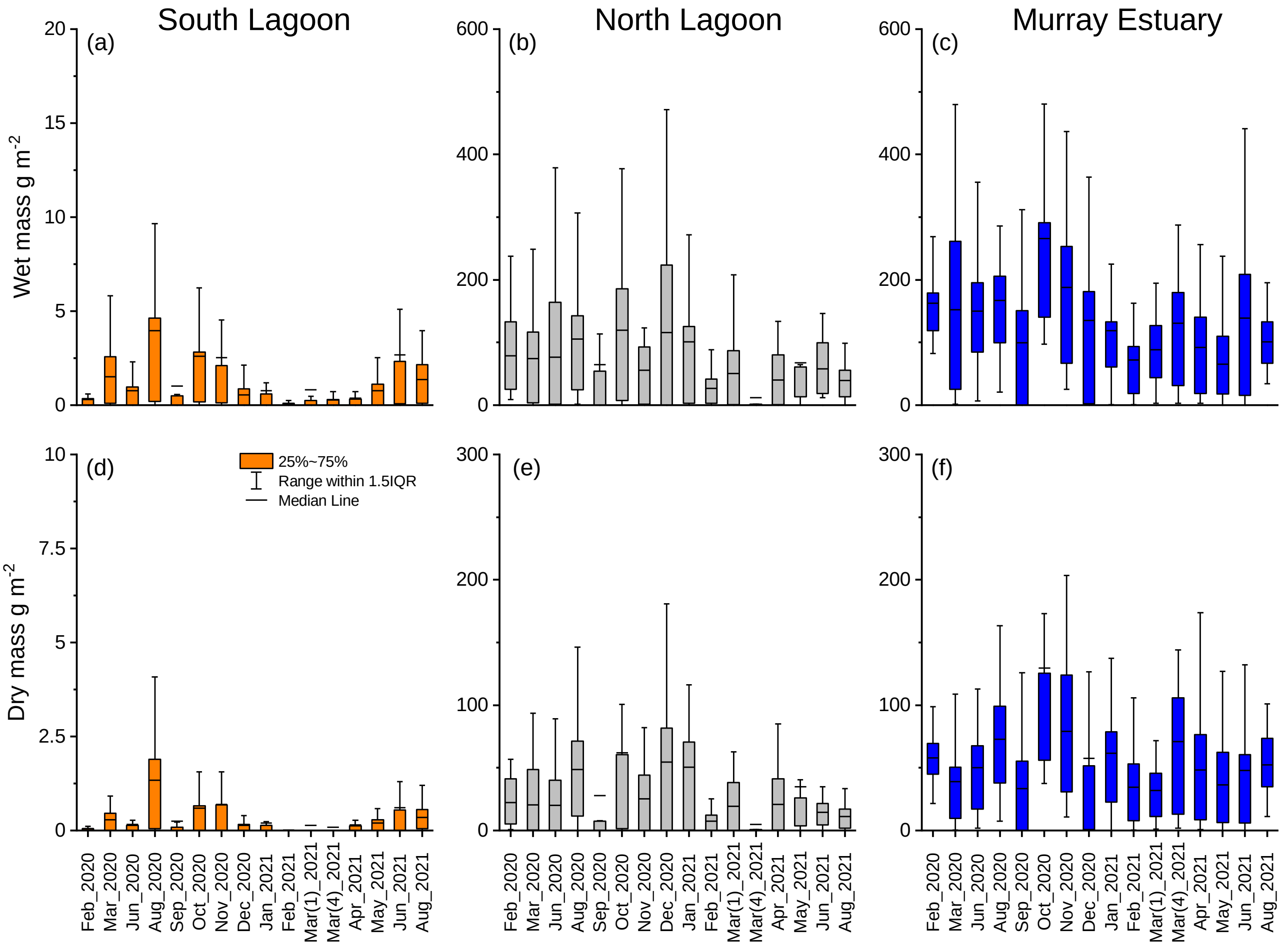

Figure 19. Box plot of macroinvertebrate biomass (g m^{-2}) in wet mass (a, b, c) and dry mass (d, e, f) for each of the regions and surveys from February 2020 to August 2021. Note the differences in y-axis scales. The whiskers display the 1.5 interquartile range IQR.

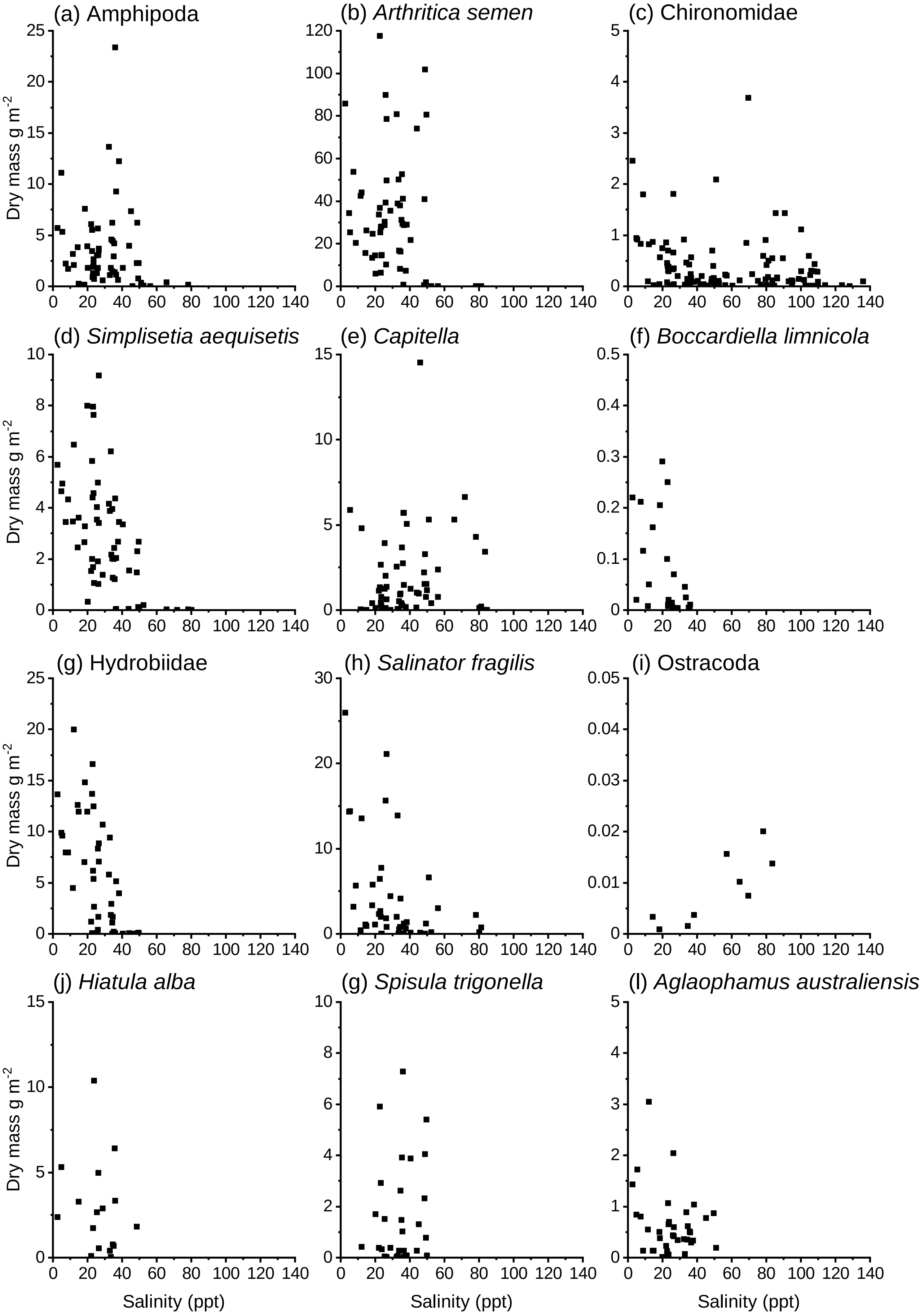

Figure 20. Scatterplot of biomass (dry weights g m^{-2}) of key macroinvertebrate species and taxa against salinities recorded in the field for all surveys and sites from February 2020 to August 2021. Note the different y-axis scales. Zero values for biomass were not included.

Table 16. Test results from permutational ANOVA (PERMANOVA) on differences in macroinvertebrate biomass, by total individual biomass and prey type categories, across the three regions (Re) of the Coorong and over the surveys (Su) from February 2020 to August 2021. Biomass differences were tested for both wet and dry mass. Significant P-values are shown in bold.

		WET MASS			DRY MASS		
MAIN TEST	df	MS	PSEUDO-F	$P_{(PERM)}$	MS	PSEUDO-F	$P_{(PERM)}$
WET MASS							
Region (Re)	2	747.13	953.60	**0.0001**	523.52	921.64	**0.0001**
Survey (Su)	15	8.71	11.11	**0.0001**	5.73	10.08	**0.0001**
Re x Su	30	2.20	2.81	**0.0001**	1.81	3.18	**0.0001**
Residual	1410	0.78			0.57		

The 'Surface-small' prey type accounted for most biomass in the Murray Estuary and North Lagoon and, to a lesser extent, in the South Lagoon (Figure 21a). No biomass of other macroinvertebrate prey types was available for higher trophic levels in the South Lagoon (Figure 21). In the North Lagoon and particularly in the Murray Estuary, biomass of larger macroinvertebrates living deeper in the sediment was also high, as this prey type was mostly composed of *Simplisetia aequisetis* and the larger bivalves *Spisula trigonella* and *Hiatula alba* (Figure 21b). Biomass for all prey types was significantly different across regions and surveys (Table 17).

Table 17 Test results from permutational ANOVA (PERMANOVA) on differences in macroinvertebrate biomass by prey type and trophic groups (see Table 9 for species allocated to each prey type and trophic group), across the three regions (Re) of the Coorong and over the surveys (Su) from February 2020 to August 2021. The prey types are S-M = Surface-Medium, S-S = Surface-Small, S-L = Surface-Large, E-L = Epifauna-Large, D-L = Deep-Large. The trophic groups are B-p-C for Benthic-pelagic Crustacea, B-A for Benthic Annelida, B-df-A for Benthic deposit feeding Annelida, B-m-M for Benthic micro-Mollusca, S-M for Subtidal benthic molluscs, I-lp for Insect larvae/pupae, B-D for Benthic Decapoda. Ficopomatus and 'other' trophic groups were rarely encountered in the surveys and not tested. Significant P-values are shown in bold.

		PREY TYPES					TROPHIC GROUPS					
		S-M	S-S	S-L	E-L	D-L	B-p-C	B-A	B-df-A	B-m-M	S-M	I-LP
MAIN TEST	df	$P_{(PERM)}$	$P_{(PERM)}$	$P_{(PERM)}$	$P_{(PERM)}$	$P_{(PERM)}$	$P_{(PERM)}$	$P_{(PERM)}$	$P_{(PERM)}$	$P_{(PERM)}$	$P_{(PERM)}$	$P_{(PERM)}$
WET MASS												
Region (Re)	2	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**
Survey (Su)	15	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**
Re x Su	30	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**
Residual	1410											

The 'Benthic micro-molluscs' trophic group, comprising *Arthritica semen*, hydrobiid snails and *Salinator fragilis*, was recorded throughout in high biomass (Figure 22c), followed by 'Benthic annelids' (Figure 22e), 'Benthic-pelagic crustaceans' (Figure 22a) and 'Benthic deposit-feeding annelids' (Figure 22f). Biomass of 'Insect larvae/pupae' occurred in the South Lagoon with similar biomass values as in the North Lagoon and Murray Estuary for several surveys (Figure 22b). Biomass of this trophic group was, however, mostly low (note y-axis scale in Figure 22b). Biomass by trophic groups also varied significantly between regions and surveys (Table 17).

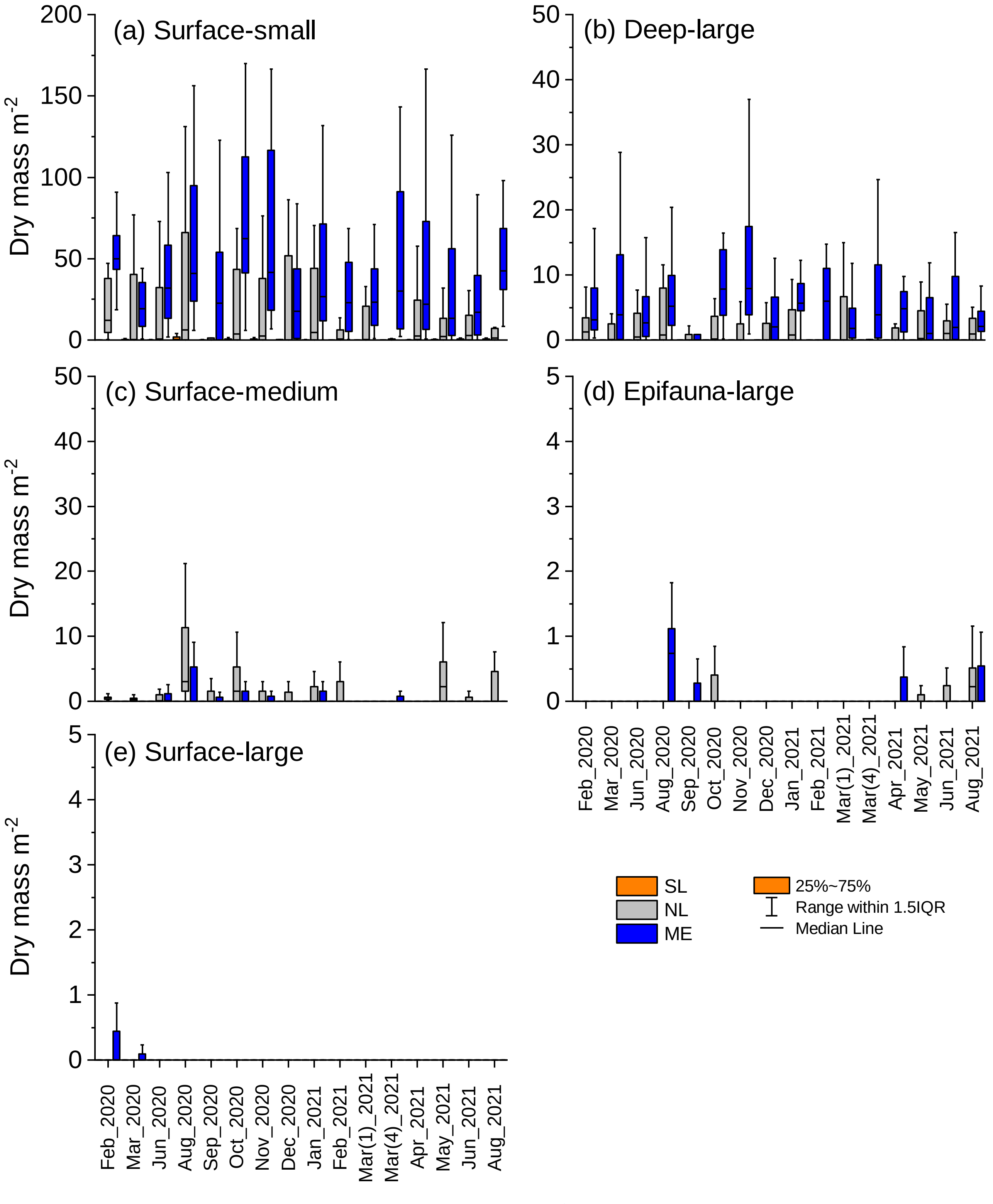

Figure 21. Box plot of macroinvertebrate biomass (dry mass g m^{-2}), grouped into prey access types based on their habitat and size, across regions and surveys from February 2020 to August 2021. See Table 9 for species allocated to each prey type. The regions are ME – Murray Estuary, NL – North Lagoon and SL – South Lagoon of the Coorong. Note the differences in y-axis scales. The whiskers display the 1.5 interquartile range IQR.

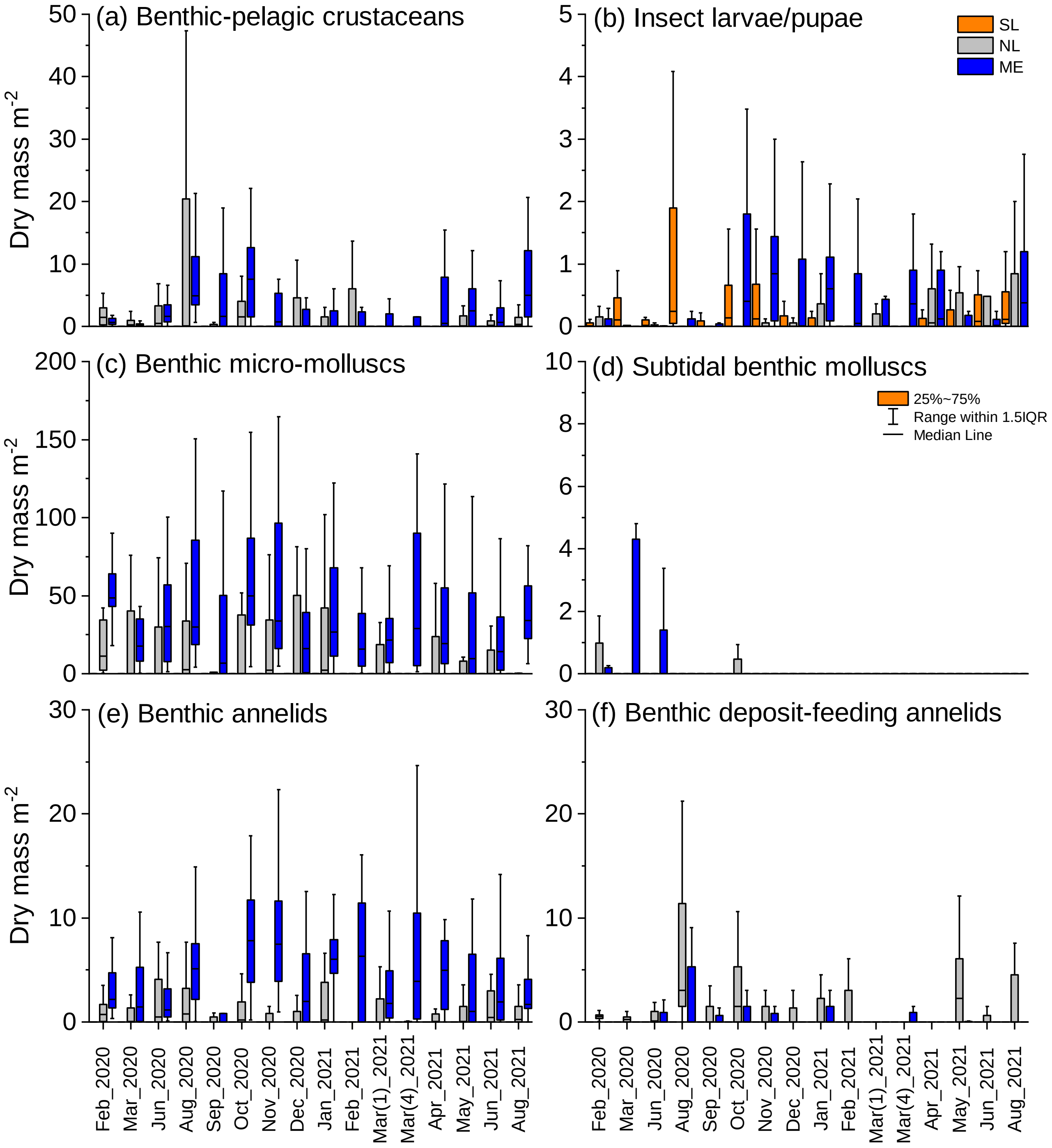

Figure 22. Box plot of macroinvertebrate biomass (dry mass g m^{-2}), grouped into trophic groups, across regions and surveys from February 2020 to August 2021. See Table 9 for species allocated to each prey type. The regions are ME – Murray Estuary, NL – North Lagoon and SL – South Lagoon of the Coorong. Note the differences in y-axis scales. The whiskers display the 1.5 interquartile range IQR.

Macroinvertebrate density to biomass conversion

To facilitate future assessments of biomass and energy density calculations, equations relating individual counts, wet and dry mass were developed for 18 macroinvertebrate species in the Coorong (Table 18). Correlations between wet mass and dry mass were best (highest R^2) for almost all taxa (Table 18). For several taxa, including key species like amphipods and *Arthritica semen*, correlations were also good between individual counts and mass. For those taxa which often occur with different individual sizes in the samples, such as *Simplisetia aequisetis* and *Salinator fragilis*, however, the conversion from individual counts to mass was poor (low R^2 in Table 18) and cannot be recommended. Scatterplots with linear fits for the taxa and conversion given in Table 18 are provided in Appendix A (i.e. for Annelida: Figures A.4 and A.5, for Mollusca Figure A.6, for Crustacea Figure A.7 and for Hexapoda Figure A.8).

Table 18. Equations to convert from individual count to wet mass or dry mass, or from wet mass to dry mass, for macroinvertebrates in the Coorong. The samples size for each taxon is given by 'n'. The conversions are based on frozen sample material. R^2 is the coefficient of determination showing the strength of the linear relationship.

		INDIVIDUALS TO WET MASS		INDIVIDUALS TO DRY MASS		WET MASS TO DRY MASS	
TAXA	n	EQUATION	R^2	EQUATION	R^2	EQUATION	R^2
Annelida							
Oligochaeta	5	y=0.00067*x	1.00	y=0.00004*x	0.99	y=0.06403*x	1.00
Aglaophamus australiensis	48	y=0.05485*x	0.75	y=0.00408*x	0.75	y=0.07315*x	0.97
Boccardiella limnicola	31	y=0.00056*x	0.40	y=0.00005*x	0.50	y=0.07402*x	0.95
Capitella	214	y=0.00053*x	0.67	y=0.00003*x	0.72	y=0.05023*x	0.87
Phyllodoce novaehollandiae	30	y=0.02472*x	0.75	y=0.00192*x	0.68	y=0.07779*x	0.92
Simplisetia aequisetis	243	y=0.00241*x	0.55	y=0.00021*x	0.49	y=0.08852*x	0.95
Mollusca							
Arthritica semen	232	y=0.00146*x	0.95	y=0.00080*x	0.94	y=0.54989*x	0.99
Hiatula alba	38	y=0.38644*x	0.59	y=0.05755*x	0.59	y=0.14421*x	0.94
Spisula trigonella	29	y=0.19545*x	0.71	y=0.03132*x	0.75	y=0.13756*x	0.92
Hydrobiidae	169	y=0.00203*x	0.70	y=0.00105*x	0.61	y=0.55018*x	0.98
Salinator fragilis	102	y=0.01494*x	0.19	y=0.00592*x	0.18	y=0.39702*x	0.99
Crustacea							
Amphipoda	237	y=0.00027*x	0.94	y=0.00004*x	0.93	y=0.14498*x	0.95
Mysidae	64	y=0.00606*x	0.85	y=0.00089*x	0.82	y=0.14303*x	0.92
Ostracoda	19	y=0.00017*x	0.70	y=0.00002*x	0.67	y=0.08963*x	0.51
Hexapoda							
Ceratopogonidae	23	y=0.00059*x	1.00	y=0.00012*x	0.97	y=0.19971*x	0.97
Chironomidae	352	y=0.00058*x	0.62	y=0.00011*x	0.60	y=0.19293*x	0.93
Dolichopodidae	22	y=0.00348*x	0.58	y=0.00077*x	0.45	y=0.23836*x	0.91
Stratiomyidae	21	y=0.00389*x	0.70	y=0.00105*x	0.69	y=0.27354*x	1.00

Macroinvertebrate production

Production of macroinvertebrates in the Coorong was estimated based on biomass from the monthly surveys. Production was highest for 'Benthic micro-molluscs' trophic group, due to the high production of *Arthritica semen*, followed by 'Benthic-pelagic crustaceans' which had a high production of amphipods (Table 19). 'Subtidal-benthic molluscs' had the lowest production, reflecting their low individual density and biomass in the Coorong. Production of 'Insect larvae/pupae' was also low, but their P:B ratio was relatively high (Table 19). Weighted P:B ratios ranged from 2.56 for 'Subtidal molluscs' to 8.55 for benthic-pelagic crustaceans (Table 19).

Table 19. Production, Biomass, and Production:Biomass (P:B) ratios of macroinvertebrates in the Coorong. Means of trophic groups are weighted by biomass density. As the P:B ratios were to inform the T&I food web model, the regions as used in the model were used here, whereby NC (North Coorong) comprises the Murray Estuary and North Lagoon.

TROPHIC GROUP	TAXA	REGION	PRODUCTION (g AFDM / m2 /YEAR)	OVERALL MEAN BIOMASS DENSITY (g AFDM / m^2)	P:B RATIO	WEIGHTED MEAN PRODUCTION (g AFDM / m2 /YEAR)	WEIGHTED MEAN P:B
Benthic annelids							
	Simplisetia aequisetis	NC	9.66	1.43	6.75	6.94	5.82
	Nephtyidae	NC	1.36	0.37	3.66		
	Phyllodoce	NC	0.07	0.02	3.07		
	Boccardiella	NC	0.34	0.04	8.33		
	Arenicolidae	NC	0.67	0.21	3.27		
	Australonereis ehlersi	NC	0.04	0.02	2.68		
Benthic deposit-feeding annelids							
	Capitella	NC	13.91	1.74	7.98	13.79	7.99
	Oligochaeta	NC	0.14	0.02	8.90		
Bentho-pelagic crustaceans							
	Amphipoda	NC	36.79	4.27	8.61	36.20	8.55
	Mysidae	NC	0.37	0.07	5.15		
Insect larvae/pupae							
	Chironomidae	NC	3.61	0.42	8.52	3.01	8.30
	Chironomidae	SL	2.30	0.28	8.16		
	Stratiomyidae	SL	0.11	0.02	5.67		
Benthic micro-molluscs							
	Arthritica semen	NC	102.65	16.66	6.16	87.28	5.95
	Hydrobiidae	NC	10.01	1.53	6.54		
	Salinator fragilis	NC	5.72	1.69	3.39		
Subtidal benthic molluscs							
	Spisula trigonella	NC	2.00	0.70	2.85	1.56	2.56
	Hiatula alba	NC	0.73	0.37	1.99		

Macroinvertebrate community

The macroinvertebrate community showed strong regional differentiation, with a clear separation of the South Lagoon from other regions (Figure 23). Within the northern regions of the Coorong, the North Lagoon and Murray Estuary also had distinct communities over most surveys (Figure 23). The communities were significantly different across regions and surveys (Table 20), and all pairwise test combinations between regions and surveys (Appendix Table B.6).

The communities were characterised by coherent species groups (Figure 24). The Murray Estuary and North Lagoon shared community similarity due to having similar species groups but, with several more species and relatively higher densities, the communities in the Murray Estuary were distinct. The key species *Simplisetia* *aequisetis*, amphipods, *Arthritica semen* and *Capitella* were the main species group, and a further group composed of *Boccardiella limnicola*, hydrobiid snails, *Salinator fragilis* and *Aglaophamus* (*Nephtys*) *australiensis* was typical for the Murray Estuary. Chironomids and Dolichopodidae were identified as a group present throughout the regions and surveys (Figure 24). The South Lagoon community had a further species group of salt tolerant ostracods, isopods (*Haloniscus searli*) and other insect larvae, which all occurred in relatively low density.

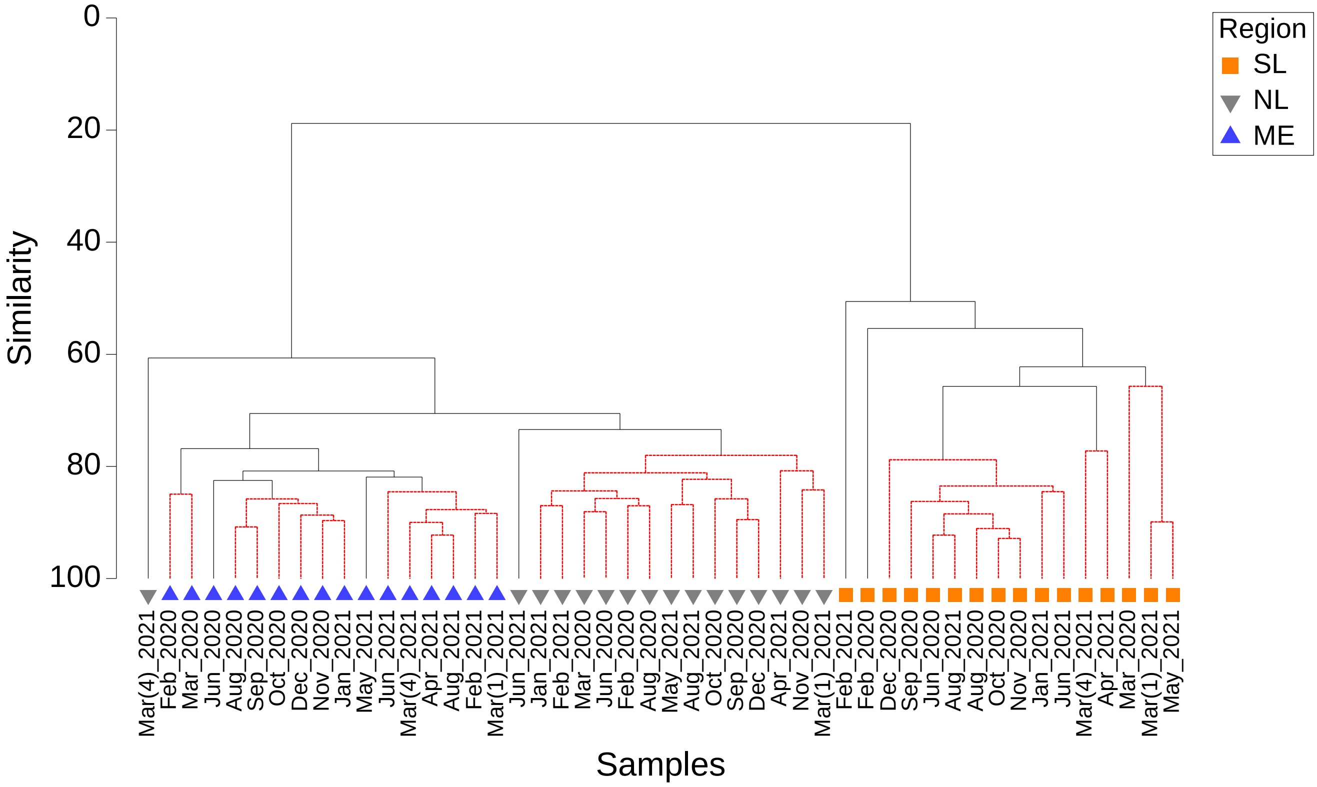

Figure 23. Dendrogram from a cluster analysis of macroinvertebrate community data for all surveys, grouped by region (SL = South Lagoon, NL = North Lagoon, ME = Murray Estuary). The black lines indicate significantly different communities based on SIMPROF tests, whereas red dotted lines indicate no community difference. Similarity is Bray-Curtis Similarity.

Table 20. Test results from permutational ANOVA (PERMANOVA) on differences in macroinvertebrate communities across the three regions (Re) of the Coorong and over the surveys (Su) from February 2020 to August 2021. Significant P-values are shown in bold.

MAIN TEST	df	MS	PSEUDO-F	P(PERM)
Region (Re)	2	747.13	953.60	**0.0001**
Survey (Su)	15	8.71	11.11	**0.0001**
Re x Su	30	2.20	2.81	**0.0001**
Residual	1405	0.78		

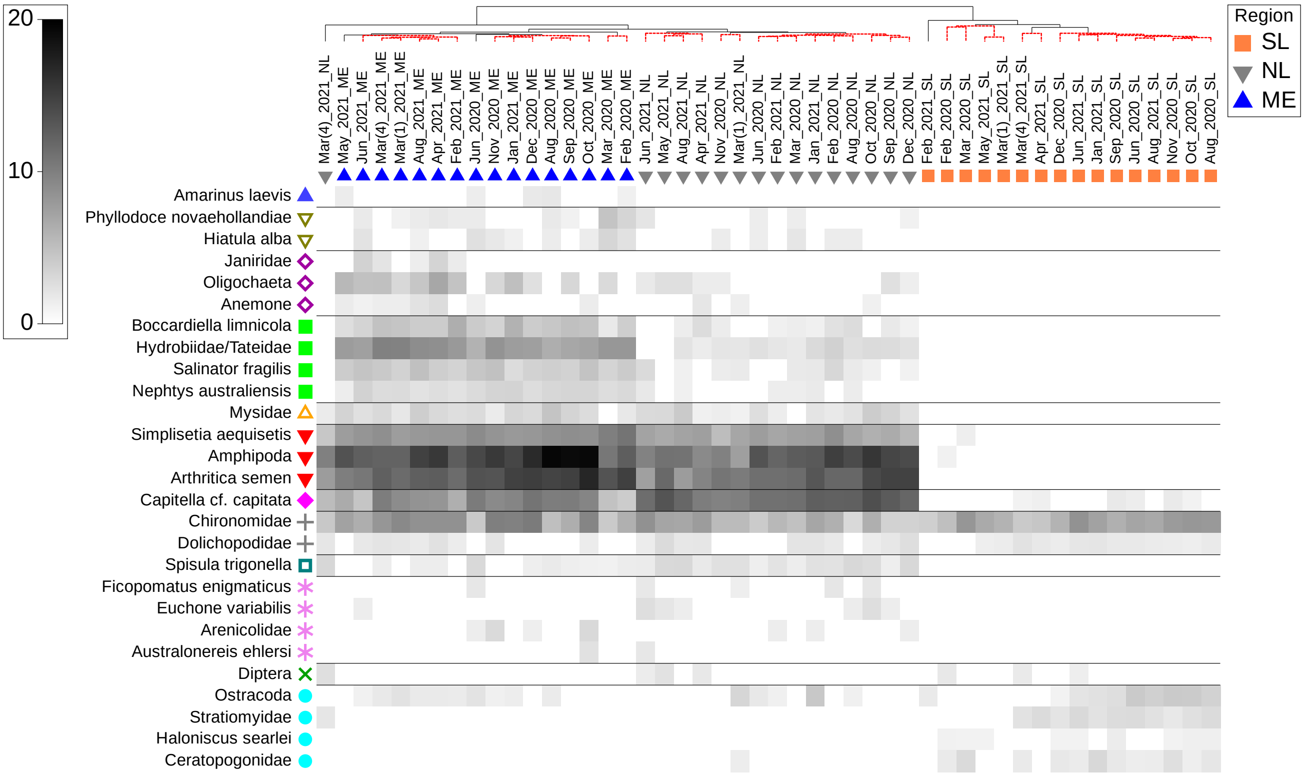

Figure 24. Shade plot for macroinvertebrate communities with coherent groups of species, indicated by colour symbols and separated by black lines. The samples (grouped by survey and region) are ordered through a cluster analysis with SIMPROF test (as in Figure 23). The 27 most abundant taxa found over all surveys are displayed in the plot. The depth of the shading corresponds to relative densities.

Environmental influences for macroinvertebrate communities

Environmental drivers for macroinvertebrate communities were analysed with water quality and flow parameters included for all surveys, and water quality and sediment properties included for December 2020 and June 2021 (surveys for which sediment characteristics were available). The strong separation of macroinvertebrate communities along the Coorong was significantly defined by salinity. The first axis explained 61.5% of the total variation, and salinity explained about 60% of this variation (Figure 25, Appendix Table B.7). The second axis explained <2% of the total variation in macroinvertebrate communities, and the other variables had no significant contributions (Appendix Table B.7).

Multivariate regression demonstrated that the main splits differentiating macroinvertebrate communities largely aligned with the three regions and were driven by salinity (Figure 26, Table 21). Salinity of <64.4 ppt split the North Lagoon and Murray Estuary from the South Lagoon (split 'A' in Figure 26), and salinity <33.8 ppt split the Murray Estuary from the North Lagoon (split 'D' in Figure 26). Further splits separated single survey months within regions and were mostly attributed to splits by water level, dissolved oxygen (DO) and barrage flow (Figure 26, Table 21). Within the South Lagoon, salinities >122 ppt split the community from February 2021, and further divisions occurred separating communities by salinities, with most surveys falling into a group with salinity <104 ppt. Barrage flow (using the monthly total for the survey month) had significant contribution to differentiating communities in the South Lagoon as well, splitting off single surveys (Figure 26, Table 21). The survey from August 2021 for the South Lagoon grouped with the North Lagoon, as the higher flows, including the Salt Creek flow, had lowered salinities in the South Lagoon and increased the water level.

The surveys for the North Lagoon were more homogenous and formed mostly one group defined by salinities >34.8 and < 64.4 ppt (split 'N' in Figure 26, Table 21). June 2021 split off because of higher water level and DO. For a few surveys, the North Lagoon sites grouped with the Murray Estuary, for example in August 2021. Macroinvertebrate communities in the Murray Estuary were characterised by salinities <33.8 ppt (split 'D' in Figure 26, Table 21), and communities from October 2020 to March 2021 and August 2021 were characterised by salinities <24.2 ppt (split 'I' in Figure 26), following the flows in spring and summer 2020-21. Water level and barrage flow variations accounted for further divisions of the Murray Estuary macroinvertebrate communities between surveys (Figure 26, Table 21).

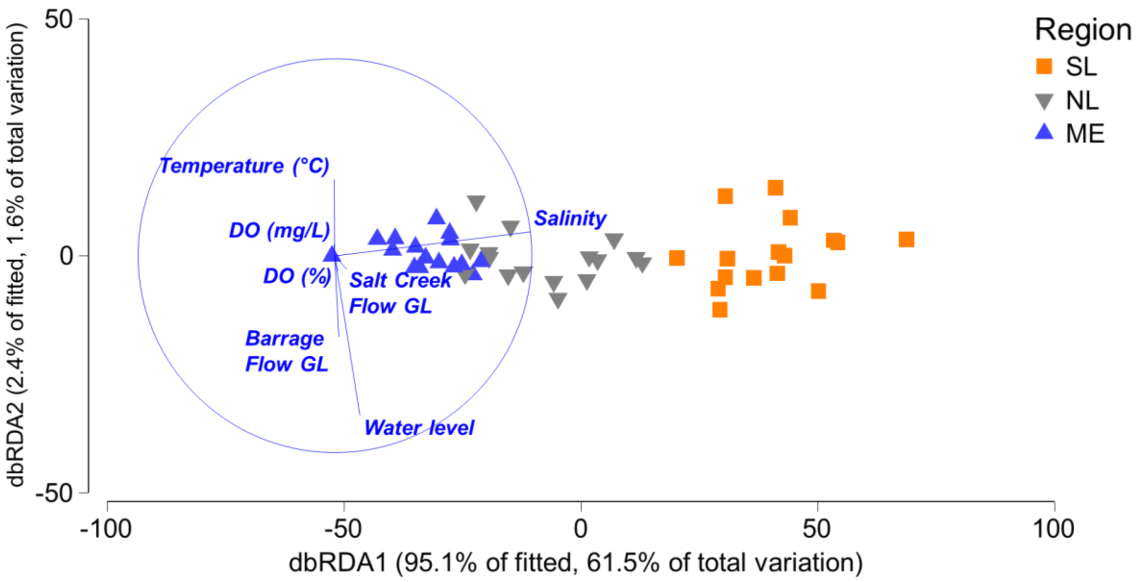

Figure 25. dbRDA plot (distance-based redundancy analysis) based on all surveys from February 2020 to August 2021 (grouped by survey-region), showing a constrained ordination of macroinvertebrate communities subject to the environmental predictor variables displayed in the vector overlay. DO = dissolved oxygen. Regions are ME = Murray Estuary, NL = North Lagoon, SL = South Lagoon.

Table 21. Outcome of LINKTREE analysis (Figure 26) with details of the environmental variables characterising the splits in macroinvertebrate communities. R is the ANOSIM R statistic and B% an absolute measure of group differences. Details are only shown for significant splits in the tree diagram.

SPLIT	R	B%	VARIABLE
A	0.92	97	Salinity<64.4(>73.8)
B	1.00	99	Water level<0.581(>0.607)
C	0.55	41	Salinity<33.8(>34.8)
D	0.57	42	Water level<0.371(>0.581)
E	0.58	36	Water level<0.232(>0.244)
F	1.00	66	Water level>0.232(<0.136) or
G	0.50	25	Barrage Flow GL<30.4(>35.2)
H	0.56	18	Barrage Flow GL<35.2(>40.3)
I	0.48	15	Salinity <24.2(>32.6)
J	0.51	12	Water level<0.244(>0.254)
N	0.90	39	DO (mg/L)>11.9(<10.4) or
T	0.86	68	Salinity >122(<110)
U	0.78	65	Barrage Flow GL<13.8(>20.4)
V	0.50	55	Barrage Flow GL>35.2(<30.4)
W	0.95	56	Salinity<104(>107)

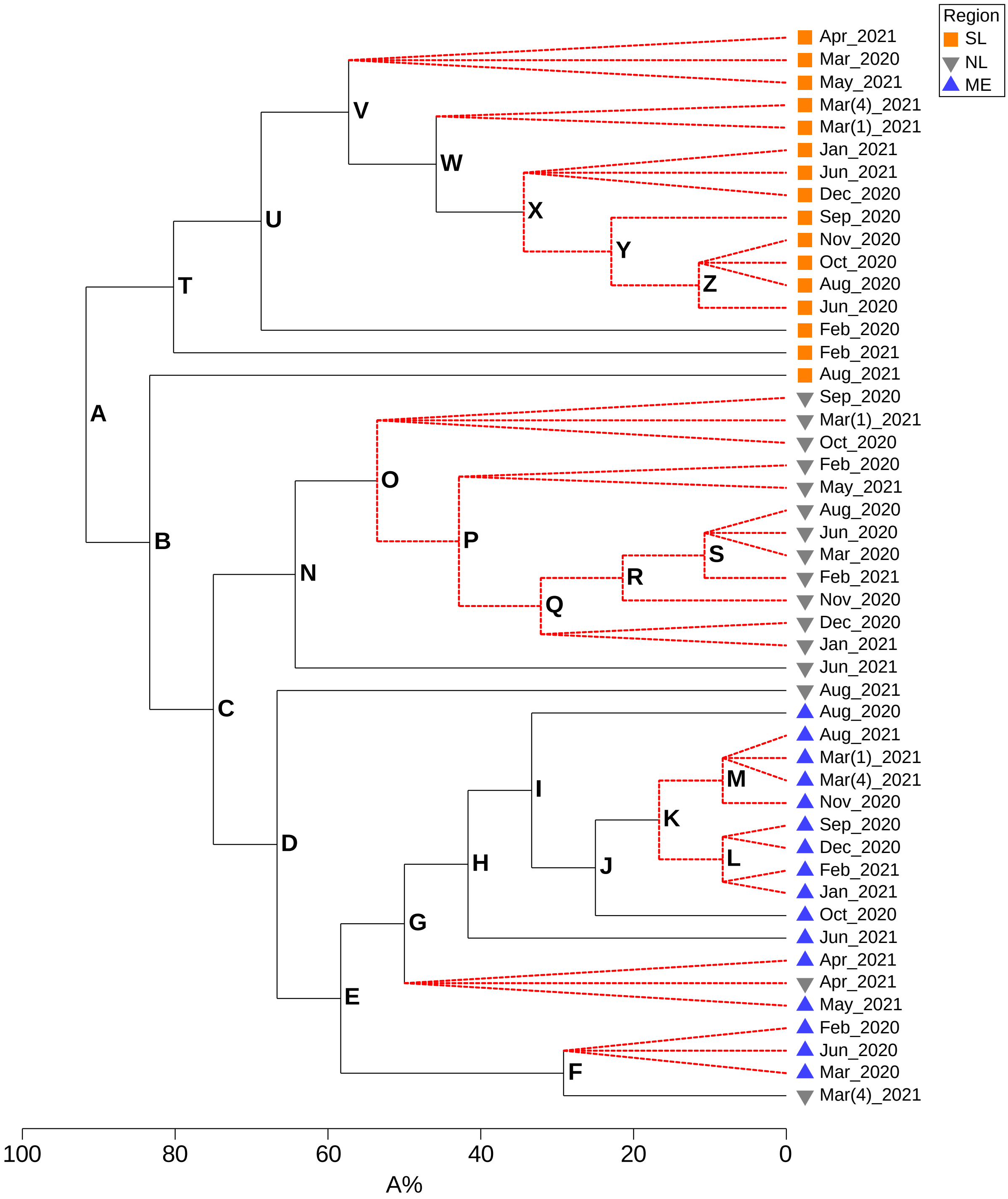

Figure 26. LINKTREE of macroinvertebrate community data for all surveys from February 2020 to August 2021 (grouped by survey and region ME = Murray Estuary, NL = North Lagoon, SL = South Lagoon). The environmental variables included for this analysis were dissolved oxygen (DO, in mg/L), salinity, average flow (monthly total in gigalitres GL), Salt Creek flow (monthly total) and average water level by region for each survey month. The A% scale displays a group split by equal spacing of dissimilarities. Red lines indicate groups that are not significantly different and black lines are separating significantly different groups based on SIMPROF tests. The splits are explained by environmental variables, see Table 21.

With sediment properties included as explanatory environmental variables for macroinvertebrates, salinity was still the main driver for the separation of communities between the South Lagoon and the North Lagoon and Murray Estuary, explaining about 49% of the variation in the macroinvertebrate community data (Figure 27, Appendix Table B.8). Water level, which was higher in the Murray Estuary and North Lagoon, further contributed to the distinction, but was not significant in sequential tests (Figure 27, Appendix Table B.8). The first axis in the dbRDA plot explained most of the variation (51% of total variation) (Figure 27). The concentration of DO, which was higher in the North Lagoon and Murray Estuary, and the median sediment grain size, which was coarser at Jack Point in particular, also significantly explained the differentiation of the macroinvertebrate communities (Appendix Table B.8).

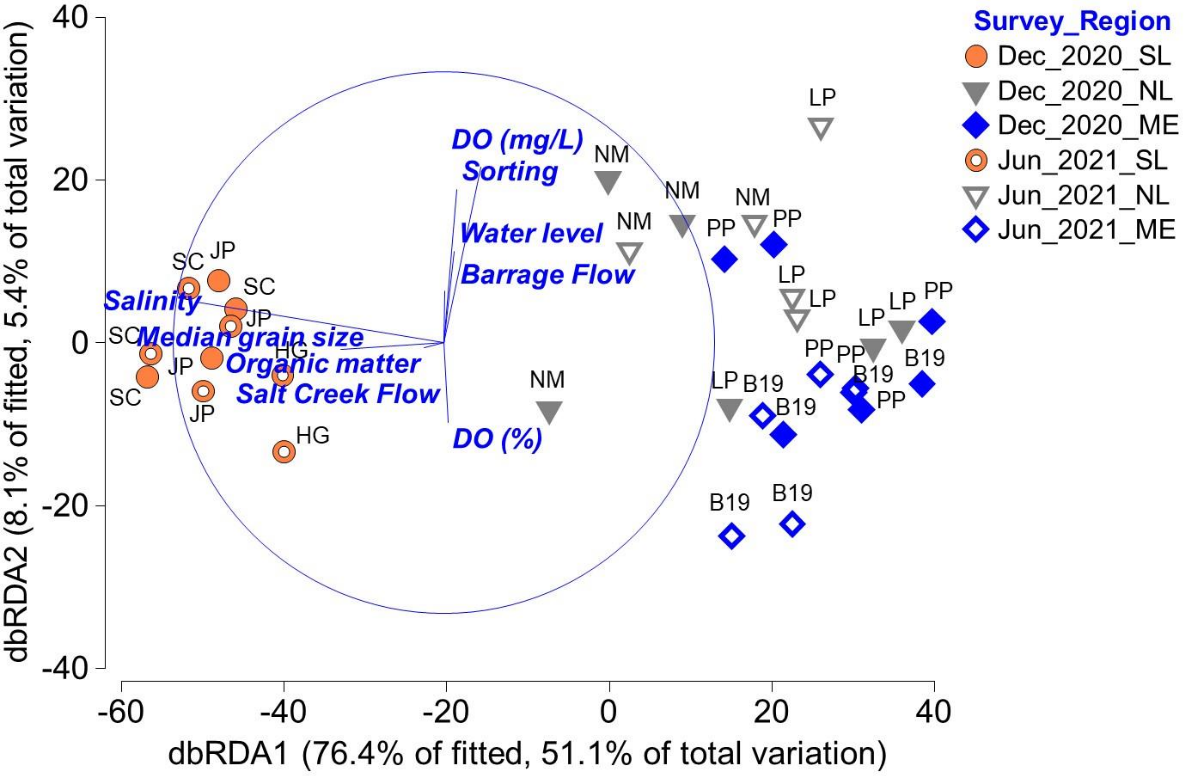

Figure 27. dbRDA plot (distance-based redundancy analysis) for two macroinvertebrate surveys, December 2020 and June 2021, showing a constrained ordination of macroinvertebrate communities subject to the environmental predictor variables displayed in the vector overlay. The sampling sites for each of the regions are indicated on the plot, with SC = Salt Creek and JP = Jack Point for the South Lagoon (SL) (note Hells Gate not included in December 2020 as not all environmental data available), NM = Noonameena and LP = Long Point for the North Lagoon (NL), and PP = Pelican Point and B19 = Beacon 19 for the Murray Estuary (ME). DO = dissolved oxygen.

3.2.3 Fish

Key results:

- A total of 33 fish species were sampled during this study. Although seasonally variable, fish species richness showed a general decrease from the Murray Estuary to the South Lagoon along the increasing salinity gradient in the Coorong (from brackish to hypersaline).
- Individual densities and biomass for key species were also higher in the Murray Estuary and North Lagoon than in the South Lagoon, except for smallmouth hardyhead, a highly salt-tolerant species.
- Fish abundance (by number) was primarily driven by two small-bodied species, with smallmouth hardyhead dominating the South Lagoon, sandy sprat dominating in the Murray Estuary, and both species present in the North Lagoon. These two species are important prey for piscivorous fish and waterbirds in the Coorong.
- Large-bodied fish were mostly (81% by number) sampled in the Murray Estuary, with 18% from the North Lagoon and <1% from the South Lagoon. The most abundant species included yelloweye mullet, congolli, bony herring and redfin perch.
- The spatio-temporal variation of fish assemblage structure in the Coorong was primarily driven by salinity, while temperature, DO and transparency were also influential at times. Fish assemblages in the South Lagoon (defined by salinities >66 ppt) were distinct from those in the North Lagoon and Murray Estuary. For most species, there was a pronounced decrease in individual and biomass densities when salinities exceeded 50 ppt, and highest densities were recorded at salinities <40 ppt.
- While temporal variability was high between fish surveys with different patterns between regions, flow-related responses in species richness and the abundance of some species were evident. Higher River Murray and Salt Creek inflows to the Coorong, were followed by increases in the diversity and individual densities of fish. The South Lagoon fish assemblages were more similar to those in the North Lagoon when higher water releases from Salt Creek occurred in spring 2021. River Murray inflow through the barrages also brought additional freshwater fish into the Murray Estuary, further diversifying prey availability to piscivorous predators.
- This study reinforces the importance of freshwater flow and salinity as the pivotal drivers for fish assemblage dynamics in the Coorong, which subsequently influences the food web.

Fish diversity

A total of 32 fish species were encountered in the Coorong, with 28 in 2020 and 25 in 2021 (Tables 22 and 23). In each sampling season, species richness ranged between 1–3 in the South Lagoon, 9–15 in the North Lagoon, and 12–19 in the Murray Estuary. The temporal pattern (i.e. throughout eight seasonal trips) in species richness varied across three regions, as shown by a significant interaction term (P=0.001) (Table 24). Nevertheless, the lowest species richness was always evident in the South Lagoon, and the highest species richness generally occurred in the Murray Estuary (Tables 22 and 23; Figure 28). The only species caught in the South Lagoon were smallmouth hardyhead, congolli, greenback flounder, Tamar goby and bluespot goby.

Fish individual densities

A total of 306,701 fish were sampled during this study, with small-bodied species (<150 mm TL) being most abundant, representing 97% of total fish caught (by number) (Tables 22 and 23). Smallmouth hardyhead and sandy sprat dominated the catch of small-bodied fish (99.4%), representing 55.6% and 43.8% of the total number, respectively. Smallmouth hardyhead was the most abundant species in the North and South lagoons, whereas sandy sprat was the most abundant in the Murray Estuary. For large-bodied species (≥150 mm TL), the numbers caught in the Murray Estuary represented 82% of the catch, whereas only 18% was from the North Lagoon and negligible numbers were from the South Lagoon (Tables 22 and 23). The most abundant species caught was yelloweye mullet, representing 52% of the catch (by number), followed by redfin perch, bony herring, congolli and greenback flounder. The two freshwater species redfin perch and bony herring were almost solely caught in the Murray Estuary, whereas the other three species (marine estuarine opportunistic and catadromous) were caught in both the Murray Estuary and North Lagoon, and congolli were also caught in the South Lagoon.

The density (i.e. individuals 1000 m^{-2}) of all fish species combined varied greatly among eight sampling trips and across three regions in the Coorong (Figure 28), and the significant 'Season-Year x Region' interaction terms (P=0.001), suggests different temporal patterns among regions (Table 24). For example, in the Murray Estuary, total fish density was the highest during June 2020 (winter), whereas in the North Lagoon and South Lagoon, the highest density occurred during March 2020 or 2021 (autumn) (Figure 28).

For the six key species, smallmouth hardyhead, sandy sprat, yelloweye mullet, congolli, Tamar and lagoon gobies, individual densities varied significantly across regions and/or between seasonal trips (i.e. season-year) during 2020 and 2021 (Table 25; Figure 29a-f). The highest densities of smallmouth hardyhead occurred in the North Lagoon in March 2020 in the North Lagoon and in the South Lagoon March 2021 (Figure 29a). The densities of this species were an order of magnitude lower in the Murray Estuary compared to the other two regions in all seasonal trips except for March 2021. Contrastingly, the densities of sandy sprat were higher in the Murray Estuary than in the North Lagoon in almost all seasonal trips, and no sandy sprat were sampled in the South Lagoon in this study (Figure 29b).

The densities of yelloweye mullet varied between seasonal trips although with no significant temporal difference (P=0.11) (Table 25). However, there was a significant difference among the regions (P=0.001), with greater densities in the Murray Estuary than in the North Lagoon, while this species was not caught in the South Lagoon (Figure 29c). Congolli was present across all three regions with the densities varying in time and space (Figure 29d). Compared to the seasonal trips in 2020, the densities of congolli appeared to be lower during 2021 except in December 2021. Tamar goby and lagoon goby were mostly confined to the Murray Estuary and North Lagoon, with a low number of Tamar goby caught in the South Lagoon only in December 2020 (Figure 29e-f). The densities of Tamar goby were generally greater in the Murray Estuary, compared to the North Lagoon and South Lagoon, whereas for lagoon goby, the densities were highly variable in space and time.

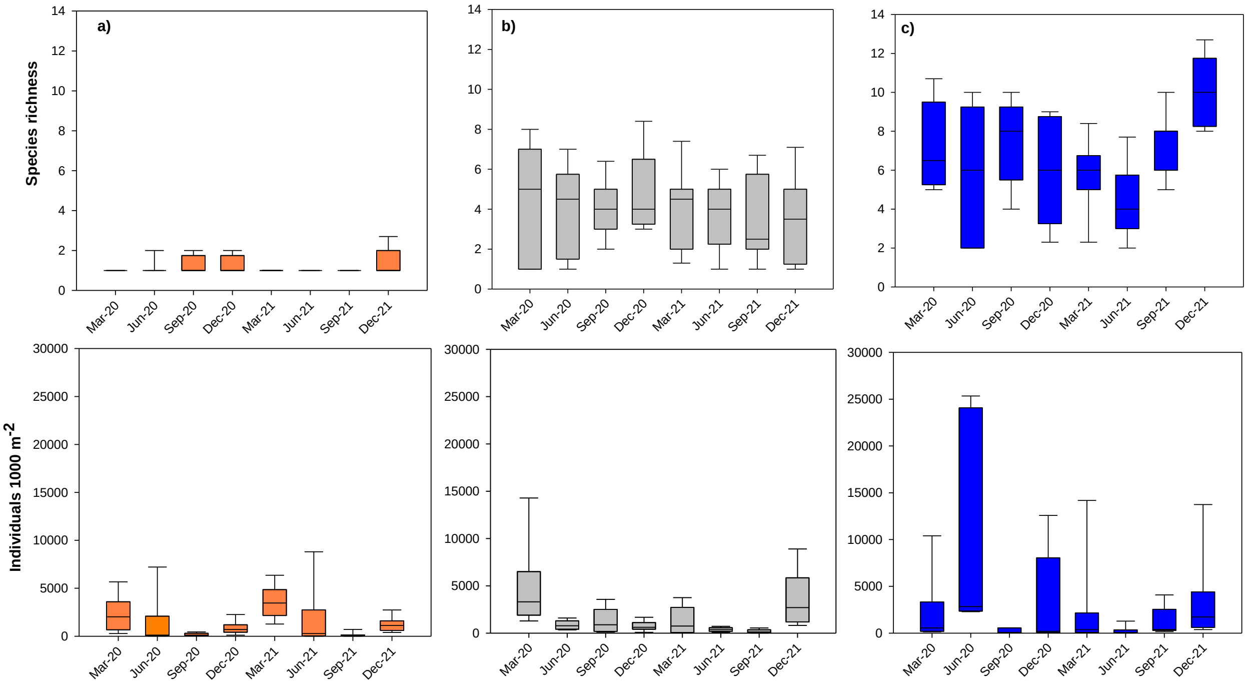

Figure 28. Species richness (top) and individual density (all species combined) (bottom) recorded at each region sampled in the Coorong between March 2020 and December 2021. a) South Lagoon, b) North Lagoon and c) Murray Estuary. Boxplot displays the distribution of data based on the median (horizontal line in the box), the first (lower box end) and third quartile (higher box end), and whiskers showing the minimum (lower end line) and maximum value (higher end line).

Table 22. The fish species and total number caught in each region of the Coorong during surveys from March 2020 to December 2020. The three regions were SL = South Lagoon, NL = North Lagoon and ME = Murray Estuary.

		March			June			September			December	
	SL	NL	ME	SL	NL	ME	SL	NL	ME	SL	NL	ME
Small-bodied species												
Australian anchovy			18									
Australian herring												7
Australian smelt					30			3	185		2	4
Bluespot goby		36				17			7		2	2
Bridled goby		51	3		1	1			1		49	2
Bridled leatherjacket					1							
Common galaxias			1						3			5
Flat-headed gudgeon			1		1	2					1	1
Sandy sprat		7,597	14,712		2,275	34,650		4,334	80		526	24,430
Scary's Tasman goby		154			13	16		14	33			1
Smallmouth hardyhead	17,060	26,710	364	9,456	3,464	137	1,246	4,312	147	6,229	4,568	98
Tamar goby		2	6		1	18			9	4		9
Large-bodied species												
Black bream		2										
Bony herring			187		1						5	89
Carp												3
Congolli		127	21	5	11	6	4	4	4	1	16	79
Goldspot mullet			1									
Greenback flounder		5	7		1	15		12	62		36	3
Longsnout flounder			1			1					2	
Prickly toadfish			12		4	6		3			1	
Red gurnard			1									
Redfin perch												3
River garfish		21	8		146						8	10
Smooth toadfish		1	33		1			1				
Soldier			2									
Southern garfish			5									
Western Australian salmon			132					2	45		5	5
Yelloweye mullet		15	797		59	245		457	201		14	93
Grand Total	**17,060**	**34,721**	**16,312**	**9,461**	**6,009**	**35,114**	**1,250**	**9,142**	**777**	**6,234**	**5,235**	**24,844**
Number of species	**1**	**12**	**20**	**2**	**15**	**12**	**2**	**10**	**12**	**3**	**14**	**18**

Table 23. The fish species and total number caught in each region of the Coorong during surveys from March 2021 to December 2021. The three regions were SL = South Lagoon, NL = North Lagoon and ME = Murray Estuary.

	March			June			September			December		
	SL	NL	ME	SL	NL	ME	SL	NL	ME	SL	NL	ME
Small-bodied species												
Australian herring			3									
Australian smelt			2		7	3		2	81			68
Barred toadfish						1						
Bluespot goby		5	1		9	1		9	25	3	48	27
Bridled goby		7									2	6
Common galaxias			2			2			8			212
Flathead sandfish						1						
Flat-headed gudgeon			1		1	1			34			141
Sandy sprat		240	11,994		717	130		2	6,845		936	20,763
Scary's Tasman goby			1		2			5	37			3
Smallmouth hardyhead	25,800	8,582	5,384	12,183	1,671	501	1,689	950	365	8,761	25,500	384
Tamar goby		8	53		45	5		99	7		1	15
Large-bodied species												
Black bream									1		1	
Bony herring			8						301			375
Carp									2			6
Congolli		8	12			1					10	232
Greenback flounder		9	9		2	4		23	141	3	8	16
Horseshoe leatherjacket			1									
Longsnout flounder						2						
Prickly toadfish			6		1	16		1	1			
Redfin perch									8			1,882
River garfish		1	20		4	1						
Smooth toadfish			11									
Southern crested weedfish			1									
Western Australian salmon		1	22		4	1			4			
Yelloweye mullet		35	378		180	1,206		319	616		128	129
Grand Total	**25,800**	**8,896**	**17,909**	**12,183**	**2,643**	**1,876**	**1,689**	**1,410**	**8,476**	**8,767**	**26,634**	**24,259**
Number of species	**1**	**10**	**19**	**1**	**12**	**16**	**1**	**9**	**16**	**3**	**9**	**15**

Table 24. Test results from permutational ANOVA (PERMANOVA) on differences of fish species richness, individual density of all species combined and assemblage structure, during the different seasons and across the regions. Significant P-values are shown in bold.

		SPECIES RICHNESS	TOTAL DENSITY	FISH ASSEMBLAGE
MAIN TEST	df	$P_{(PERM)}$	$P_{(PERM)}$	$P_{(PERM)}$
Season-Year	7	**0.001**	**0.001**	**0.001**
Region	2	**0.001**	**0.017**	**0.001**
Season-Year x Region	14	**0.001**	**0.001**	**0.001**
Residual	258			

Table 25. Test results from permutational ANOVA (PERMANOVA) on differences of key fish individual densities during the different seasons and across the regions. Significant *P*-values are shown in bold.

		SMALLMOUTH HARDYHEAD	SANDY SPRAT	YELLOWEYE MULLET	CONGOLLI	TAMAR GOBY	LAGOON GOBY
MAIN TEST	df	$P_{(PERM)}$	$P_{(PERM)}$	$P_{(PERM)}$	$P_{(PERM)}$	$P_{(PERM)}$	$P_{(PERM)}$
Season-Year	7	**0.001**	**0.019**	0.11	**0.001**	0.486	**0.001**
Region	2	**0.001**	**0.001**	**0.001**	**0.001**	**0.02**	**0.001**
Season-Year x Region	14	**0.001**	**0.001**	0.126	**0.001**	0.05	**0.001**
Residual	258						

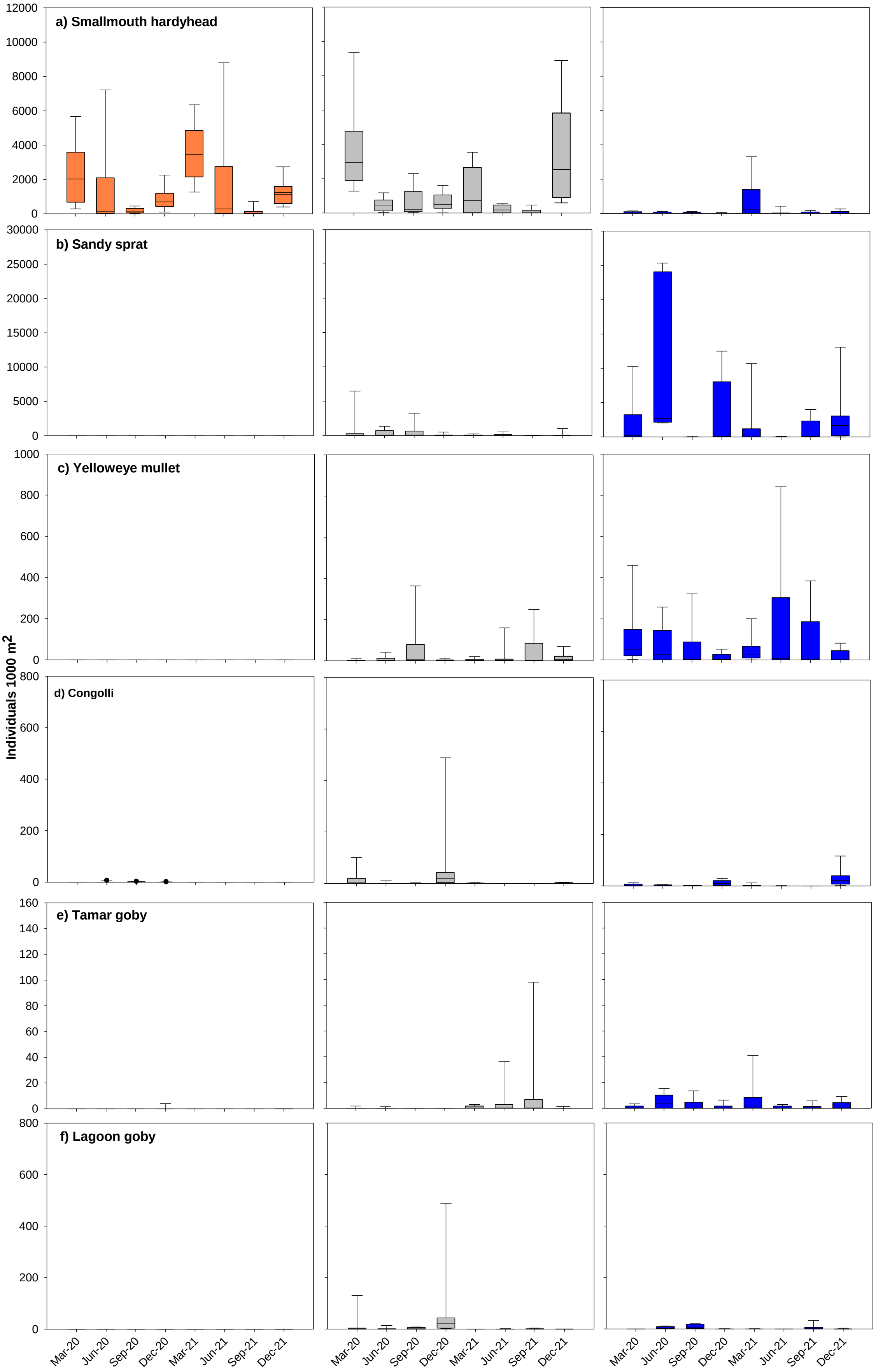

Figure 29. Individual densities of smallmouth hardyhead (a), sandy sprat (b), yelloweye mullet (c), congolli (d), Tamar goby (e) and lagoon goby (f) recorded at each region sampled in the Coorong between March 2020 and December 2021. Left - South Lagoon, middle - North Lagoon and right - Murray Estuary. Boxplot displays the distribution of data based on the median (horizontal line in the box), the first (lower box end) and third quartile (higher box end), and whiskers showing the minimum (lower end line) and maximum value (higher end line).

Fish biomass

The wet biomass (i.e. g 1000 m^{-2}) of nine fish species varied significantly across regions and between seasonal trips with significant interaction terms for most species (*P*<0.01), suggesting that the temporal pattern varied among regions (Table 26). The exceptions included yelloweye mullet, which consistently showed significantly (*P*=0.001) greater wet mass densities in the Murray Estuary than in the North Lagoon (nil in the South Lagoon) and no mass difference (*P*=0.184) across seasonal trips (Figure 31a), and lagoon goby, which showed a significant temporal difference (*P*=0.001) but not among regions (*P*=0.312). Additionally, for black bream and longsnout flounder, no significant difference in wet mass was detected, likely due to very low numbers of fish sampled during this study.

The highest wet biomass densities of smallmouth hardyhead occurred in the North or South lagoons, while those of sandy sprat occurred in the Murray Estuary (Figure 30a and c). For yelloweye mullet, being a large-bodied fish, the wet mass densities were comparable to those of the highly abundant small-bodied fish (e.g. smallmouth hardyhead) with highest densities occurring in the Murray Estuary (Figure 31a). The wet mass densities of congolli were generally much higher in the Murray Estuary and North Lagoon than in the South Lagoon, although they were highly variable between sampling seasons, with higher densities usually occurring in summer (December) and autumn (March) (Figure 31c). Wet mass densities were similarly low for Tamar goby and lagoon goby (Figure 32a and c) compared to the other four key species.

The spatio-temporal patterns of the dry mass densities of the six key species (Figures 30-32b and d) and the statistical results of the eleven species (Table 27) resemble those of the wet mass densities (Figures 30-32a and c; Table 26). Examining spatio-temporal variability in wet and dry mass densities 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 biomass data are critical for further assessment of associated energy supply to support piscivorous fish and waterbirds in the Coorong.

Table 26. Test results from permutational ANOVA (PERMANOVA) on differences of key fish species wet weight (biomass) during the different seasons and across the regions. Season df =7, region df= 2, season x region df = 14, Residual = 252. Significant P-values are shown in bold.

	SEASON-YEAR	REGION	SEASON-YEAR X REGION
	P$_{(PERM)}$	*P*$_{(PERM)}$	*P*$_{(PERM)}$
Black bream	1	0.414	0.476
Tamar goby	**0.43**	**0.001**	**0.006**
Yelloweye mullet	0.184	**0.001**	0.73
Longsnout flounder	0.587	0.078	0.118
Western Australian salmon	**0.001**	**0.001**	**0.001**
Smallmouth hardyhead	**0.001**	**0.001**	**0.001**
River garfish	**0.003**	**0.001**	**0.002**
Sandy sprat	**0.005**	**0.001**	**0.001**
Congolli	**0.001**	**0.001**	**0.001**
Greenback flounder	**0.019**	**0.001**	**0.01**
Lagoon goby	**0.001**	0.312	**0.007**

Table 27. Test results from permutational ANOVA (PERMANOVA) on differences of key fish species dry weight (biomass) during the different seasons and across the regions. Season df =7, region df= 2, season x region df = 14, Residual = 252. Significant P-values are shown in bold.

	SEASON-YEAR	REGION	SEASON-YEAR X REGION
	$P_{(PERM)}$	*$P_{(PERM)}$*	*$P_{(PERM)}$*
Black bream	1	0.392	0.514
Tamar goby	**0.41**	**0.001**	**0.005**
Yelloweye mullet	0.391	**0.001**	**0.019**
Longsnout flounder	0.57	0.089	0.111
Western Australian salmon	**0.001**	**0.001**	**0.001**
Smallmouth hardyhead	**0.001**	**0.001**	**0.001**
River garfish	**0.001**	**0.001**	**0.002**
Sandy sprat	**0.001**	**0.001**	**0.001**
Congolli	**0.001**	**0.001**	**0.001**
Greenback flounder	**0.021**	**0.001**	**0.08**
Lagoon goby	**0.004**	0.32	**0.004**

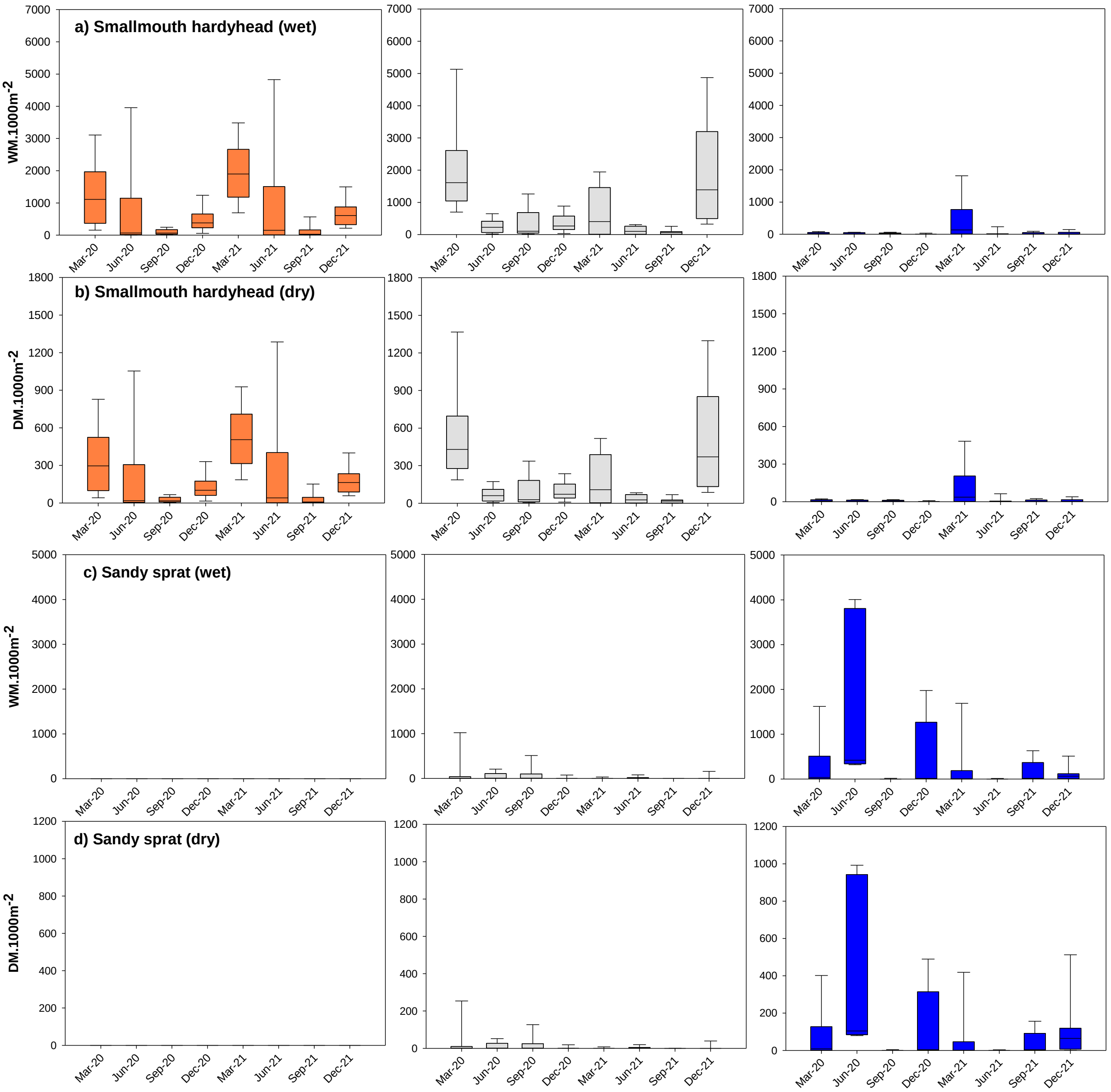

Figure 30. Wet and dry mass densities (g. 1000 m^{-2}) of smallmouth hardyhead (a and b) and sandy sprat (c and d) in the three regions of the Coorong between March 2020 and December 2021. Left - South Lagoon, middle - North Lagoon and right - Murray Estuary. Boxplot displays the distribution of data based on the median (horizontal line in the box), the first (lower box end) and third quartile (higher box end), and whiskers showing the minimum (lower end line) and maximum value (higher end line).

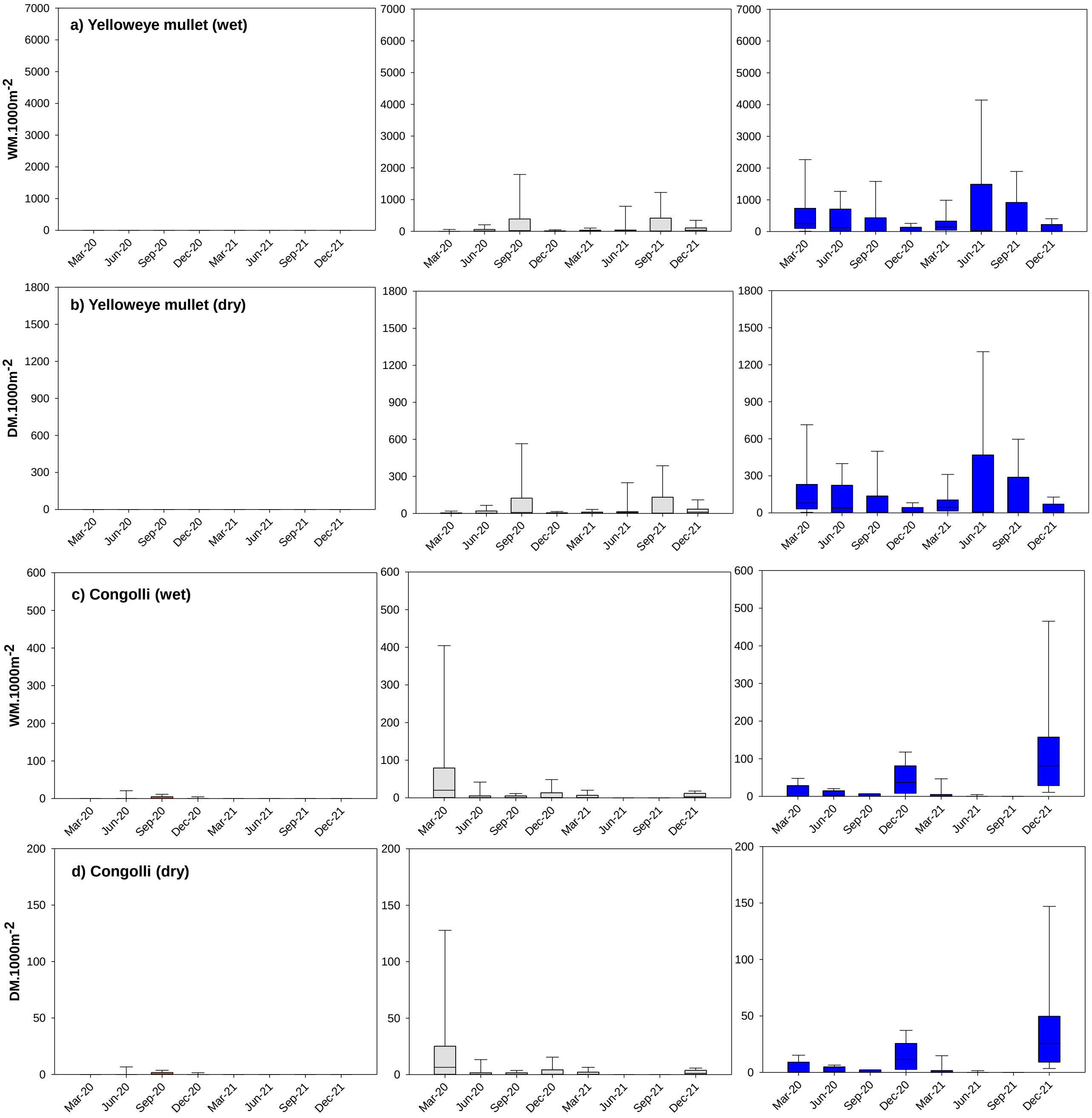

Figure 31. Wet and dry mass densities (g. 1000 m^{-2}) of yelloweye mullet (a and b) and congolli (c and d) in the three regions of the Coorong between March 2020 and December 2021. Left - South Lagoon, middle - North Lagoon and right - Murray Estuary. Boxplot displays the distribution of data based on the median (horizontal line in the box), the first (lower box end) and third quartile (higher box end), and whiskers showing the minimum (lower end line) and maximum value (higher end line).

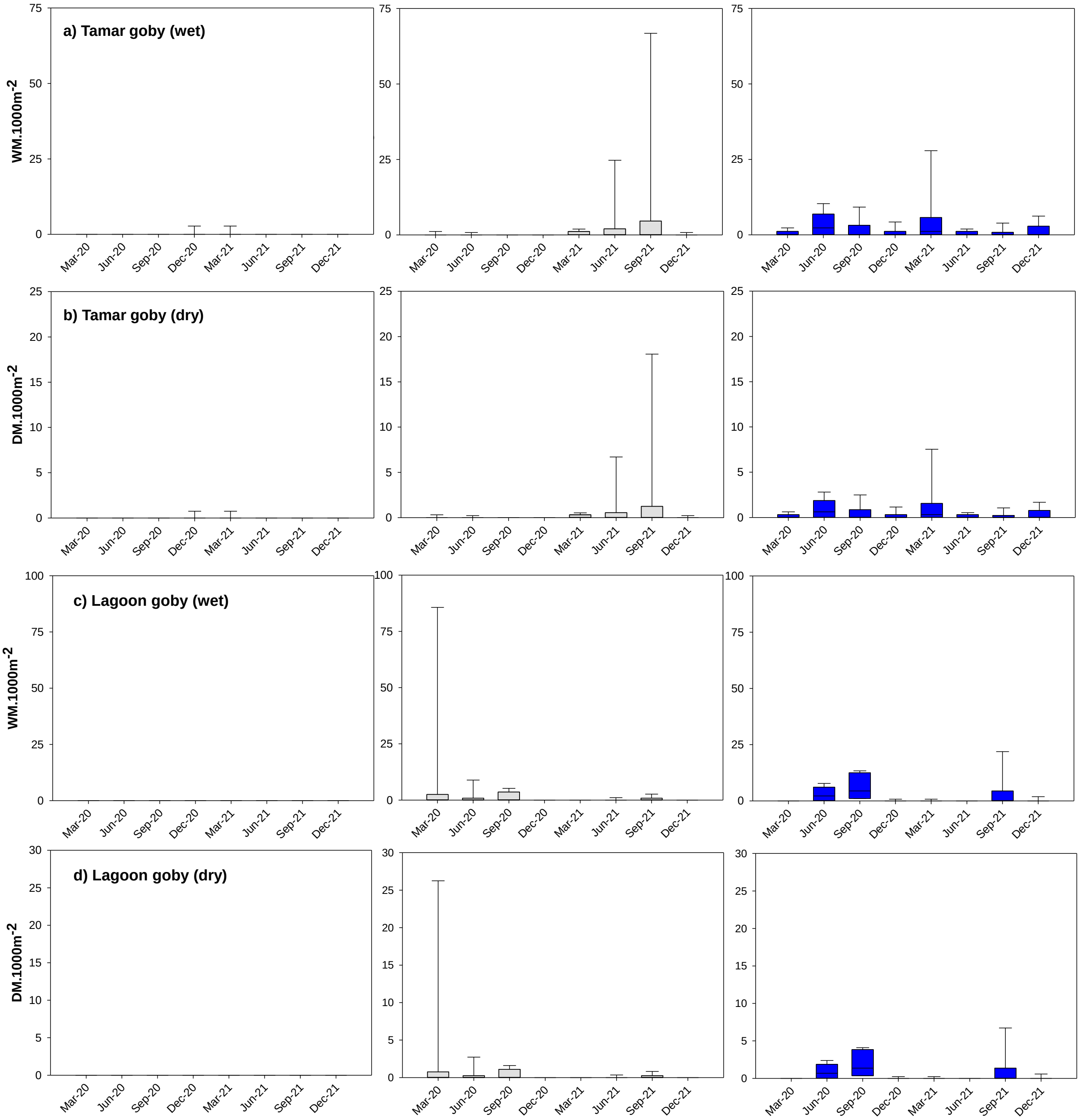

Figure 32. Wet and dry mass densities (g. 1000 m^{-2}) of Tamar goby (a and b) and lagoon goby (c and d) in the three regions of the Coorong between March 2020 and December 2021. Left - South Lagoon, middle - North Lagoon and right - Murray Estuary. Boxplot displays the distribution of data based on the median (horizontal line in the box), the first (lower box end) and third quartile (higher box end), and whiskers showing the minimum (lower end line) and maximum value (higher end line).

Fish community

Fish assemblage structure showed significant variation between the three regions of the Coorong and across eight seasonal trips in 2020 and 2021 (Table 24; Figure 33). Assemblages in the Murray Estuary, North Lagoon and South Lagoon were distinct, although there were some interspersed points in the data clouds for the North and South lagoons (Figures 33 and 34). This interspersion indicates that fish assemblages in the North Lagoon in some seasons may be similar to those in the South Lagoon in other seasons. For instance, the South Lagoon assemblage in summer 2021 was similar to the North Lagoon assemblage in autumn 2021, and the South Lagoon assemblage in autumn 2021 was similar to the North Lagoon assemblage in summer 2021. In general, the spring and winter samples were less widely dispersed among three regions than summer/autumn samples except for the Murray Estuary sample in winter 2020.

The spatio-temporal differences in fish assemblages were influenced mainly by highly abundant small-bodied species (i.e. smallmouth hardyhead and sandy sprat) and a large-bodied freshwater species (bony herring) with moderate densities (Figure 34). The Principal Coordinate Analysis (PCO) graph of fish assemblage data accounted for 87.2% of the total variation in the first two axes (Figure 34). In the South and North lagoons, fish assemblages were strongly characterised by smallmouth hardyhead while in the Murray Estuary, they were driven by sandy sprat and bony herring.

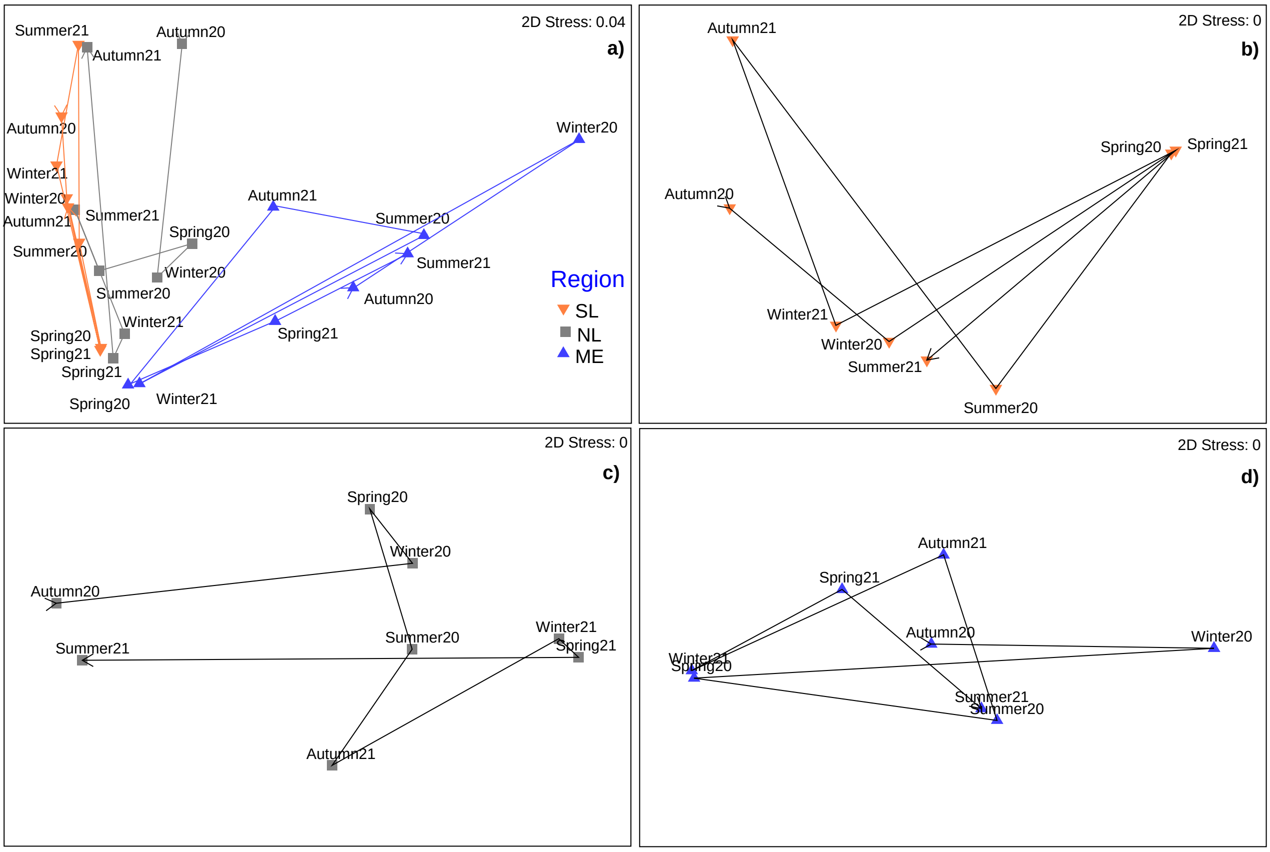

Figure 33. Multidimensional scaling ordination with trajectory overlay showing grouping of fish assemblage by season and year grouped in three regions in the Coorong. a) All regions, b) South Lagoon (SL), c) North Lagoon (NL) and d) Murray Estuary (ME).

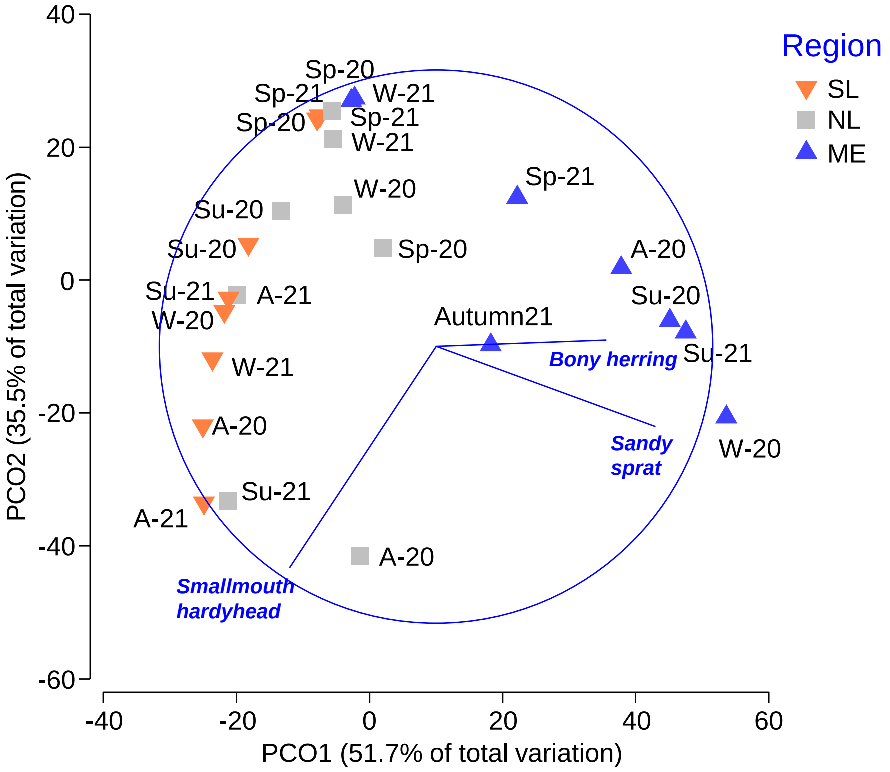

Figure 34. PCO of abundance samples of fish species collected by seine net in all seasons and regions (ME = Murray Estuary, NL = North Lagoon, SL = South Lagoon). The vector overlay indicates Pearson rank correlations between species and PCO axes 1 and 2 (correlations >0.5, with respect to a unit circle). Labels indicate season-year (A = Autumn, W = Winter, Sp = Spring and Su = Summer; 20 = 2020 and 21 = 2021).

Environmental influences for fishes

BEST test using five water quality parameters (water temperature, salinity, pH, dissolved oxygen and transparency) indicated that a combination of four parameters (salinity, water temperature, DO and transparency) best predicted the spatio-temporal variations in fish assemblage structure in the Coorong (Table 28). Salinity best explained the horizontal separation of the samples (i.e. a broad regional separation), with assemblages linking to decreasing salinities from the South Lagoon to Murray Estuary; Water temperature explained the vertical distribution of the data cloud. Distinct seasonal separation was evident, with winter assemblages linking with cooler temperatures and summer/autumn assemblages with warmer temperatures (Figure 35).

The LINKTREE analysis resulted in seven statistically significant groups presented in black lines; insignificant groups (red lines) are presented, but not interpreted (Figure 36). The first grouping (A) separated the South Lagoon samples (J), which were associated with salinities >66 ppt, from the remainder of the samples (i.e. the North Lagoon and Murray Estuary), which were from salinities <52 ppt. The second grouping (B) divided the samples to two groups: Group C was linked with brackish to just above marine salinities (<42 ppt) and included all Murray Estuary samples and the North Lagoon samples except for autumn 2020 and summer 2021, with salinities >45 ppt. Group C was further separated by water temperature with summer 2020 and 2021 samples from the Murray Estuary linking to temperatures >21 °C, whereas the remaining samples (D) were associated with temperatures <21 °C. Group D was further separated by salinity, with most Murray Estuary samples and one North Lagoon sample (summer 2020) associated with salinities <30 ppt, whereas the remaining samples of Group H were associated with salinities >31 ppt and included mostly North Lagoon samples and one Murray Estuary sample. Transparency influenced the separation of Group H, with two distinct samples (Murray Estuary winter 2020 and North Lagoon spring 2020) characterised by turbid water (Secchi disc depth <1 m) while the remaining North Lagoon samples had less turbid water (Secchi disc depth >1.2 m). For the South Lagoon samples (J), salinity once again was responsible for the further separation with two spring samples distinctly linked to salinities <75 ppt, whereas the remaining samples (K) had salinities

>75 ppt. Further separation of Group K was influenced by both salinity and DO (e.g. autumn 2020 and 2021 South Lagoon samples were associated with salinities >105 ppt and DO <7.7).

Table 28. BEST test results for all five environmental parameters (pH, DO, salinity, temperature, and transparency). RSS = residual sum of squares.

R^2	RSS	NUMBER OF VARIABLES	VARIABLE SELECTION
0.55794	10875	4	DO, salinity, temperature, transparency
0.54997	11071	5	pH, DO, salinity, temperature, transparency
0.53727	11383	3	Salinity, temperature, transparency
0.5301	11560	4	pH, salinity, temperature, transparency
0.52723	11630	3	DO, salinity, temperature
0.5246	11695	3	DO, salinity, transparency
0.51936	11824	4	pH, DO, salinity, temperature
0.51541	11921	4	pH, DO, salinity, transparency
0.49919	12320	2	Salinity, temperature,
0.49254	12459	3	pH, salinity, temperature

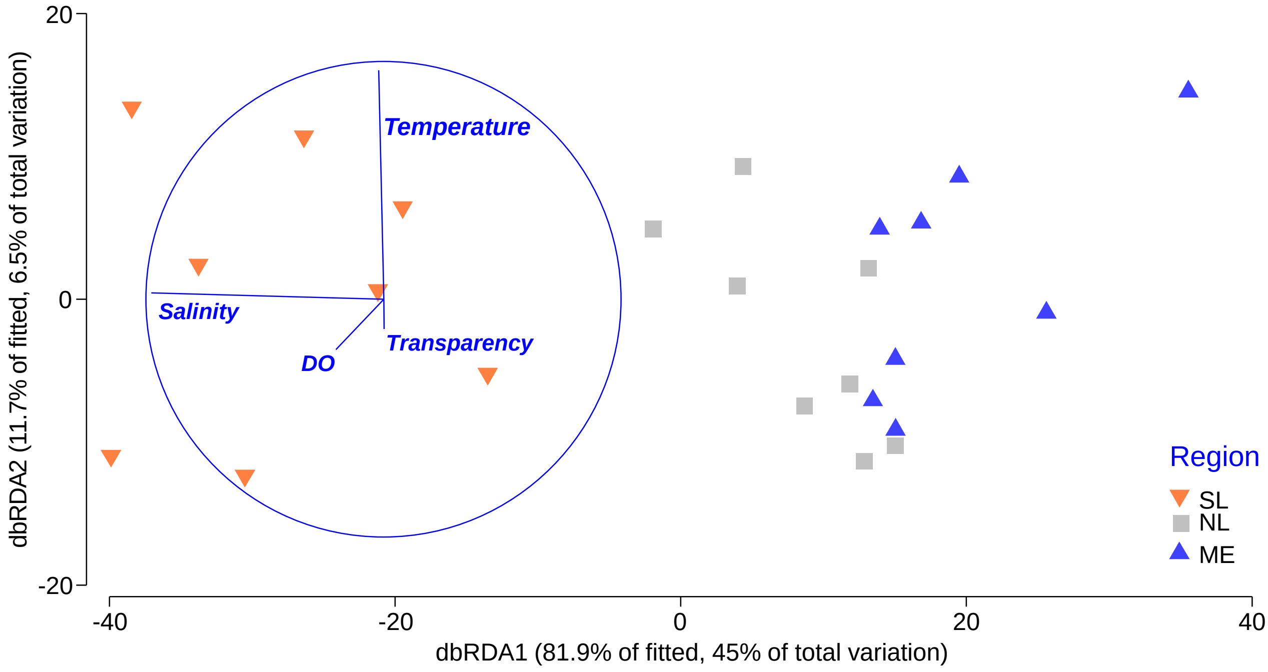

Figure 35. Distance-based redundancy analysis (dbRDA) ordination of the fitted model of species abundance data from different regions versus the predictor variables salinity, temperature, dissolved oxygen (DO) and transparency. ME = Murray Estuary, NL = North Lagoon, SL = South Lagoon. The vector overlay indicates multiple partial correlations between the predictor variables and dbRDA axes 1 and 2. Labels indicate season-year (A = Autumn, W = Winter, Sp = Spring and Su = Summer).

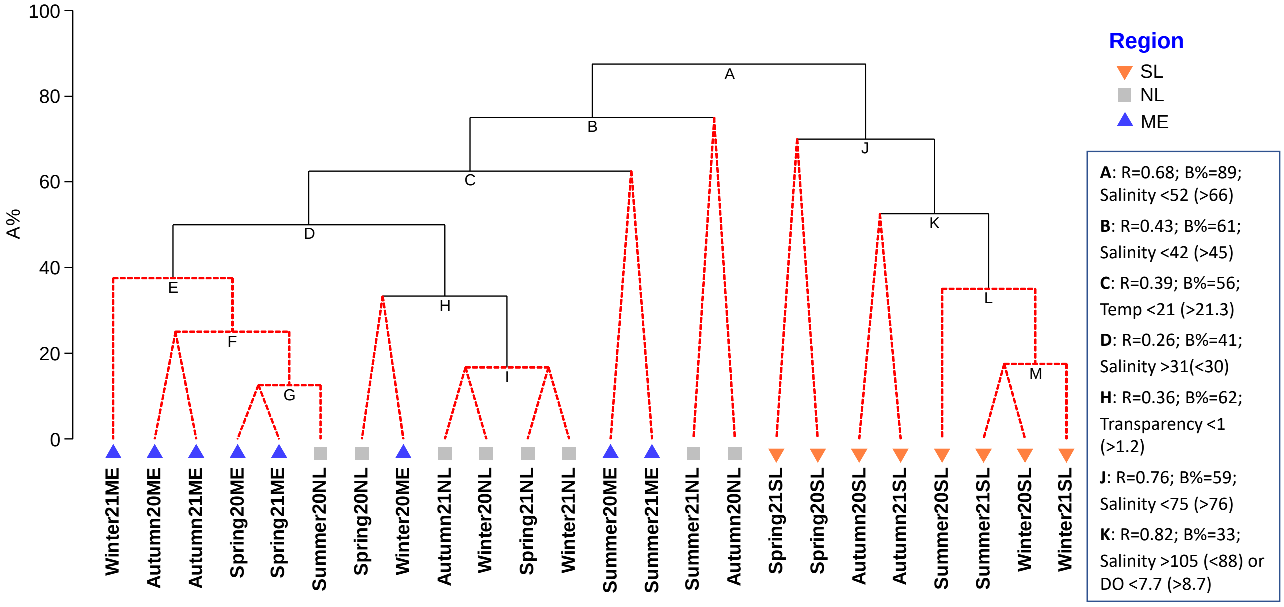

Figure 36. LINKTREE analysis using salinity and transparency (significant environmental parameters) showing divisive clustering of fish assemblages (above), constrained by inequalities in water quality variables (below). Seven statistically significant groups are presented in black lines; insignificant groups are presented in red lines. ME = Murray Estuary, NL = North Lagoon, SL = South Lagoon.

Salinity is the primary driver influencing fish assemblages in the Coorong, therefore, we graphed salinity with individual number and wet mass densities of six key fish species as dependent variables to explore its influence on fish density and biomass (Figures 37 and 38). High densities of smallmouth hardyhead (both numbers and wet mass) occurred at a broad range of salinities from brackish to 117 ppt. In contrast, all other species had substantially lower individual and biomass densities at salinities greater than ~50 ppt, and highest densities mostly occurred at salinities less than ~40 ppt (i.e. brackish to just above marine salinities).

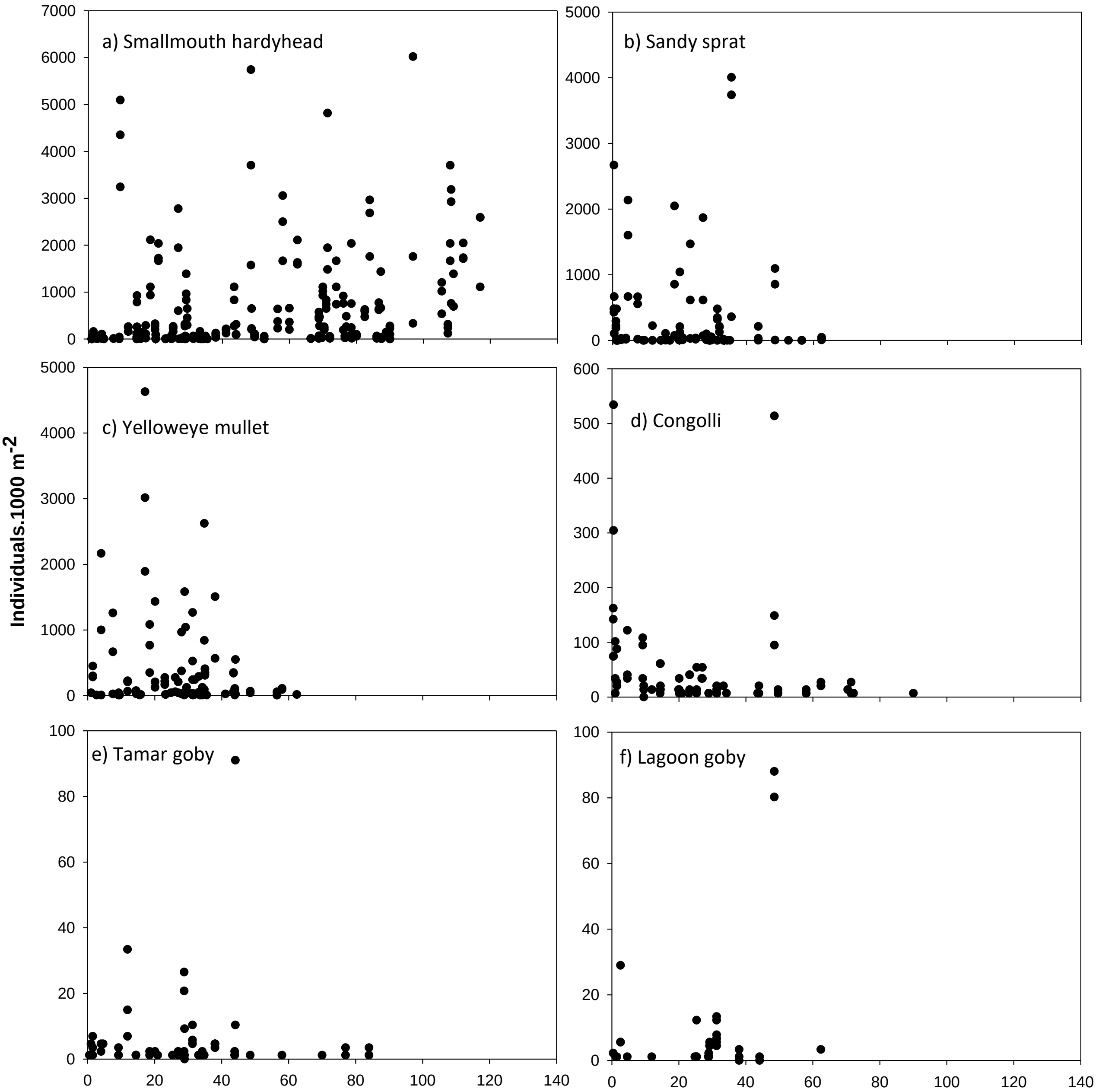

Figure 37. Scatter plots of fish individual densities (individuals 1000 m-2) against salinities for six key species in the Coorong. Note the differences in y-axis scales. Zero values for densities were not included.

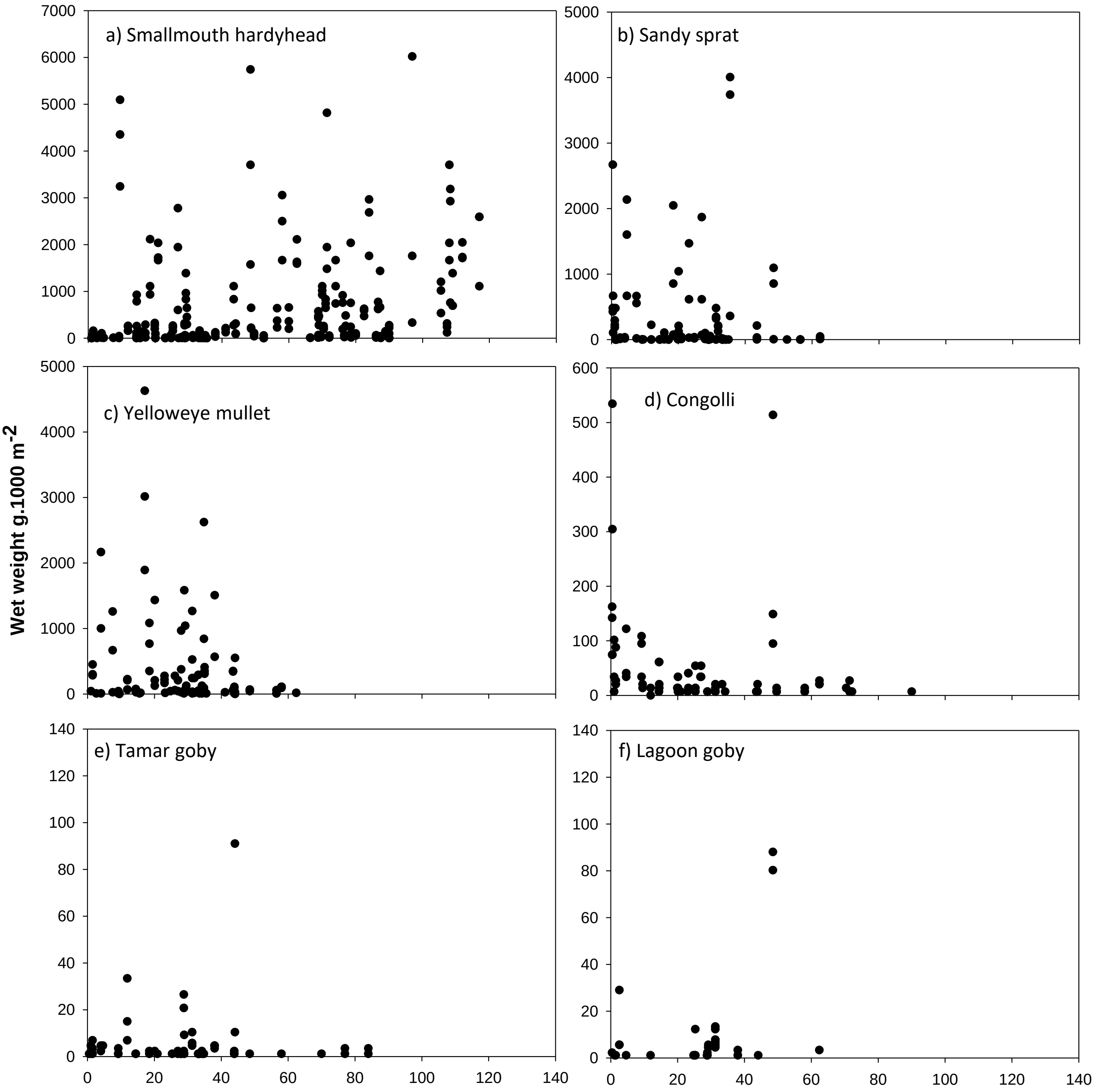

Figure 38. Scatter plots of fish wet mass densities (g. 1000 m-2) against salinities for six key species in the Coorong. Note the difference in y-axis scales. Zero values for biomass were not included.

Prey-related patterns in fish community: Zooplankton and macroinvertebrate prey as predictor for fishes

The distribution of fish communities can not only be affected by environmental conditions but by prey availability. Densities of zooplankton and macroinvertebrates, grouped into higher taxonomic or prey type categories, were taken as predictor variables and could explain about 60% of the variation in the fish community (Figure 39a). The distance-based linear model showed a strong separation of the fish community between the South Lagoon and the North Lagoon and Murray Estuary (Figure 39b). Vectors for prey items along this first axis pointed to the North Lagoon and Murray Estuary, and benthic macroinvertebrate prey types 'Deep-large' (D-L), 'Surface-small' (S-S) and 'Surface-medium' (see Section 3.2.2) explained 45%, 31% and 26% respectively (Figure 39, Appendix Table B.9). Microcrustaceans in the zooplankton explained 14% of the variation (Appendix Table B.9). The second axis explained only 6% of the total variation, mostly due to meroplankton (larval stages of invertebrates), as hyperbenthos (resuspended macroinvertebrates or those leaving the sediment actively) was not significant in the marginal test (Figure 39, Appendix Table B.9).

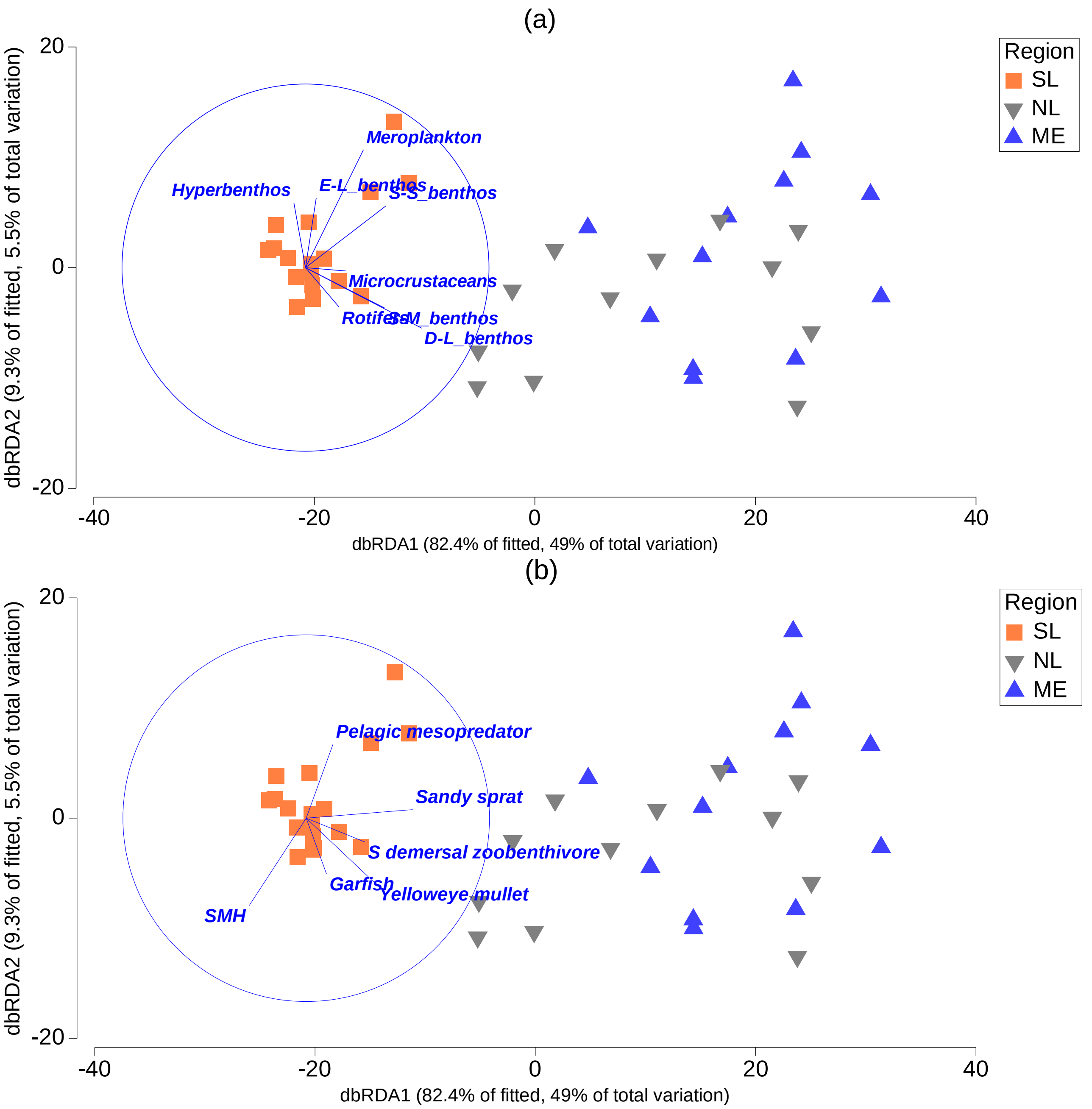

Figure 39. dbRDA plot (distance-based redundancy analysis) for the fish community, showing (a) a constrained ordination with zooplankton and macroinvertebrate prey density as predictor variables, grouped into higher categories or prey types; and (b) a vector overlay of the fish community by trophic group. The analysis is based on seasonal surveys from Autumn 2020 to Winter 2021, for the regions ME = Murray Estuary, NL = North Lagoon, SL = South Lagoon. See Table 9 for macroinvertebrate prey types. SMH = Smallmouth hardyhead.

3.3 Nutritional value and energy content of major food sources for key fish and waterbird species in the Coorong

Key results:

- This study provided the first bioenergetic values for prey occurring in the Coorong.
- Average calorific values per gram dry mass were <5 kJ for detritus, 6 kJ for plankton, 10 kJ for *Ruppia*, 12 kJ for macroinvertebrates (values for 17 taxa, range 9 – 16 kJ) and 19 kJ for fish (values for 12 taxa, range from 17 – 22 kJ).
- Ratios between wet and dry mass were calculated that support conversions of energy density needed for food web analyses.
- Combining calorific contents with biomass revealed a decrease in energy density of macroinvertebrates from the North to the South Lagoon. Macroinvertebrate energy density in the South Lagoon was negligible.
- Benthic micro-molluscs had the highest energy density in both the North Lagoon and Murray Estuary, but the lipid and protein contents of taxa in this trophic group were low. Benthic-pelagic crustaceans and benthic annelids had high energy density in the Murray Estuary, and high lipid and protein contents, thus providing nutritious and energy rich prey.
- Crude protein contents were lowest for Ruppia and filamentous algae and highest for fish.
- For fish, energy density was more similar across the regions due to the high abundance and biomass of smallmouth hardyhead which accounted for the energy density in the South Lagoon. In summer, however, the protein content of smallmouth hardyhead was significantly lower in the South Lagoon compared to the North lagoon and Murray Estuary.
- In the North Lagoon and Murray Estuary, several other fish trophic groups provided additional energy density. The protein content of yelloweye mullet varied with their size, but not season. Sandy Sprat had higher protein values in winter in both the North Lagoon and Murray Estuary.

3.3.1 Dry/wet mass ratios

As the energy content measured by calorimetry is based on dry mass (DM), but values were also needed in relation to wet mass (WM) for the T&I Component 3 food web model, ratios of DM/WM were determined to convert from kJ g^{-1} DM to kJ g^{-1} WM.

For macroinvertebrates, DM/WM ratios were obtained for 33 different taxa, whereby 14 were represented by few samples (<5 replicates), and five taxa with >200 replicates each. The ratio ranged from 0.011 to 0.5171 between species, and variation was low within most taxa (Table 29). For fish, the ratio ranged from 0.248 to 0.316 across the different species, with little variation within taxa (Table 30). For yelloweye mullet (*A. fosteri*), the DM/WM ratio was significantly different between the two size categories analysed (ANOVA, F=61.87, P<0.0001).

For samples of *Ruppia* and filamentous algae, no wet weight was available, and a ratio of wet to dry mass based on Wickham et al. (2019) for related species (*Zostera* DM/WM = 0.224, and *Ulva* DM/WM = 0.187) was used.

Table 29. Ratio (mean ± Standard error SE) of Dry Mass (DM) to Wet Mass (WM) of macroinvertebrate collected for energy content by calorimetry. N is the total number of samples for which weights were determined for each species for calorimetry. Note that there was not enough material from all species to be analysed. For each phylum/higher taxon, the species are listed by alphabetical sequence of their Latin names.

			DM/WM	
PHYLA/HIGHER TAXA	SPECIES	N	MEAN	SE
Cnidaria	**Anemone**	**1**	0.11	
Annelida	***Aglaophamus (Nepthys) australiensis***	**48**	0.07	0.00
	Arenicolidae	**3**	0.08	0.03
	Australonereis ehlersi	**2**	0.08	0.04
	Boccardiella limnicola	**28**	0.16	0.04
	Capitella capitata	**256**	0.10	0.01
	Euchone variabilis	**1**	0.40	
	Ficopomatus enigmaticus	**5**	0.10	0.04
	Oligochaeta	**3**	0.14	0.12
	Phyllodoce novaehollandiae	**31**	0.05	0.01
	Rhynchobdellida	**1**	0.01	
	Simplisetia aequisetis	**238**	0.09	0.01
Mollusca	***Arthritica semen***	**294**	0.52	0.01
	Hiatula (Soletellina) alba	**40**	0.15	0.01
	Hydrobiidae	**170**	0.53	0.01
	Liloa brevis	**2**	0.16	0.08
	Macomona deltoidalis	**1**	0.28	
	Salinator fragilis	**93**	0.34	0.01
	Spisula trigonella	**28**	0.20	0.03
Crustacea	***Amarinus laevis***	**4**	0.19	0.07
	Amphipoda	**304**	0.16	0.01
	Halicarcinus ovatus	**1**	0.13	
	Haloniscus searlei	**3**	0.21	0.06
	Janiridae	**2**	0.25	0.25
	Mysidae	**65**	0.14	0.01
	Ostracoda	**14**	0.15	0.05
	Paragrapsus gaimardii	**27**	0.40	0.03
Hexapoda	**Ceratopogonidae**	**17**	0.33	0.06
	Chironomidae	**322**	0.20	0.01
	Diptera	**6**	0.30	0.11
	Dolichopodidae	**18**	0.25	0.04
	Empididae	**2**	0.03	0.03
	Stratiomyidae	**14**	0.29	0.07

Table 30. Ratio (mean ± Standard error SE) of Dry Mass (DM) to Wet Mass (WM) of tissue from fish species analysed for energy content by calorimetry. For yelloweye mullet (A. fosteri), the DM/WM ratio was different between two size categories analysed. N is the total number of samples analysed for each species. Species are listed by alphabetical sequence of their Latin names. The common name as well as the trophic group assigned by the T&I Component 3 food web model are included.

				DM/WM	
SPECIES	COMMON NAME	TROPHIC GROUP	N	MEAN	SE
Acanthopagrus butcheri	**Black bream**	**Black bream**	**10**	0.266	0.003
Afurcagobius tamarensis	**Tamar goby**	**Demersal zoobenthivore**	**17**	0.270	0.005
Aldrichetta forsteri	**Yelloweye mullet**	**Yelloweye mullet**	**62**	0.315	0.005
<80 mm			**29**	0.286	0.005
>80 mm			**33**	0.341	0.005
Ammotretis rostratus	**Longsnout flounder**	**Flounder**	**1**	0.272	--
Argyrosomus japonicus	**Mulloway**	**Mulloway**	**5**	0.290	0.013
Arripis truttaceaus	**Australian salmon**	**Pelagic mesopredator**	**28**	0.312	0.007
Atherinosoma microstoma	**Smallmouth hardyhead**	**Smallmouth hardyhead**	**48**	0.286	0.003
Hyperlophus vittatus	**Sandy sprat**	**Sandy sprat**	**29**	0.248	0.008
Hyporhamphus regularis	**River garfish**	**Garfish**	**18**	0.305	0.012
Pseudaphritis urvillii	**Congolli**	**Demersal zoobenthivore**	**47**	0.316	0.007
Rhombosolea tapirina	**Greenback flounder**	**Flounder**	**25**	0.267	0.010
Tasmanogobius lasti	**Lagoon goby**	**Demersal zoobenthivore**	**13**	0.306	0.011

3.3.2 Energy contents

Calorific values were obtained for several levels of the food web, from primary producers (*Ruppia*, filamentous algae) to primary and secondary consumers (macroinvertebrates and fish) (Figure 40). Detritus and algae had a low calorific value (<5 kJ g^{-1} DM), plankton on average 6 kJ g^{-1} DM, and *Ruppia* 10 kJ g^{-1} DM. For macroinvertebrates, the average calorific value was 12.28 kJ g^{-1} DM, which ranged for the taxa analysed from 8.82 (*Salinator fragilis*) to 15.75 kJ g^{-1} DM (*Australonereis ehlersi*) (Table 31). The average calorific content for fish was higher at 19.05 kJ g^{-1} DM, ranging from 17.47 (longsnout flounder *Ammotretis rostratus*) to 22.11 kJ g^{-1} DM for black bream (*Acanthopagrus butcheri*) (Table 31).

Energy content values were mostly similar across the regions of the Coorong (Figure 40), where samples could be obtained from different regions (Table 3, for region specific calorific values see Tables C.1 and C.2). For chironomid larvae, the average calorific content was higher in the South Lagoon (12.81 kJ g^{-1} DM) than in the North Lagoon (8.66 kJ g^{-1} DM) and Murray Estuary (7.61 kJ g^{-1} DM) (Appendix Table C.1).

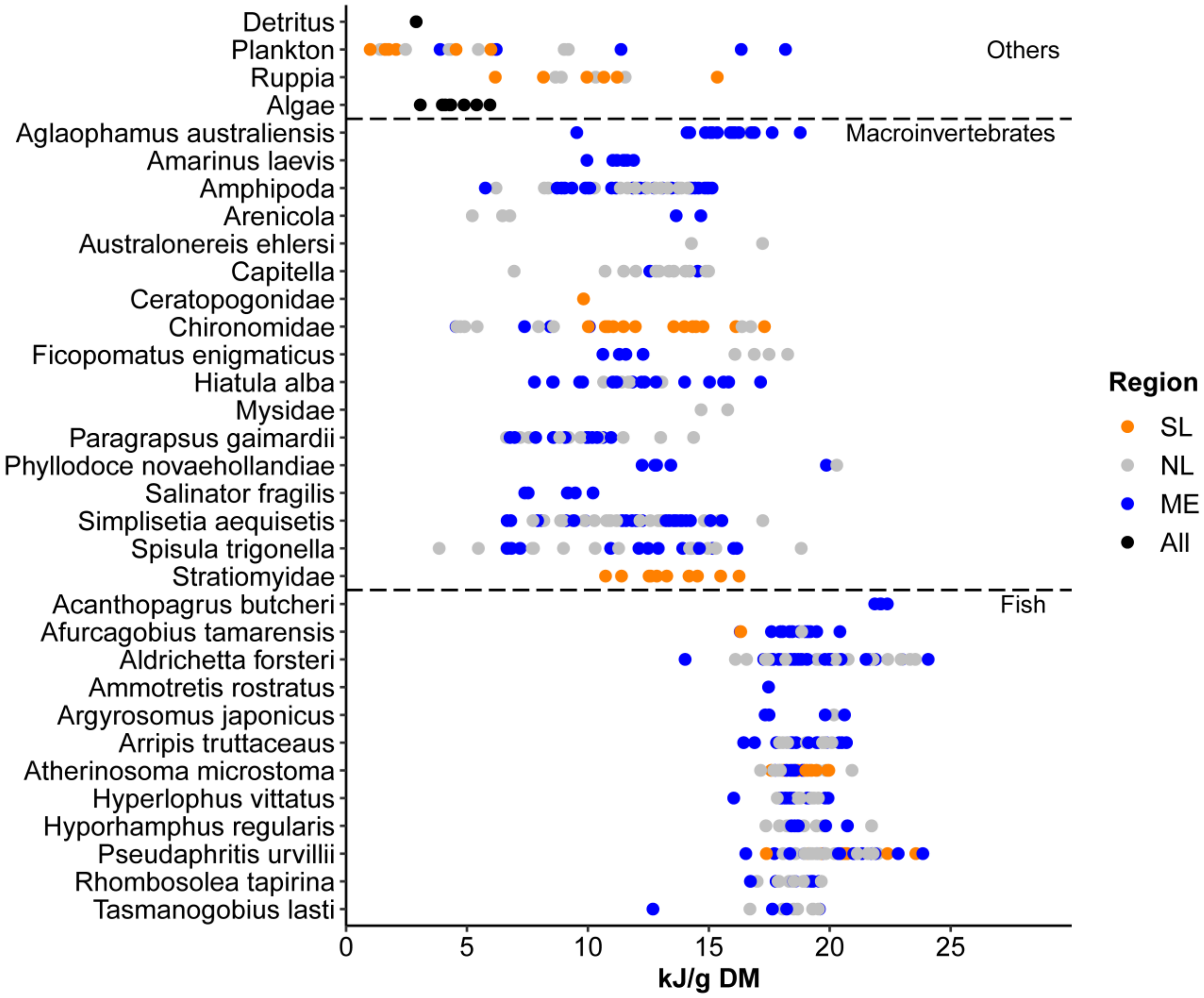

Figure 40. Energy content values as measured for taxa from all trophic levels for which sufficient material for calorimetry could be obtained. The colours indicate the region of the Coorong from where the material was sourced, with SL = South Lagoon, NL = North Lagoon, and ME = Murray Estuary. For some taxa, the source location was not known, or material had to be combined from all regions for analyses (shown in black for region). Note that not all taxa occur in all regions.

For the Coorong food web model, energy content values were needed for trophic groups. Based on the macroinvertebrate and fish taxa within each trophic group for which calorific content could be analysed, average energy contents were calculated (Table 32). Note that the trophic groups are represented by further taxa in the Coorong for which energy content could not be analysed. Applying the value per trophic group to other taxa within that trophic group occurs under the assumption that the energy content will be similar, which is supported by the low standard error for most trophic groups (Table 32). For trophic groups of macroinvertebrates, tubeworms (*Ficopomatus enigmaticus*) had a high energy content based on dry mass, but not on wet mass, where benthic decapods had the highest average energy content, followed by benthic-micro molluscs. Black bream had the highest energy content based on dry mass but based on wet mass, yelloweye mullet had a higher content. Flounder, sandy sprat and smallmouth hardyhead had some of the lowest energy contents of all fish (Table 32).

Table 31. Energy content (mean ± standard error SE) in kJ/g dry mass as well as kJ/g WM for detritus, plankton, macrophytes and filamentous algae, macroinvertebrates and fish from samples in the Coorong, and differentiated by region. See Table 3 for number of samples.

		kJ/g DRY MASS			kJ/g WET MASS		
PREY TYPE	SPECIES/TAXA	MEAN		SE	MEAN		SE
Detritus		2.90			1.49		
Plankton		6.06	±	1.12	1.75	±	0.32
Plant	*Ruppia*	10.09	±	0.77	2.26	±	0.17
	Filamentous algae	4.50	±	0.32	0.84	±	0.06
Macroinvertebrates	*Amarinus laevis*	11.08	±	0.26	2.13	±	0.05
	Amphipoda	12.12	±	0.36	1.95	±	0.06
	Arenicolidae	9.35	±	1.98	0.76	±	0.16
	Australonereis ehlersi	15.75	±	1.47	1.28	±	0.12
	Capitella capitata	12.79	±	0.52	1.27	±	0.05
	Ceratopogonidae	9.82			3.20		--
	Chironomidae	10.81	±	0.76	2.22	±	0.16
	Ficopomatus enigmaticus	14.31	±	1.12	1.45	±	0.11
	Mysidae	15.23	±	0.55	2.20	±	0.08
	Aglaophamus (Nepthys) australiensis	15.69	±	0.37	1.07	±	0.03
	Paragrapsus gaimardii	9.42	±	0.39	3.77	±	0.16
	Phyllodoce novaehollandiae	15.24	±	1.54	0.83	±	0.08
	Salinator fragilis	8.82	±	0.46	3.02		0.16
	Simplisetia aequisetis	11.80	±	0.32	1.04	±	0.03
	Hiatula (Soletellina) alba	11.97	±	0.41	1.77	±	0.06
	Spisula trigonella	11.14	±	0.73	2.18	±	0.14
	Stratiomyidae	13.38	±	0.55	3.89	±	0.16
Fish	*Acanthopagrus butcheri*	22.11	±	0.11	5.88	±	0.03
	Afurcagobius tamarensis	18.52	±	0.25	5.01	±	0.07
	Aldrichetta forsteri	19.37	±	0.25	6.11	±	0.13
	Ammotretis rostratus	17.47			4.76		
	Argyrosomus japonicus	19.08	±	0.69	5.54	±	0.20
	Arripis truttaceaus	18.95	±	0.20	5.91	±	0.06
	Atherinosoma microstoma	18.64	±	0.11	5.32	±	0.03
	Hyperlophus vittatus	18.68	±	0.16	4.63	±	0.04
	Hyporhamphus regularis	19.04	±	0.31	5.81	±	0.09
	Pseudaphritis urvillii	20.13	±	0.23	6.36	±	0.07
	Rhombosolea tapirina	18.63	±	0.16	4.97	±	0.04
	Tasmanogobius lasti	18.02	±	0.60	5.52	±	0.18

Table 32. Energy content (mean ± standard error SE) for trophic groups of macroinvertebrate and fish, by assigning taxa for which calorific content was obtained to the trophic group (see Sections 3.2.2 and 3.2.3). Energy content are given in both kJ/g dry mass and kJ/g wet mass.

		kJ/g DRY MASS			kJ/g WET MASS		
PREY TYPE	TROPHIC GROUP	MEAN		SE	MEAN		SE
Macroinvertebrates	Benthic decapods	9.84	±	0.33	3.36	±	0.17
	Bentho-pelagic crustaceans	12.25	±	0.36	1.96	±	0.06
	Benthic annelids	12.90	±	0.32	1.03	±	0.02
	Benthic deposit-feeding annelids	12.79	±	0.52	1.27	±	0.05
	Insect larvae/pupae	11.46	±	0.59	2.68	±	0.17
	Ficopomatus	14.31	±	1.12	1.45	±	0.11
	Benthic micro-molluscs	8.82	±	0.46	3.02	±	0.16
	Subtidal benthic molluscs	11.54	±	0.43	1.98	±	0.08
Fish	Pelagic mesopredator	18.95	±	0.20	5.91	±	0.06
	Small Demersal zoobenthivore	19.44	±	0.20	5.93	±	0.09
	Flounder	18.58	±	0.16	4.96	±	0.04
	Mulloway	19.08	±	0.69	5.54	±	0.20
	Garfish	19.04	±	0.31	5.81	±	0.09
	Sandy sprat	18.68	±	0.16	4.63	±	0.04
	Smallmouth hardyhead	18.64	±	0.11	5.32	±	0.03
	Yelloweyed Mullet	19.37	±	0.25	6.11	±	0.13
	Black bream	22.11	±	0.11	5.88	±	0.03

3.3.3 Energy density

Corresponding with the patterns for biomass of macroinvertebrates (Figure 19) and fish (Figure 30-32), the energy density increased from the South Lagoon towards the North Lagoon (Figure 41), with the temporal pattern varying between regions (Figures 42 and 43; Table 33).

Macroinvertebrate energy density was negligible in the South Lagoon (median 0 kJ m^{-2}, mean 3.59 kJ m^{-2} across all surveys), low at Noonameena (median 5.19 kJ m^{-2}) in the North Lagoon (for entire North Lagoon: median 59.19 kJ m^{-2}, mean 193.93 kJ m^{-2}), and exceeded 200 kJ m^{-2} (median values) from Long Point and through the Murray Estuary (Figures 41a and 42). The macroinvertebrate energy density was high in the Murray estuary (median 275.07 kJ m^{-2}, mean 355.45 kJ m^{-2}). Macroinvertebrate energy density varied significantly between regions and surveys (Table 33) but was similar between the Murray Estuary and North Lagoon on several surveys (Appendix Table B.5).The 'Surface-small' macroinvertebrate pry type provided the highest energy density in the North Lagoon and Murray Estuary, and were also found, although in low abundance, in the South Lagoon (Figure 43a). The prey types 'Surface-medium' and 'Deep-large' also had higher energy density in the North Lagoon and Murray Estuary than in the South Lagoon, while other prey types ('Surface-large' and 'Epifauna-large') had negligible energy density in all regions (Figure 43a). Energy density of macroinvertebrate trophic groups was also not evenly provided across the regions (Figure 43b). 'Benthic micro-molluscs' had the highest energy density in both the North Lagoon and Murray Estuary. 'Benthic-pelagic crustaceans' and 'Benthic annelids' also had high energy density in the Murray Estuary. 'Insect larvae/pupae' had a low energy density in each region, including the South Lagoon (Figure 43b).

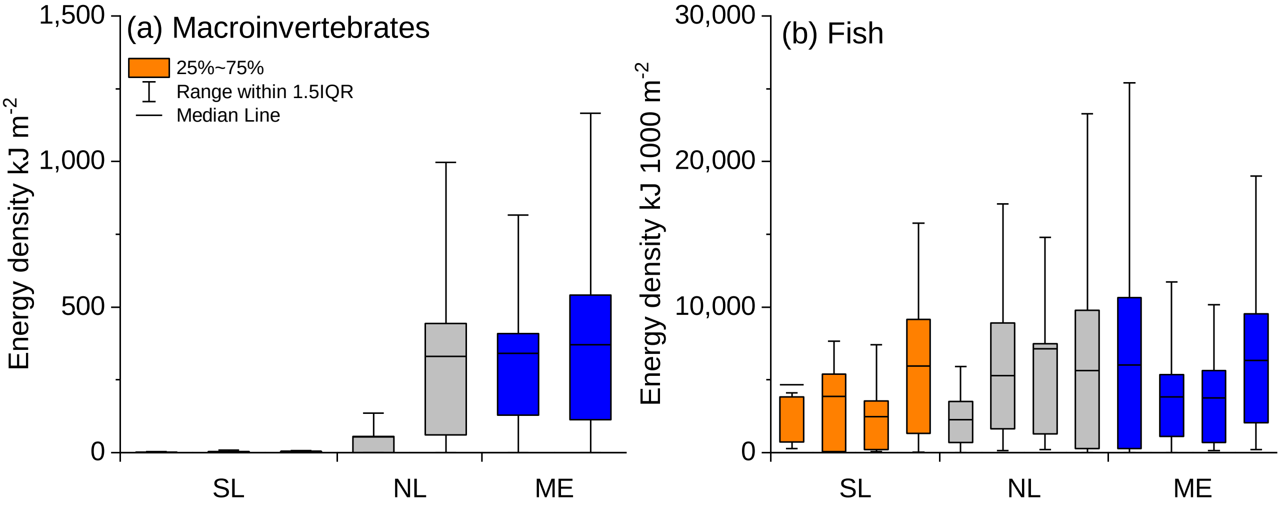

Figure 41. Box plot of total energy density for (a) macroinvertebrates and (b) fish across the gradient of the Coorong, with seven sites surveyed for macroinvertebrates and 12 sites for fish. Boxplots of macroinvertebrates are based on surveys from February 2020 to August 2021, and for fish from Autumn 2020 to Summer 2021. Energy density for macroinvertebrates is based on dry mass and for fish on wet mass, and calorific content by taxa (Table 42). The regions are SL = South Lagoon, NL = North Lagoon, ME = Murray Estuary. Note the different scales in the y-axes. The whiskers display the 1.5 interquartile range IQR.

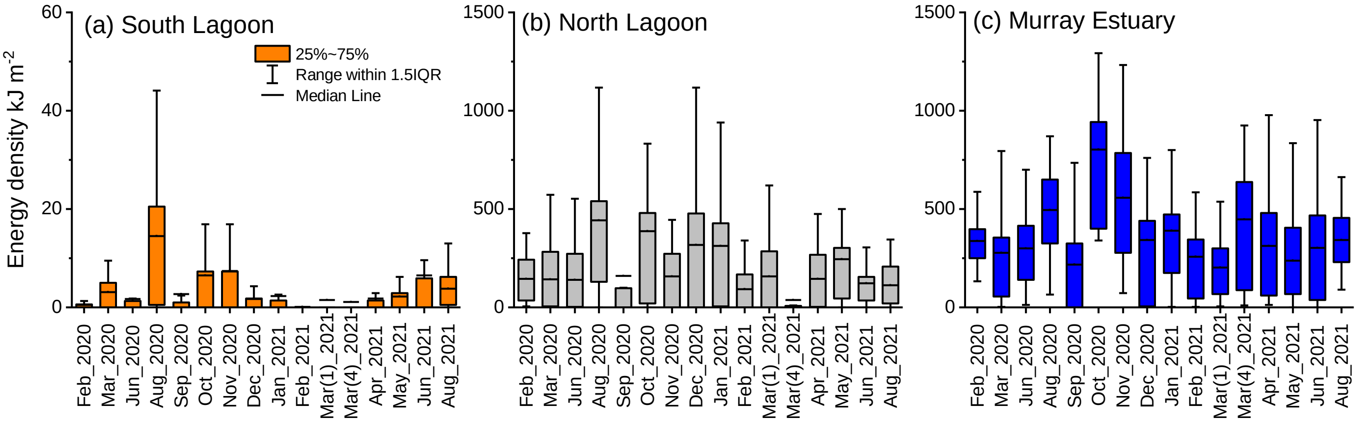

Figure 42. Box plots of energy density (kJ m^{-2}, based on dry mass) for macroinvertebrates for each of the regions and surveys from February 2020 to August 2021. Note the different scales in the y-axes. The whiskers display the 1.5 interquartile range IQR.

Table 33. Test results from permutational ANOVA (PERMANOVA) on differences in energy density for macroinvertebrates and fish across the three regions (Re) of the Coorong and over the surveys (Su). Significant P-values are shown in bold.

	MACROINVERTEBRATES				FISH			
MAIN TEST	df	MS	PSEUDO-F	P$_{(PERM)}$	df	MS	PSEUDO-F	P$_{(PERM)}$
Region (Re)	2	1320.80	896.82	**0.0001**	2	565.01	2.69	0.0470
Survey (Su)	15	17.02	11.56	**0.0001**	7	2569.60	12.24	**0.0001**
Re x Su	30	5.11	3.47	**0.0001**	14	669.84	3.19	**0.0001**
Residual	1404				252			

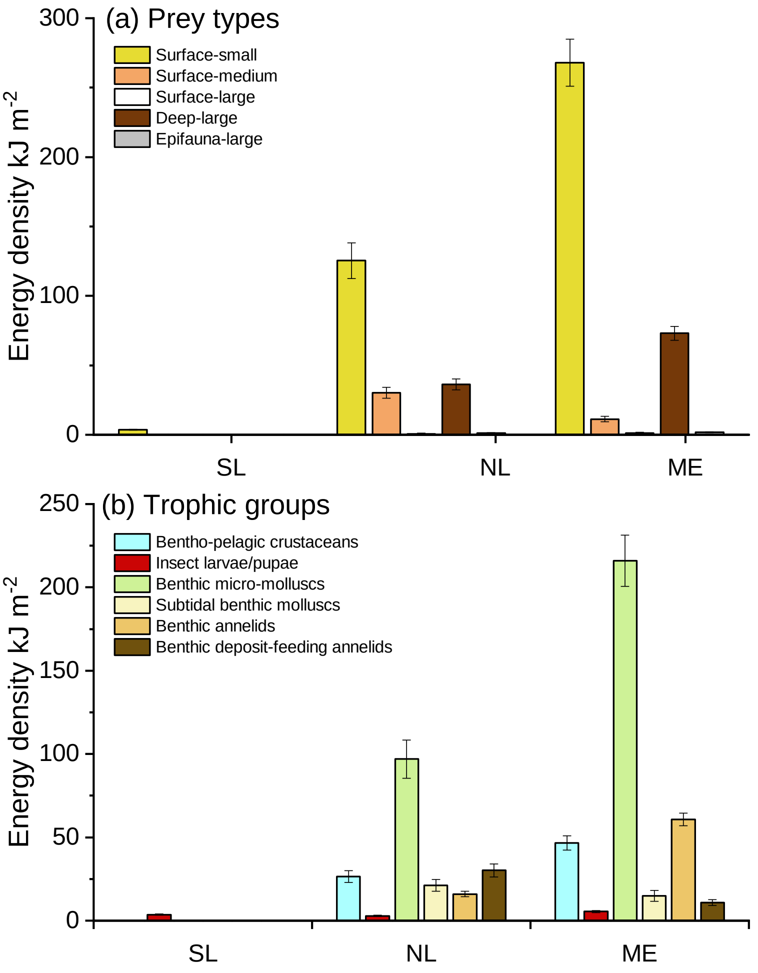

Figure 43. Energy density (average ± standard error) for macroinvertebrates grouped (a) by prey types, and (b) by trophic groups, per region of the Coorong, based on all surveys from February 2020 to August 2021. The regions are SL = South Lagoon, NL = North Lagoon, ME = Murray Estuary. See Table 9 for species allocated to each prey type and trophic group.

For fish, variability in energy density was high, and differences were more pronounced between the surveys than between regions (Figure 44, Table 33), but some significant differences occurred between regions across the surveys (Appendix Table B.10). Over all surveys, the median energy density in the South Lagoon was 1489 kJ 1000 m^{-2}, 2334 kJ 1000 m^{-2} in the North Lagoon, and 2876 kJ 1000 m^{-2} in the Murray Estuary. Smallmouth hardyhead accounted for the energy density in the South Lagoon, and most of the energy density in the North Lagoon (Figures 44 and 45). In the North Lagoon, and especially in the Murray Estuary, several other trophic groups provided energy density, with the highest energy density in the Murray Estuary from yelloweye mullet and sandy sprat (Figure 45).

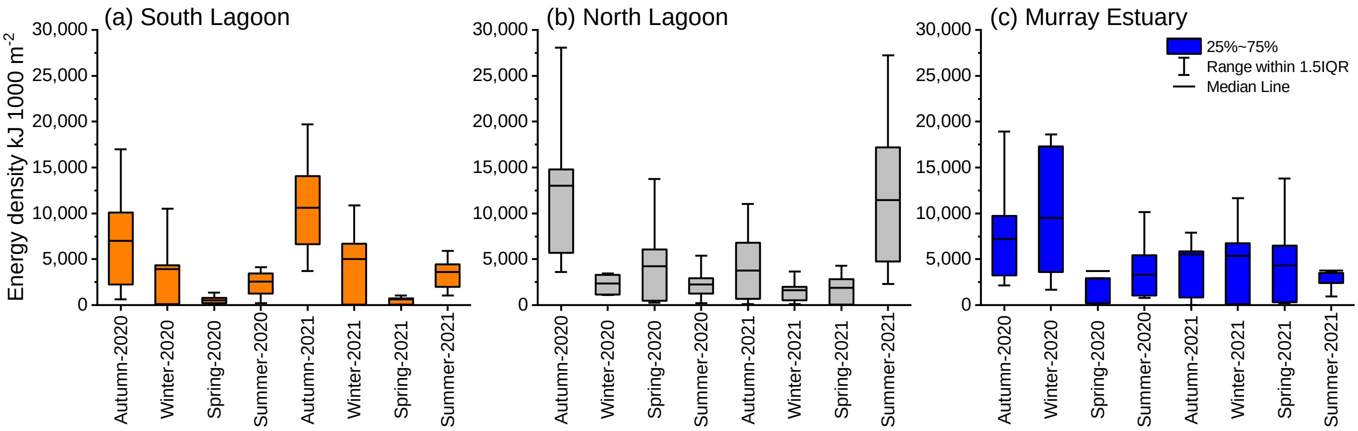

Figure 44. Box plots of energy density (kJ 1000 m^{-2}, based on wet mass) for small and large bodied fish for each of the regions and seasonal surveys from Autumn 2020 to Summer 2021. The whiskers display the 1.5 interquartile range IQR.

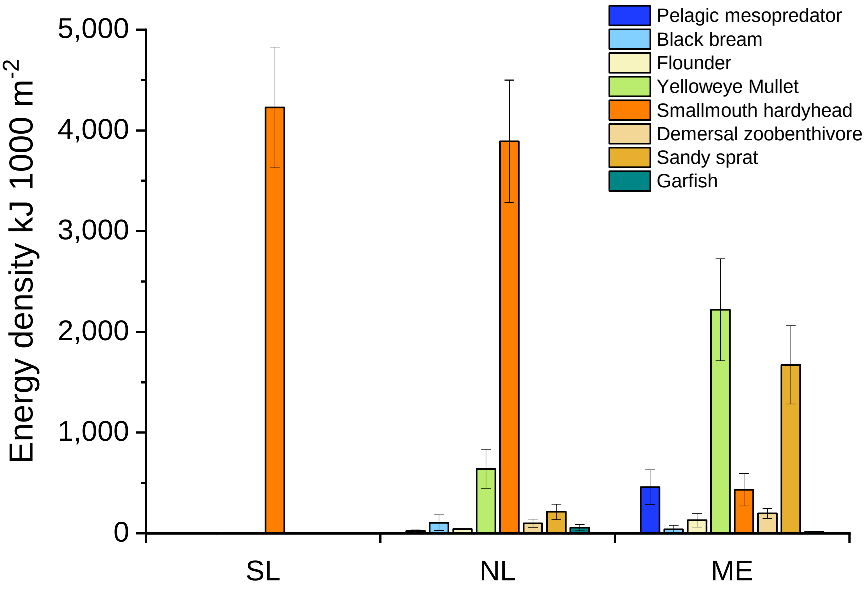

Figure 45. Energy density (average ± standard error) for fish by trophic groups (see Table 30 for detail), per region of the Coorong, based on all surveys from March 2020 to December 2021. The regions are SL = South Lagoon, NL = North Lagoon, ME = Murray Estuary.

3.3.4 Lipid and protein contents

The nutritional value of prey items was further characterised by their lipid and protein contents. For macroinvertebrates, the average crude lipid content across all species was 4.78% DM (dry mass), ranging from 0.68% DM for *A. semen* to 11.87% DM for *Ficopomatus enigmaticus* (Figure 46, Table 34). Several species in the trophic group 'Benthic micro-molluscs', which accounted for most of the macroinvertebrate energy density (Figure 43), had low lipid and protein contents (Figures 46 and 47, Table 34). Amphipods had relatively high lipid (7.46% DM) and protein (39.72% DM) content, which aligned with a high calorific content (Table 31). Several species of benthic annelids (*Australonereis ehlersi, S. aequisetis, A. australiensis*) contained both high lipid (values from 5 to 12% DM) and protein (>40% DM) contents, and also had high calorific values (Figures 46 and 47, Tables 31 and 34). The larger bivalves *H. alba* and *S. trigonella* were relatively low in lipid, but high in protein contents (Table 34). Where lipid and protein contents could be determined in macroinvertebrates for the two seasons, the values were mostly similar between seasons, apart from lower values in winter for *S. aequisetis* (Figure 46, Table 34).

Crude lipid (<2% DM) and crude protein (<10% DM) contents were lowest for *Ruppia* and filamentous algae, (Figures 46 and 47, Table 34). Crude lipid and protein contents were highest for fish (>70% DM on average for protein and >13% DM for lipid) (Figures 46 and 47, Table 34). There was no seasonal difference in the protein content for yelloweye mullet, but in summer the protein content was significantly higher for small than large mullet (PERMANOVA, Pseudo-F = 17.25, P = 0.0003). Large yelloweye mullet had very high lipid contents (28% DM on average). There was no seasonal difference in the lipid content for sandy sprat and smallmouth hardyhead (Figure 46). The protein content for sandy sprat was different between seasons with significantly higher values in winter, but not different between the Murray Estuary and North Lagoon where this species occurs (Figure 47, Appendix Tables B.11). Smallmouth hardyhead, which occur throughout the Coorong, had significantly different protein content between regions and seasons, which was due to significantly lower protein content in the South Lagoon compared to the North Lagoon and Murray Estuary in summer (Figure 48, Appendix Table B.11). Between the two seasons, there was no difference in the protein content in the Murray Estuary, a significant increase from winter to summer in the North Lagoon, and a significant decrease from winter to summer in the South Lagoon (Figure 48, Appendix Table B.12).

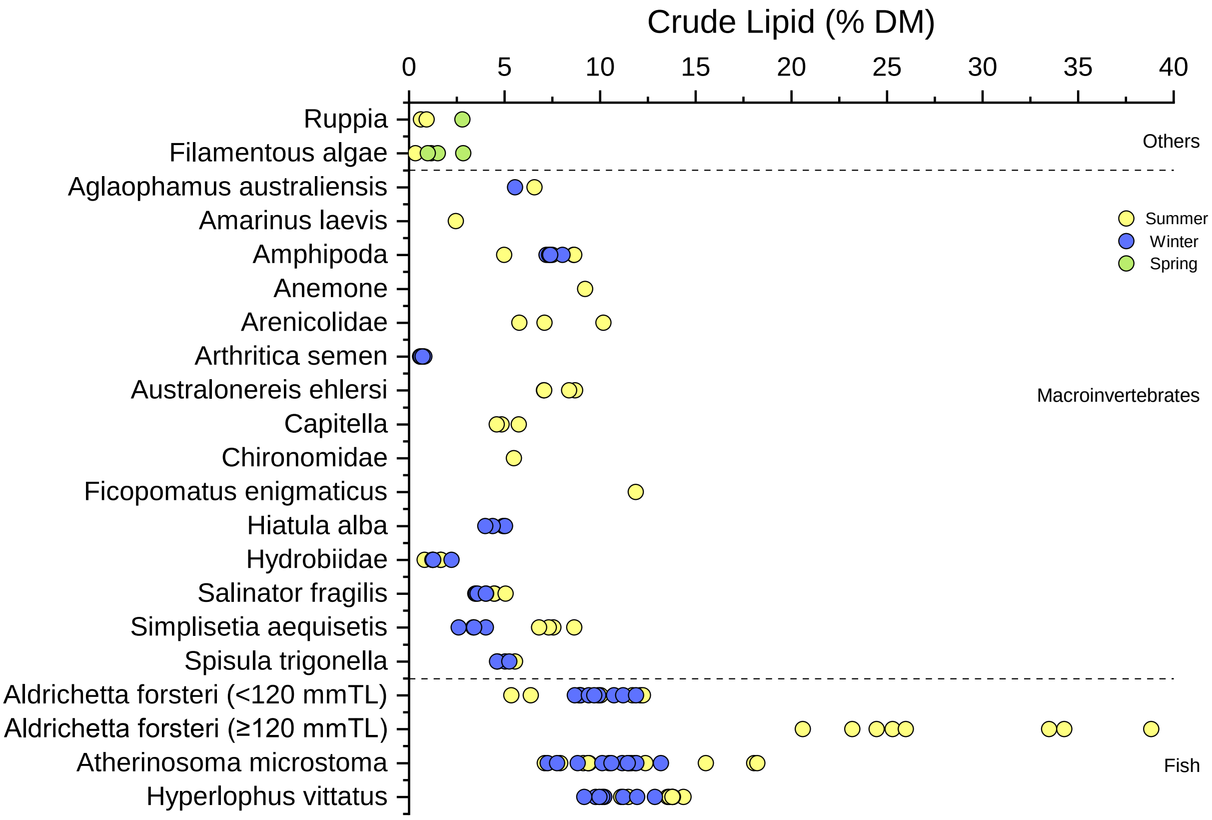

Figure 46. Crude lipid content (% dry mass DM) of plant, macroinvertebrate and fish taxa from several trophic levels for which sufficient material could be obtained for analysis. The colours indicate whether the material was collected in summer (yellow) winter (blue), or spring (green). See Table 4 in Section 2.3.4 for sample size.

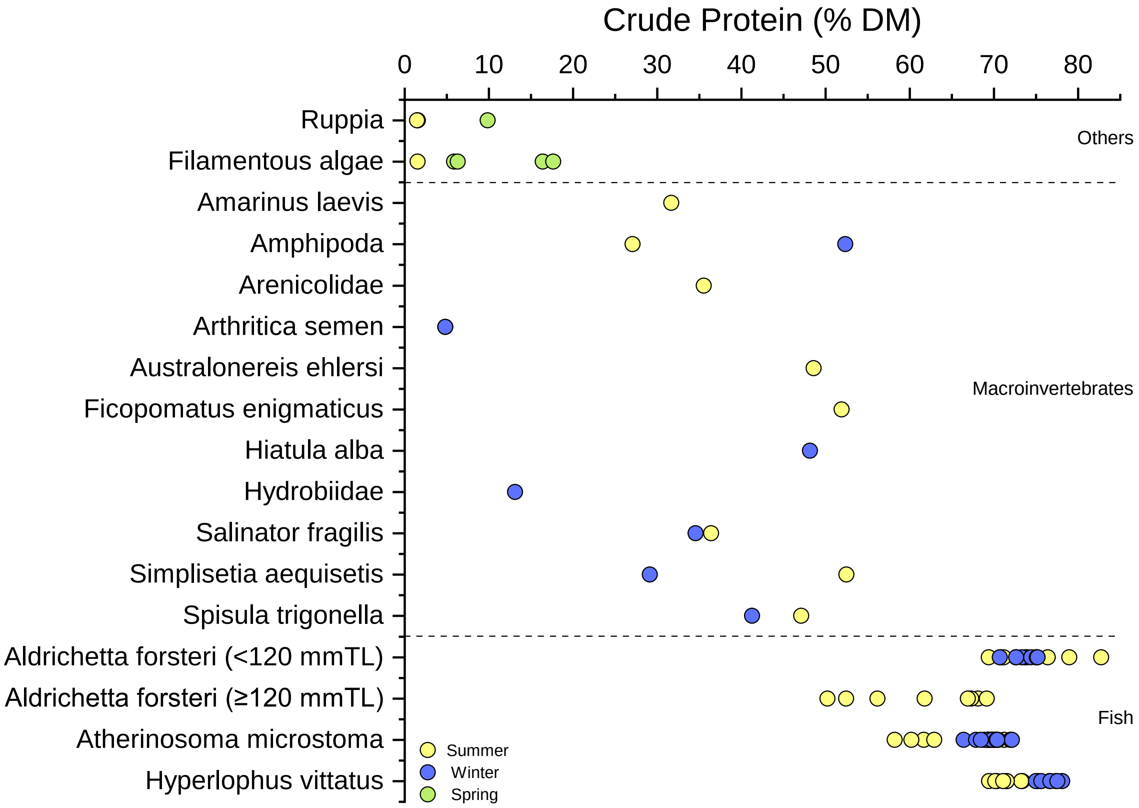

Figure 47. Crude protein content (% dry mass DM) of plant, macroinvertebrate and fish taxa from several trophic levels for which sufficient material could be obtained for analysis. The colours indicate whether the material was collected in summer (yellow), winter (blue), or spring (green). See Table 4 in Section 2.3.4 for sample size.

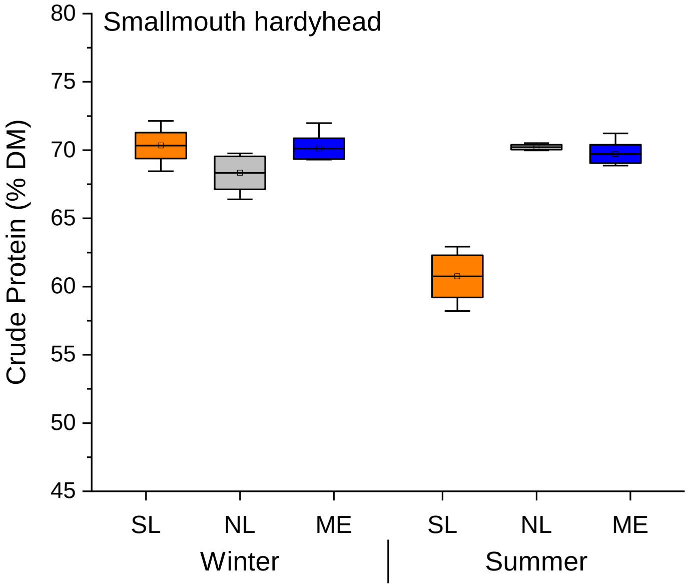

Figure 48. Box plot of crude protein content (% dry mass DM) of smallmouth hardyhead from the South Lagoon (SL), North Lagoon (NL) and Murray Estuary (ME) in two seasons, winter 2021 and summer 2022. The whiskers display the 1.5 interquartile range IQR.

Table 34. Crude Lipid (in % dry mass DM) and Crude Protein (%DM) contents (mean ± standard error) for different food items. Samples were obtained where possible from the winter (W) and summer (S) season in 2021. A * indicates that the sample amount was minimal and values are to be interpretated with caution. Size for yelloweye mullet (*Aldrichetta fosteri*) is given in mm Total Length (TL).

FOOD CATEGORY	SPECIES	SIZE mm TL	SEASON	CRUDE LIPID (% DM)	CRUDE PROTEIN (% DM)
Plants	*Ruppia*			1.45 ± 0.68	4.30 ± 2.78
	Filamentous algae			1.37 ± 0.41	9.56 ± 3.17
Macroinvertebrates	*Amarinus laevis*		S	2.45	31.68
	Amphipoda		S	7.44 ± 0.86	27.09
			W	7.49 ± 0.19	52.35
	Anemone		S	9.22*	
	Arenicolidae		S	7.68 ± 1.30*	35.52
	Arthritica semen		S	0.68 ± 0.04	4.83
			W	0.69 ± 0.05	4.82
	Australonereis ehlersi		S	7.80 ± 0.43*	48.59
	Capitella capitata		S	5.06 ± 0.35*	
	Chironomidae		S	5.49*	
	Ficopomatus enigmaticus		S	11.87	51.90
	Hydrobiidae		S	1.39 ± 0.28*	
			W	1.50 ± 0.25	13.12
	Aglaophamus (Nepthys) australiensis		S	6.57*	
			W	5.56	
	Salinator fragilis		S	4.51 ± 0.21	36.40
			W	3.65 ± 0.12	34.56
	Simplisetia aequisetis		S	7.58 ± 0.39	52.50
			W	3.35 ± 0.29	29.12
	Hiatula (Soletellina) alba		W	4.58 ± 0.24	48.16
	Spisula trigonella		S	5.54	47.12
			W	4.88 ± 0.18	41.28
Fish	*Aldrichetta forsteri*	<120	S	9.46 ± 0.92	74.52 ± 1.61
		≥120	S	28.27 ± 2.27	61.52 ± 2.68
		<120	W	10.06 ± 0.40	73.77 ± 0.54
	Atherinosoma microstoma		S	11.54 ± 1.06	66.90 ± 1.36
			W	10.61 ± 0.52	69.59 ± 0.46
	Hyperlophus vittatus		S	13.19 ± 0.42	71.35 ± 0.50
			W	10.66 ± 0.44	76.54 ± 0.40

4 Discussion

4.1 Food resource availability and associated habitat requirements, including environmental influences

4.1.1 Zooplankton

This study was designed to investigate patterns in the zooplankton community within the Coorong, including the South Lagoon, North Lagoon and Murray Estuary, and relate these to changes in season and freshwater flow. In general, density and taxonomic richness were similar to what has been measured in previous studies under similar conditions (e.g. Geddes et al. 2016). In the South Lagoon and Murray Estuary, there was no evidence of consistent seasonal trends in the zooplankton community. However, densities in the South Lagoon in 2021, and the Murray Estuary in 2020 and 2021, did increase at times of higher freshwater flow. In the South Lagoon, total zooplankton and microcrustacean density was significantly greater in September 2021 than during any other survey during this study. These greater densities were associated with high flow via Salt Creek and decreases in salinity. The greater densities were most likely driven by the decreases in salinity rather than the importation of organisms via Salt Creek, as there was no evidence of freshwater taxa. The few taxa present at the time were immature copepods, ostracods and the marine rotifer, *Synchaeta neapolitana*. In the Murray Estuary, total, microcrustacean and rotifer density was greater in December 2020 and September 2021 than what was detected during surveys conducted earlier in the corresponding years. These results were associated with high freshwater flow via barrages and were most likely driven by a combination of decreases in salinity and the importation of organisms with freshwater flows. The greater densities measured were driven primarily by freshwater taxa including the rotifers *Filinia longiseta* and *Keratella australis*, and the microcrustaceans *Boeckella triarticulata* and *Ceriodaphnia* cf. *quadrangula*. This importation of freshwater taxa contributed considerably to the highest taxonomic richness (12 taxa) recorded for the study across regions at the Murray Estuary in September 2021. Interestingly, the North Lagoon demonstrated vastly different trends in total, microcrustacean and rotifer density than the other two regions. Similarly, there was no evidence of consistent seasonal trends, however in contrast to the other two regions, greater densities were measured during periods of low flow, despite indiscernible differences in water quality in comparison to sites within the Murray Estuary.

The zooplankton of the South Lagoon was depauperate in density and taxonomic richness, presumably due to limited inflows to the region and resulting hypersaline conditions. Densities, taxonomic richness, and the community assemblage detected in this study were very similar to that reported by Shiel and Tan (2013b), who collected zooplankton samples from a single site in the South Lagoon (Villa de Yumpa) from September 2012 to March 2013. The hydrological conditions experienced in 2012-13 were also similar to those that occurred during this study with freshwater inflows to the Coorong occurring through spring and early summer. Shiel and Tan (2013b) detected 1-9 taxa and measured densities of 0-1.34 x 10^5 ind. m^{-3} in comparison to 1-7 taxa and 4.34 x 10^3 – 1.13 x 10^5 ind. m^{-3} in this study. Additionally, in both studies the community assemblage was predominantly comprised of halophile *Synchaeta* species, copepodites, copepod nauplii, the estuarine/marine calanoid *Acartia* and ostracods. As in this study, Shiel and Tan (2013b) measured the highest densities in the month of September when freshwater flow through Salt Creek was highest (~300-500 ML day^{-1} in both studies). In this study, the freshwater flows via Salt Creek, in addition to freshwater flows via the barrages, resulted in a decrease in salinity in the South Lagoon, from ~80-90 ppt in June 2021 to ~60-70 ppt in September 2021. These results demonstrate how reductions in salinity, whether due to unregulated flows or management actions, are likely to enhance the availability of zooplankton as a food resource for higher trophic organisms in the South Lagoon, similar to other hypersaline systems (Tweedley et al. 2019; Brookes et al. 2022). The densities of zooplankton required to result in positive outcomes for higher trophic organisms is unknown and should be considered as a focus for future research.

The North Lagoon had the most dense and dynamic zooplankton in comparison to the other two regions throughout the study, however not necessarily the most taxa rich. During this study, the zooplankton community within the North Lagoon did not demonstrate short-term responses to increases in freshwater flow (unlike the Murray Estuary and the South Lagoon). Interestingly, densities were high from June 2020 until September 2021. These greater values were due to high densities of an undescribed species of *Synchaeta*, which has previously been detected in the lower River Murray, the Lower Lakes and the Coorong region, and appears to be salt tolerant. In this study, this species thrived in salinities <45 ppt, whereas in March 2020 and December 2021, when salinities were near to or greater than 45 ppt, this species was almost completely absent. Previous studies have also found this and other *Synchaeta* species to contribute significantly to zooplankton densities within the North Lagoon, and for this particular species to peak in density at similar salinities (Furst et al. 2019; Geddes et al. 2016; Shiel and Aldridge 2011; Shiel and Tan 2013b, 2013a). The higher densities within the North Lagoon were also driven significantly by microcrustacean densities, largely copepod nauplii, which increased from $2.96 \times 10^4 \pm 3.11 \times 10^3$ ind. m^{-3} in September 2020 to $3.39 \times 10^5 \pm 1.92 \times 10^4$ ind. m^{-3} in December 2020. Following December 2020, nauplii densities steadily decreased until September 2021. It is most likely these copepod nauplii belonged to a species of calanoid copepod, possibly *Gladioferens pectinata*, as calanoid copepodites were also detected throughout the period as well as adult *G. pectinata* in the June 2021 samples. As found in previous studies, even during times in which nauplii are abundant, adults were rare, possibly due to top-down (predation) and/or bottom-up (e.g nutrient limitation) pressures or water quality, which can impact the development of immature copepods (Hemraj et al. 2018).

The results from this study, when considered in context with previous studies, suggest that over the long-term, zooplankton densities in the North Lagoon tend to be lower during persistent low flow periods and greater during high flow periods. Geddes et al. (2016) measured densities of $3.4 \times 10^3 – 3.70 \times 10^5$ ind. m^{-3} at Long Point in 2004-05, similar to densities measured at Long Point and Noonameena in this study ($5.56 \times 10^3 – 4.44 \times 10^5$ ind. m^{-3}) and both measured after approximately four years of low freshwater flow. Additionally, taxonomic richness, and the taxa present were very similar, with only a few taxa present including *Synchaeta* species, copepod nauplii and copepodites. After an additional three years of low freshwater flow, Geddes et al. (2016) measured even lower densities at Long Point and Noonameena in 2007-08 (50 – 565 ind. m^{-3}). Investigations were also conducted in 2010-11 and 2011-12 that sampled at Mark Point (north of Long Point however still within the North Lagoon) (Shiel and Aldridge 2011; Shiel and Tan 2013a). Both 2010-11 and 2011-12 were years of high freshwater flow and the densities and taxonomic richness measured were considerably greater than those seen during this study (~1×10^5 - 4.5×10^6 and $8 \times 10^3 – 9.15 \times 10^5$ ind. m^{-3} and ~2-18 and 5-25 taxa, respectively). However, it is important to note that these two studies also included protists, which contributed considerably, at times, to both the reported high densities and taxonomic richness.

The Murray Estuary is the most well-connected region to barrage flows, and the zooplankton community responded rapidly to increases in freshwater flow with increases in total, microcrustacean and rotifer densities, characterised by freshwater taxa. Flow to the Coorong was very low from March until early July 2020. During this period, as well as in September 2020, total density was low ($2.3 \times 10^4 – 6.4 \times 10^4$ ind. m^{-3}) and comparable to densities found by Geddes et al. (2016) at Pelican Point in late 2003 ($1.2 \times 10^4 – 1.91 \times 10^5$ ind. m^{-3}) and 2004-05 ($1.4 \times 10^4 – 1.14 \times 10^5$ ind. m^{-3}) when freshwater flow was also low. Geddes et al. (2016) measured even lower densities in January 2007 and 2008 in the Coorong at Goolwa Creek and Pelican Point, after a further three to four years of drought ($1.9 \times 10^3 – 3.9 \times 10^3$ ind. m^{-3} and 4×10^2 - 5.2×10^2 ind. m^{-3}, respectively). In this study, following a short period of moderate increases in flow to the Murray Estuary through September and December 2020, total density increased slightly to $1.27 \times 10^5 \pm 3.11 \times 10^4$ before returning to densities similar to those seen prior. Again, as seen in previous studies during barrage releases, these increases in December 2020 were characterised primarily by increases in freshwater rotifers (in this instance, *Keratella australis* and *Filinia longiseta*) and copepod nauplii (Shiel and Aldridge 2011; Shiel and Tan 2013a, 2013b). Flow increased substantially in September 2021 and total, microcrustacean and rotifer densities responded rapidly, with substantially greater densities measured in September in comparison to those seen in June 2021 (~10-fold increase in total density and ~2.5-fold increase in taxonomic richness, reaching $4.11 \times 10^5 \pm 8.97 \times 10^4$ ind. m^{-3}). These increases were much smaller than those measured by Shiel and Aldridge (2011) ($1 \times 10^5 – 5 \times 10^6$ ind. m^{-3} downstream of Goolwa Barrage and $1.25 \times 10^5 – 1.1 \times 10^6$ ind. m^{-3} at Tauwitcherie), Shiel and Tan (2013a) ($7.8 \times 10^4 – 2.82 \times 10^6$ ind. m^{-3} at Tauwitcherie) and Shiel and Tan (2013b) ($2.4 \times 10^4 – 2.04 \times 10^6$ ind. m^{-3} at Tauwitcherie) during periods of increased freshwater flow. However, the magnitude of freshwater flow was considerably greater in those years than during this study. Furthermore, the substantially greater densities measured in comparison to those measured in this study were primarily driven by protists, which were not included in this study. Interestingly, the pulse in total density measured in this study in September 2021 was largely driven by increases in three freshwater microcrustaceans (*Boeckella triarticulata, Calamoecia ampulla* and a *Ceriodaphnia* species), in addition to freshwater rotifers (*Keratella tropica*, *Keratella australis, Filinia australiensis* and a salt tolerant undescribed *Synchaeta* species). Cladocerans such as *Ceriodaphnia* and adult copepods were otherwise almost completely absent from the study. Shiel and Aldridge (2011) also found that increases in density in the Murray Estuary during high flow were in part due to increases in adult copepods and cladocerans. These increases in microcrustaceans are most likely from Lake Alexandrina, as the taxa detected have commonly been found in high densities in Lake Alexandrina, Mundoo Channel and Boundary Creek (e.g. Geddes 1984; Shiel and Tan 2013b). Additionally, the conditions within Lake Alexandrina are more likely to support the development of dense populations of these taxa (i.e. lower salinities and longer water residence times). Microcrustaceans are often viewed as preferred prey organisms for fish, however specifics around required densities and timing, preferred taxa and the importance of varying food quality between and within taxa is largely unknown. Gaining more insight in these matters will vastly improve our ability to evaluate these results and further investigate how nuances in the management of freshwater flows between Lake Alexandrina and the Coorong may translate to outcomes for higher trophic organisms in the Coorong.

Across regions, the results from this study, in combination with the results from past investigations, demonstrate the vital role that freshwater flow into the Coorong plays in driving zooplankton productivity. In the short-term, freshwater flow freshens the system, and provides pulses of freshwater zooplankton, as seen in this study. However, freshwater flow also delivers nutrients and detritus that fuels the food web over the longer term. Determining how these influences shift over time and interact with tidal, seasonal, annual and inter-annual cycles is challenging, and is best answered through multi-year studies. This study hoped to shed some light on seasonal influences however clear trends within the time period were not evident. It is likely that sampling needs to occur over a greater period than two years and possibly at a higher frequency to untangle these trends.

4.1.2 Macroinvertebrates

Macroinvertebrates are essential prey items for many fish and waterbird species in the Coorong, particularly migratory shorebirds (Giatas et al. 2018, 2022; Ye et al. 2020), but the availability of macroinvertebrate prey varies throughout the Coorong subject to environmental drivers (Dittmann et al. 2015). Both the overall number of macroinvertebrate species and the species density across samples was higher in the Murray Estuary and North Lagoon than in the South Lagoon. This pattern of higher diversity in the estuarine section of the Coorong compared to the southern hypersaline South Lagoon aligns with long-term monitoring records (Dittmann et al. 2015, 2021). The significant decrease in the number of species as salinities increase to hyper- or ultrahaline is known from estuaries (Whitfield et al. 2012) and hypersaline lagoons (Tweedley et al. 2019).

The diversity of prey options was higher in the estuarine regions of the Coorong, with more trophic groups and prey types available for benthivorous fish and shorebirds with different foraging strategies. The feeding specialisation of shorebirds is related to their bill lengths (Dann 1987, Durell 2000), and for shorebirds with longer bills, such as curlews, harvestable prey was only available in the Murray Estuary and North Lagoon with a high biomass and energy density of ‘Deep-large’ prey types. The intensive sampling effort for macroinvertebrates, which included subtidal sediments as well as the peninsula side of the Coorong (which was rarely included in previous investigations), increased the total number of species known to occur in the Coorong. Of the six marine/estuarine species newly recorded in the Coorong, the large-bodied lugworms (Arenicolidae) can be important prey for shorebirds (Zwarts & Wanink 1993) and improve sediment conditions due to their bioturbation (Volkenborn et al. 2009).

In the South Lagoon, individual densities and biomass were several orders of magnitude lower than in the North Lagoon and Murray Estuary. The higher macroinvertebrate individual densities and biomass in the Murray Mouth and North Lagoon compared to the South Lagoon were similar to a pattern seen over long-term monitoring (Dittmann et al. 2015, 2021). The higher sampling frequency detected a seasonal increase in macroinvertebrate individual densities over spring and summer, which was aligned with higher freshwater flows and most pronounced in the Murray Estuary. Amphipods and mysid shrimp numbers increased in response to flow and accounted for higher densities of 'Surface-small' and 'Epifauna-large' prey types and as trophic group, of 'Benthic-pelagic crustaceans'.

Surface sediments contained the highest densities of macroinvertebrate prey of small to medium size. In the South Lagoon, only small surface living insect larvae and pupae provided food, whereas more taxa contributed to the higher densities of this prey type the North Lagoon and Murray Estuary. Macroinvertebrate prey of larger body size and occurring deeper in the sediment are possible prey for long-billed shorebirds in the Murray Estuary where they were more abundant than in other regions. Chironomid larvae occurred over the entire salinity range but with lower density and biomass compared to other macroinvertebrate taxa. While chironomids were the main, or only, macroinvertebrate prey available in the South Lagoon, the energy density they provided was very low. Improved food availability for shorebirds and benthivorous fish in the Coorong arises from higher prey diversification under lower salinities.

Salinity was the main driver determining the macroinvertebrate community and prey availability in the Coorong. The communities characterising the North Lagoon and Murray Estuary were split from those in the South Lagoon at a salinity of 64 ppt, similar to findings by Lester and Fairweather (2009) and Dittmann et al. (2015). Coherent groups of macroinvertebrate species occurred in the Coorong, with a group of key species (*Simplisetia aequisetis*, amphipods and *Arthritica semen*) present throughout the North Lagoon and Murray Estuary, and a further group comprising species of micro-molluscs, benthic annelids and mysid shrimp present mainly in the Murray Estuary. Within the Murray Estuary, nine of the monthly surveys during the higher flow in spring and summer, were separated as a distinct cluster by salinities <24 ppt. While the main division with a salinity of 64 ppt has been used for management considerations, our findings indicate that much lower salinities provide a more diverse and abundant macroinvertebrate community and food availability. Based on our extensive sampling, it emerged that macroinvertebrate diversity, individual and biomass densities were highest at salinities <40 ppt. Lowering salinity to below 40 or 50 ppt could have a beneficial outcome for the Coorong food web, similar to findings from salinity reductions in other estuaries (Breaux et al. 2019; Tweedley et al. 2019).

With low prey diversity and energy density, the food web in the South Lagoon is simpler and less resilient to perturbations than the more diverse prey communities in the North Lagoon and Murray Estuary, where energy density of several prey types was higher. As the pattern of food availability of macroinvertebrates along the Coorong gradient was driven by salinity, lower salinity in the South Lagoon (<60 or ideally <40 ppt) can increase the food resources for key fish and waterbird species, as shown for the management of other hypersaline systems (Breaux et al. 2019; Smith et al. 2021).

Our study revealed variability in macroinvertebrate data within study regions, which could be partially explained by localised impacts of filamentous algal mats and occurrence of monosulfidic black ooze, which occurred especially in subtidal sediments during this study. Filamentous algae can thrive under eutrophic conditions which characterise the Coorong (Mosley et al. 2020) and affect macroinvertebrates (Kanaya et al. 2016). Lowering nutrient influx and nutrient loads within the Coorong will have beneficial effects for macroinvertebrates, which can also be part of the solution through their ecological functions that can remediate sediment conditions (Lam-Gordillo et al. 2022).

Secondary production (production by heterotrophic organisms) integrates growth and mortality, reflecting numerous population processes, biotic interactions, and environmental conditions; thereby providing insight into ecosystem function (Dolbeth et al. 2012). Production studies provide insights into trophic dynamics of communities and ecosystems, reveal important information about the flow of matter and energy, and are an important step in the development of quantitative food webs (Benke 2011; Downing 1984).

Benthic macroinvertebrate production is important for sustaining populations of higher trophic predators in estuaries, such as birds and fish. Species contributing most to this production in the Coorong are the micro-mollusc, *A. semen*, and the bentho-pelagic crustaceans, Amphipoda, with the Polychaetes *Capitella* and *S. aequisetis* also important. These species cover a range of different trophic groups and prey types, providing food for predators with different feeding modes, however the bulk of macroinvertebrate production in the Coorong is contained in surface-small prey (*A. semen* and Amphipoda).

Annual production and production:biomass (P:B) ratios calculated based on Edgar's (1990) empirical equation were generally within the range of values reported in the literature for the same or related species in other parts of the world (Appendix Table C.6). Notable exceptions to this were *A. semen* and *S. aequisetis*. For *A. semen*, both production and the P:B ratio were high relative to other bivalves, while for *S. aequisetis* the P:B ratio was higher than conspecifics from other systems and other Nereids. This relatively high productivity may be linked to the generally small size of macroinvertebrates in the Coorong. Benthic communities made up of larger species have been associated with lower productivity (Downing 1984). High rates of secondary production may also be facilitated by low species diversity in benthic communities (Paterson and Walker 1974), which may explain the higher productivity seen for these species in the Coorong. As mentioned earlier, Edgar's (1990) model may be less reliable for species which display greater variation in individual size, such as *S. aequisetis*.

The only taxon for which production and P:B estimates could be obtained for both the Northern (North Lagoon and Murray Estuary) and Southern Coorong (South Lagoon) was Chironomidae. Production for this taxon was lower in the Southern Coorong, likely due to lower biomass densities. The P:B ratio was also slightly lower in the Southern Coorong, mostly due to a slightly lower mean mass per individual, which may result from the hypersaline conditions in the South Lagoon (Shadrin et al. 2019). Water temperature is the only environmental variable input into Edgar's (1990) model, and is similar across the Coorong. Salinity is the primary driver of benthic communities in the Coorong; however, few studies have specifically investigated patterns of secondary production along estuarine salinity gradients, especially under hypersaline conditions. Hypersalinity impacts recruitment, growth, and mortality of many species (Hoeksema et al. 2006; Shadrin et al. 2019; Trape et al. 2017) and is likely to affect secondary production.

4.1.3 Fish

Freshwater inflows (particularly from the River Murray) impact fishes in the Coorong by influencing the following critical factors: (1) salinity; (2) connectivity within, and between, marine, estuarine and lake environments; and (3) productivity, by transporting carbon, nutrients and microbiota from upstream (Ye et al. 2016; Bice et al. 2018). 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. 2020). During this 2-year study, fish species richness showed a general reduction from the Murray Estuary to South Lagoon and varied between seasonal trips. Such a distinct pattern coincided with the increasing salinity gradient from the north to south in the Coorong, which was also well demonstrated by our long-term monitoring data (autumn 2006–2020) (Ye et al. 2020). This suggests a strong negative effect of salinity on species richness, and indeed, at salinities >70 ppt, the mean species number was no more than four in the Coorong (Ye et al. 2020). This could be explained by the greater osmoregulatory stress and diminishing food resources due to the increasing salinity, which probably limit the opportunity to extend their ecological niche into the South Lagoon to only a few highly salt-tolerant species (Whitfield 1999). Under current conditions, salinities are typically >70 ppt in the South Lagoon, thus the species diversity is limited, and food web dynamics (e.g. complexity and resilience) may be compromised in this region. Improved habitat connectivity with freshwater flows has been shown to maintain or increase resilience of fish populations (Colombano et al. 2020). The seasonal trend of species richness showed a distinct increase in the Murray Estuary in December 2021, associated with increased barrage flow. Additionally, a minor increase in species richness was also observed in the South Lagoon in December 2021, likely due to the influence of elevated water flow via Salt Creek during this season, but also the substantially greater barrage flow from the River Murray. This highlights the importance of freshwater flow and salinity in maintaining/restoring biodiversity and enhance food resources in the Coorong.

During this study period, fish abundance (individual density) was strongly driven by two small-bodied fishes, with smallmouth hardyhead dominating the South Lagoon, and to a less extent the North Lagoon, and sandy sprat being more abundant in the Murray Estuary. This is consistent with the findings from our long-term monitoring in this region (Ye et al. 2020). Smallmouth hardyhead is the most salt tolerant fish species in the

Coorong with an upper tolerance threshold of 108 (50% lethal concentration, LC_{50}) (Lui 1969), therefore, they were often the only species present in the South Lagoon during dry years (Ye et al. 2020). Smallmouth hardyhead and other small atherinids are important fish species in many temperate Australian estuaries, where they are often the dominant species (>50% of total number of fish), particularly where salinities are near or above that of seawater (e.g. Potter and Hyndes 1994; Griffiths and West 1999; Young and Potter 2002; Hoeksema and Potter 2006). Sandy sprat is a marine-estuarine opportunist species, which spawns in inshore waters of southern Australia, and frequently enters and uses estuaries as a feeding and nursery ground (Rogers and Ward 2007). High densities of sandy sprat were observed in the Murray Estuary, typically following high barrage flows (e.g. in 2011–2013), and their distribution also extended into the North Lagoon, with peak numbers generally associated with marine salinity (35 ppt) (Ye et al. 2020). Smallmouth hardyhead and sandy sprat are the two most abundant prey species, playing an important role in supporting piscivorous fish and waterbird species in the Coorong (Giatas et al. 2018).

For the large-bodied species, >80% (by number) were sampled in the Murray Estuary with the remainder mainly found in the North Lagoon. The most abundant species was yelloweye mullet, which is a marine-estuarine opportunist species that is also consistently abundant in south-western Australian estuaries, particularly as juveniles (see Potter and Hyndes 1999, and references therein). This species can tolerate high salinities up to 82 ppt (LC_{50} at 23 °C) (McNeil et al. 2013), although the field data from this study suggest that they generally prefer salinities <40 ppt (Figure 37). Congolli, a catadromous species, was found in moderate densities in the Murray Estuary and North Lagoon. Although this species also has high salinity tolerance (94 LC_{50} at 23 °C) (McNeil et al. 2013), most individuals were found at salinities <45 ppt in this study (Figure 37). Consequently, yelloweye mullet and congolli were not detected in the South Lagoon during 2020 and 2021 except for very lower numbers of congolli collected in 2020, suggesting negligible abundances. Yelloweye mullet and congolli are important food items for fish predators (e.g. mulloway, Giatas and Ye 2015) and support piscivorous waterbirds in the Coorong (Ye et al. 2020). Furthermore, two freshwater species, bony herring and redfin perch, showed a distinct increase in abundance in the Murray Estuary, particularly during spring and summer 2021, following high barrage flows. Bony herring is a native freshwater-estuarine opportunist species, often present in the Murray Estuary and North Lagoon with increased numbers during high flow years (e.g. Ye et al. 2012). Under wet conditions, bony herring may play an important role, providing food resource subsidy to the Coorong food web.

In the Coorong, fish biomass distribution across three regions was influenced by both fish abundance (numbers, presented as individual density) and size/weight of individual species. In this study, the biomass in the South Lagoon was predominantly from high numbers of smallmouth hardyhead, whereas in the Murray Estuary, the biomass was driven by both small-bodied fish (e.g. abundant sandy sprat) and large-bodied fish species (e.g. yelloweye mullet, congolli, bony herring). In the North Lagoon, the biomass was also influenced by the composition of both large- and small-bodied fishes. Given this region was typically characterised by high abundances of both smallmouth hardyhead and sandy sprat with a moderate abundance of large-bodied species, the overall biomass density was higher than in the Murray Estuary (13%), and slightly higher than in the South Lagoon (1.3%). Such pattern was consistent with the finding from our previous investigations of food resource availability in the Coorong in 2019 (Ye et al. 2019). It should be noted that in both studies, the biomass in the North Lagoon and Murray Mouth may have been underestimated due to sampling method (seine netting) bias toward small-bodied fish and juveniles of large-bodied fish, and the focus of the study selecting key species that are likely to occur in the South Lagoon in order to inform ecological restoration. As large-bodied fish were generally absent in the South Lagoon under current conditions with extreme hypersalinity, the overall fish biomass would have been greater in the northern Coorong (Murry Estuary and North Lagoon), where salinities largely ranged from brackish to moderately hypersaline.

Fish assemblage structure differed distinctly from the Murray Estuary to the South Lagoon, primarily driven by the north-south increasing salinity in the Coorong during 2020 and 2021. This is supported by previous studies (e.g. Geddes and Butler 1984; Geddes 1987; Noell et al. 2009; Ye et al. 2012 and 2016). High seasonal variability in assemblage structure was also evident, mainly influenced by the variations in water temperature, which is also a key factor affecting fish life-history processes. Overall, fish assemblage dissimilarity among regions reduced during spring and winter (cooler months), compared to autumn/summer. For most fish species in the Coorong, the typical spawning and recruitment season occurs between late spring and summer. Therefore, fish abundance (by individual number) may increase substantially after reproduction, though at different levels, along the salinity gradient of the Coorong. This could explain the greater variability in assemblage structure during summer–autumn.

In this study, four water quality parameters (salinity, water temperature, dissolved oxygen, and transparency) best characterised spatio-temporal variations in fish assemblage structure in the Coorong, with salinity being the strongest driver. Three of the four parameters were influenced by freshwater flows from the River Murray (Figure 7b). Salinity, dissolved oxygen and transparency generally decreased with increasing flows, noting the timing of responses along the Coorong may differ due to the distance of the South Lagoon from the Murray barrages. This reinforces the importance of barrage flows in driving environmental conditions and fish assemblage dynamics in the Coorong. Although water temperature regime is largely seasonal, over the last decade, higher flows from the River Murray typically occurred during winter–spring, although the 2021 high flow season extended into the summer.

Salinity was the primary factor separating South Lagoon fish assemblages (>66 ppt) from those of northern Coorong (<52 ppt) during this study. Within the South Lagoon, fish assemblages in spring (September) 2020 and 2021 were distinct from other seasons and were characterised by reduced salinities (66–75 ppt) due to increased flows from the River Murray and/or Salt Creek. In autumn (March) 2020 and 2021, smallmouth hardyhead was the sole species present in this region, associated with salinities >105 ppt or DO <7.7 mg/L. This is not surprising as such high salinity levels are beyond the tolerance thresholds of all other Coorong fish species. The lower DO in autumn was likely due to the extended warmer water temperature in March reducing saturation concentration of DO, and also potentially high ecosystem respiration rates during this season. For the Murray Estuary and North Lagoon, in addition to salinity (the primary driver), water temperature and transparency were secondary factors shaping the spatio-temporal variations in fish assemblage structure. As previously mentioned, temperature is an important factor influencing life-history and ecosystem processes. The highly varied fish assemblages across seasonal trips in this study suggest temporal dynamics of fish prey abundance, which should be considered regarding its implications for the Coorong food web, particularly the effect on piscivorous waterbirds in this region. Water transparency was also identified and better demonstrated as an influential factor for fish, based on our long-term monitoring data in the Coorong (Ye et al. 2020). Water transparency can affect behavioural and physiological aspects of fish. For instance, reduced transparency can alter visual perception of fish (Utne-Palm 2002), which may affect predator-prey interactions (Abrahams and Kattenfeld 1997), disrupt species recognition signals (Seehausen et al. 1997) and affect reproductive behaviour (Sundin et al. 2010). Variation in water transparency may also influence primary productivity, which ultimately impacts fish populations through trophic links. Many studies suggest that the protection against predators afforded by turbid water, in addition to enhanced food resources, may explain why estuaries are productive nursery grounds for many fish species (Cyrus and Blaber 1987; Marais 1988; Griffiths 1996).

This study provides insight on the spatio-temporal variations in fish species diversity, abundance, assemblage structure and biomass in the Coorong across eight seasonal surveys during 2020 and 2021, as well as the key environmental drivers. It reinforces the importance of freshwater flow and salinity being the primary factors driving fish assemblage dynamics in the Coorong, with water transparency and DO also being influential factors in some seasons and/or regions. Fish are an important component of the food web, providing prey for piscivorous taxa (fish and waterbirds) but also being a consumer of lower trophic organisms. The learnings from this study, along with the long-term data collected under varying hydrological conditions over the last two decades (synthesised in Ye et al. 2020), provide important knowledge to inform the ecological restoration, particularly to enhance food resources (diversity and abundance) in the South Lagoon and improve food web functioning and resilience in the Coorong.

4.2 Nutritional value and energy content of major food sources for key fish and waterbird species in the Coorong

Organisms need energy for maintenance, growth, and reproduction, and energy content is an important aspect of food quality, providing insight into food web structure and dynamics. The quality of prey in terms of energy content and nutritional value, rather than purely their abundance, is an important consideration when determining food web functioning. Nutritional requirements of predators can be subject to cyclical events such as reproduction or migration (Murphy 1994). Access to high energy food sources is important during these periods of high demand. Compensatory feeding mechanisms such as increasing the quantity of food consumed when food quality is low, can allow species to sustain themselves (Yeager et al. 2014). Inter- and intraspecific differences in energy content of different food types lead to differences in quality of food available to higher trophic levels.

Energy content of species in the Coorong followed trends expected based on the literature, with less mobile, lower trophic level species containing less energy than more mobile, higher trophic level species (Brey et al. 2010). The exception to this pattern was plankton, which had a lower energy content (6 kJ g^{-1} DM) than the macrophyte *Ruppia* (10 kJ g^{-1} DM). The plankton samples used for energy content analyses were not sorted and may have contained a mixture of phytoplankton and zooplankton, as well as suspended detritus, which may explain the low energy content. However, planktivorous species are likely to consume this mixture of material when feeding, therefore we deem this value representative of the energy available to such species in the Coorong.

Energy content of detritus, algae, *Ruppia*, plankton, and macroinvertebrates was generally lower than values for similar species in the literature (Appendix Tables C.3 and C.5). Environmental factors including temperature, salinity, and food availability can affect energy content of prey (Foy and Paul 1999; Urzúa et al. 2018; Wilt et al. 2014). An increase in energy content of benthic macroinvertebrates with increasing latitude in Arctic shelf waters was associated with the combined effects of higher nutrients and primary productivity, and lower temperatures (Wilt et al. 2014). The energy content of larval crabs (*Hemigrapsus crenulatus*) was reduced when female crabs were subjected to low salinities during oogenesis and embryogenesis (Urzúa et al. 2018). Numerous environmental factors influence the energy content of aquatic organisms and therefore their quality as food items for consumers. The lower energy content of certain food types in the Coorong suggests that consumers may need to consume higher quantities of these foods to meet their energy requirements. The similarity of energy contents of Coorong fishes with literature values (Appendix Table C.4), however, suggests that these apparent deficiencies in energy content may be restricted to the lower levels of the food web.

Energy content was similar across regions for most species for which multiple regions could be assessed. A notable exception was the Chironomidae, which had considerably higher energy content in the South Lagoon (12.81 kJ g^{-1} DM) than in the North Lagoon (8.66 kJ g^{-1} DM) and Murray Estuary (7.61 kJ g^{-1} DM). This may be due to higher availability of algae as a food resource, combined with lower competition in the South Lagoon.

We provided the first conversion equations for macroinvertebrates in southern temperate estuaries, which will simplify future investigations by enabling a conversion from counts or wet mass measurements for taxa to their dry mass, and energy content when multiplied by the calorific value per gram dry mass, which was also determined in this study. The equations form the foundation of a calculator for use of bioenergetic calculations for southern temperate macroinvertebrates, and could also be integrated into models and global databases originating from the Northern hemisphere (Brey et al. 2010).

Energy density (energy per unit area) was low in the South Lagoon and increased towards the Murray Estuary, following the patterns of biomass for both macroinvertebrates and fish. Macroinvertebrate energy density was negligible in the South Lagoon, low in Noonameena, and increased vastly from Long Point towards the Murray Mouth. The calculations indicated that the food web in the North Lagoon and Murray Estuary is supported by high energy density of benthic prey items, which also had high lipid and protein contents. Despite relatively low energy content of the macroinvertebrates, high biomass, especially from species such as *A. semen*, amphipods, and *S. aequisetis,* led to high energy densities in the Murray Estuary and North Lagoon. Energy transfer through macroinvertebrates to higher trophic levels is a characteristic of the food web in the Murray Estuary and North Lagoon but is currently limited in the South Lagoon.

For fish the energy density was much more even across the regions, largely due to high abundance of smallmouth hardyhead supporting the energy density in the South Lagoon. Smallmouth hardyhead had a lower protein content in the South Lagoon, however, possibly driven by the extreme hypersaline conditions posing osmoregulatory stress (Wedderburn et al. 2016), and a lack of food resources for the fish. Smallmouth hardyhead also contributed the majority of the energy density in the North Lagoon. For sandy sprat, which contributed to the energy density in the Murray Estuary, the varying protein contents with season could be related to their reproductive activities. For yelloweye mullet, the size differentiation for protein content revealed an ontogenetic shift in diet, as juveniles are carnivorous eating benthic-pelagic crustaceans which could be reflected in the higher protein content compared to the larger fish, which eat more detritus or algae (Ye et al. 2020). In the Murray Estuary there was a more even distribution of energy density across different trophic groups of fish and therefore greater diversity of prey options for larger fish and piscivorous birds. This also makes the Murray Estuary more resilient to changes in species composition and abundance as the food web is supported by a variety of species.

4.3 Conclusions

Our investigations provide a comprehensive assessment of food resources and bioenergetics for the Coorong, and of how environmental conditions affect their availability. Common spatial and temporal patterns emerged from the analyses of zooplankton, macroinvertebrates and fish, each of which had lower diversity and individual densities for most species in the South Lagoon than in the North Lagoon and Murray Estuary. Flow related patterns in abundance became apparent for all three prey categories, as higher freshwater flow, including water release from Salt Creek, was followed by increases in the diversity and individual densities of zooplankton, macroinvertebrates, and fish.

There was less choice of prey types for benthivorous fish and shorebirds in the South Lagoon, which was characterised by a food web low in diversity, individual densities, and biomass (except for a highly salt-tolerant fish species, smallmouth hardyhead), and with little energy density for higher trophic levels. Small-bodied fish in the South Lagoon were dominated by smallmouth hardyhead, and macroinvertebrates included only small, surface living prey. A greater diversity of prey with higher nutritional values was available in the Murray Estuary for predators with a range of foraging strategies. Sandy sprat were the most abundant small-bodied fish in the Murray Estuary, where large-bodied fish species also occurred. Macroinvertebrates of small, medium, and large size were abundant at the sediment surface or in greater depths in the Murray Estuary. The bulk of macroinvertebrate production in the Coorong is contained in surface-small prey (*Arthritica semen* and Amphipoda).

Energy density of macroinvertebrate prey was very low in the South Lagoon and high in the Murray Estuary, where ‘Benthic micro-molluscs’ provided the greatest contribution to energy density complemented by energy densities of other trophic groups, which were absent from the South Lagoon. Amphipods and benthic annelids had the highest nutritional value of macroinvertebrates based on their lipid and protein contents. For fish, energy densities were more similar across the regions due to high energy density provided by smallmouth hardyhead in the South Lagoon, but this species had low nutritional value in the South Lagoon in summer. A range of other fish trophic groups with high nutritional value accounted for the high energy density of fish prey items in the Murray Estuary and North Lagoon. We obtained calorific content of species and trophic groups, which provide a tool kit for food web analyses of the Coorong. Our investigations provide critical data for the development of a quantitative food web model not only on trophic group diversity, density, and biomass, but also on Coorong-specific values for production, production to biomass (P:B) ratios and energy density.

The main environmental drivers affecting zooplankton, macroinvertebrates, and fish food resources in the Coorong were salinity and freshwater flow. Additional water quality parameters affecting fish assemblages were water temperature, dissolved oxygen and transparency, and water level played a role for macroinvertebrate assemblages. The distinct split in assemblages of macroinvertebrates and fish between the South Lagoon and the North Lagoon and Murray Estuary was explained by salinities of <64-66 ppt. Similar salinity thresholds emerged for individual taxa of macroinvertebrates and fish, with a pronounced decrease in individual densities and biomass when salinities exceeded 50-60 ppt, and highest densities recorded at salinities <40 ppt. Communities characterised by high diversity and density of individuals and biomass of macroinvertebrate prey were found at marine to brackish salinities <34 ppt.

Higher freshwater flow through the barrages and from Salt Creek was associated with a reduction in salinity that had the strongest influence on the diversity and abundance of food availability and energy provision for planktivorous and benthivorous predators as well as piscivorous waterbirds in the Coorong. Higher freshwater flow through the barrages and from Salt Creek was associated with a reduction in salinity that had the strongest influence on the diversity and abundance of food availability and energy provision for planktivorous and benthivorous predators as well as piscivorous waterbirds in the Coorong. The higher complexity of the food web enabled by marine to brackish environmental conditions will make the food web more resilient than under hypersaline conditions. Lowering salinity in the South Lagoon (<60 or ideally <40 ppt) can increase food resources for key fish and waterbird species, as shown for the management of other hypersaline systems. The ecological improvements that emerged after higher flows during our study period are encouraging in that recovery can be supported by continuous and higher freshwater input to the Coorong.

List of shortened forms and glossary

AFDM	Ash-free dry mass
Benthic	Of or associated with the sediment at the bottom of an estuarine or marine system.
Benthivorous	Feeds predominantly on benthic invertebrates.
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.
Bioturbation	Reworking of sediment by macroinvertebrates which irrigates and improves the sediment
Calorimetry	A standard process for determining the energy content of organic matter, based on the heat production of samples burned in a bomb-calorimeter.
Catadromous	Catadromous fish species are those whose adult life is spent in fresh water, prior to downstream migration into the marine environment for spawning. Larvae and juveniles develop in the ocean before migrating upstream into freshwater habitats.
Copepod nauplii	The first larval stage of a copepod.
CPUE	'catch-per-unit-effort', a measure of abundance.
Demersal	Living and feeding near the seafloor, for example by fish and crustaceans
DEW	Department for Environment and Water
DM	Dry mass
DO	Dissolved oxygen
Ekman grab	A device (225 cm^2 surface area) used for sampling benthic invertebrates in subtidal habitats.
Fish, large-bodied	Fishes that have a maximum adult size typically >150 mm in total length.
Fish, small-bodied	Fishes that have a maximum adult size typically ≤150 mm in total length.
Flow year	A flow year covers the time period from 1 July to 30 June, e.g. flow year 2020-2021 is from 1 July 2020 to 30 June 2021.
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).
Haney trap	A box-like device used for sampling zooplankton in pelagic habitats.
HCHB	Healthy Coorong, Healthy Basin
Hypersaline	Water with salinity greater than sea water, i.e. over 40 parts per thousand (ppt) or grams per litre (g/L).
Intertidal	The area of the shore between the low and high water level that is regularly submerged and exposed by rising and falling tides.
Key species	Species, or taxa, of macroinvertebrates and fish which are common in the Coorong (based on abundance and occurrence), have several trophic links and are of relevance for the ecological function of the Coorong.

La Niña	Climate pattern in the Pacific Ocean bringing above-average rainfall for Australia.
Macroinvertebrate	Invertebrate fauna that are retained on sieve mesh size greater than 0.5 mm.
ME	Murray Estuary
Meiofauna	Invertebrates occurring in the porewater space of sediments, and defined by a size <0.5 mm
Millennium Drought	An Australian drought which impacted the Murray-Darling Basin over the period 1996-2010, and substantially impacted the Coorong over the period 2001-2010.
Monosulfidic black ooze	Organic gel-like sediments with high acid volatile sulfide
NL	North Lagoon
Ontogenetic	During a life cycle, e.g. developments of individual organism in their life time
PET jar	Plastic sample jars made of polyethelene terephthalate.
Planktivorous	Predominantly feed on zooplankton.
ppt	Parts per thousand, a measure of salinity in water
Production	Primary production is the process of producing organic material by plants. Secondary and tertiary production is the rate of production of animal tissue by herbivorous or carnivorous animals respectively.
Productivity	Energy (e.g. calories) and its movement into, out of and within (e.g. across levels of) food webs. The rate of secondary production which can be derived from annual production-to-biomass ratios.
Region	Spatial units, based on geomorphology, that divide the Coorong estuary. For the Coorong, moving from North to South, these are: the Murray Estuary, North Lagoon and South Lagoon regions.
Seiching	The process in which standing waves are created in an enclosed or partially enclosed body of water that alter water level. Enclosed, shallow and narrow waterbodies such as the Coorong are prone to wind-caused seiches.
SFDM	Shell-free dry mass
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.
SL	South Lagoon
Spatial	Refers to the dimension of space or area.
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 Project
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.
Ultrahaline	Extremely hypersaline conditions with salinities >80 ppt
Waterbirds	A group of birds that are aquatic, i.e. live around the water. This group includes shorebirds.

WM	Wet mass
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.

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Appendix A – Additional tables and figures

Table A1. Sampling sites and food item categories (zooplankton, macroinvertebrates, fish) collected. √ indicates that sites were sampled during all surveys for the respective category. # indicates sites which were only sampled for macroinvertebrates on some seasonal surveys (December 2020, March and June 2021 for Mount Anderson; March and June 2021 for Mark Point).

SITE	ZOOPLANKTON	MACROINVERTEBRATES	FISH
South Lagoon			
Salt Creek	√	√	√
Jack Point	√	√	√
Villa de Yumpa			√
Hells Gate	√	√	√
North Lagoon			
Mount Anderson		#	√
Noonameena	√	√	√
Long Point	√	√	√
Mark Point		#	√
Murray Estuary			
Pelican Point	√	√	√
Godfreys Landing			√
Boundary Creek			√
Beacon 19	√	√	√

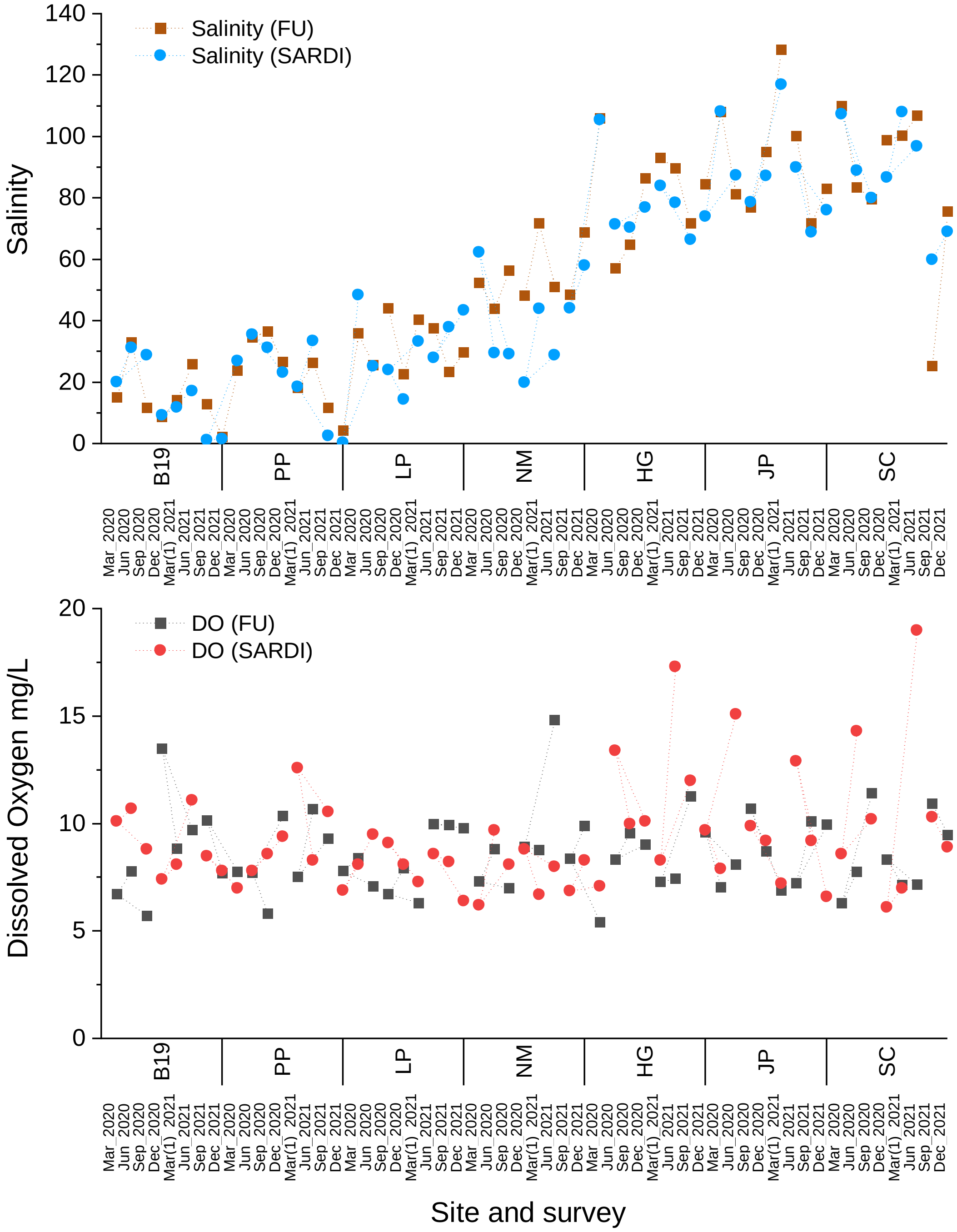


Figure A.1. Water quality data (Salinity and Dissolved Oxygen concentration DO) as measured by the team from Flinders University (FU, macroinvertebrates) and SARDI Aquatic Sciences (SARDI, zooplankton and fish) respectively during field surveys over the study period, based on average values from replicate measurements using handheld electronic meters or refractometer for salinity. Note that sampling for seasonal surveys aligned as best as possible within a fortnight.

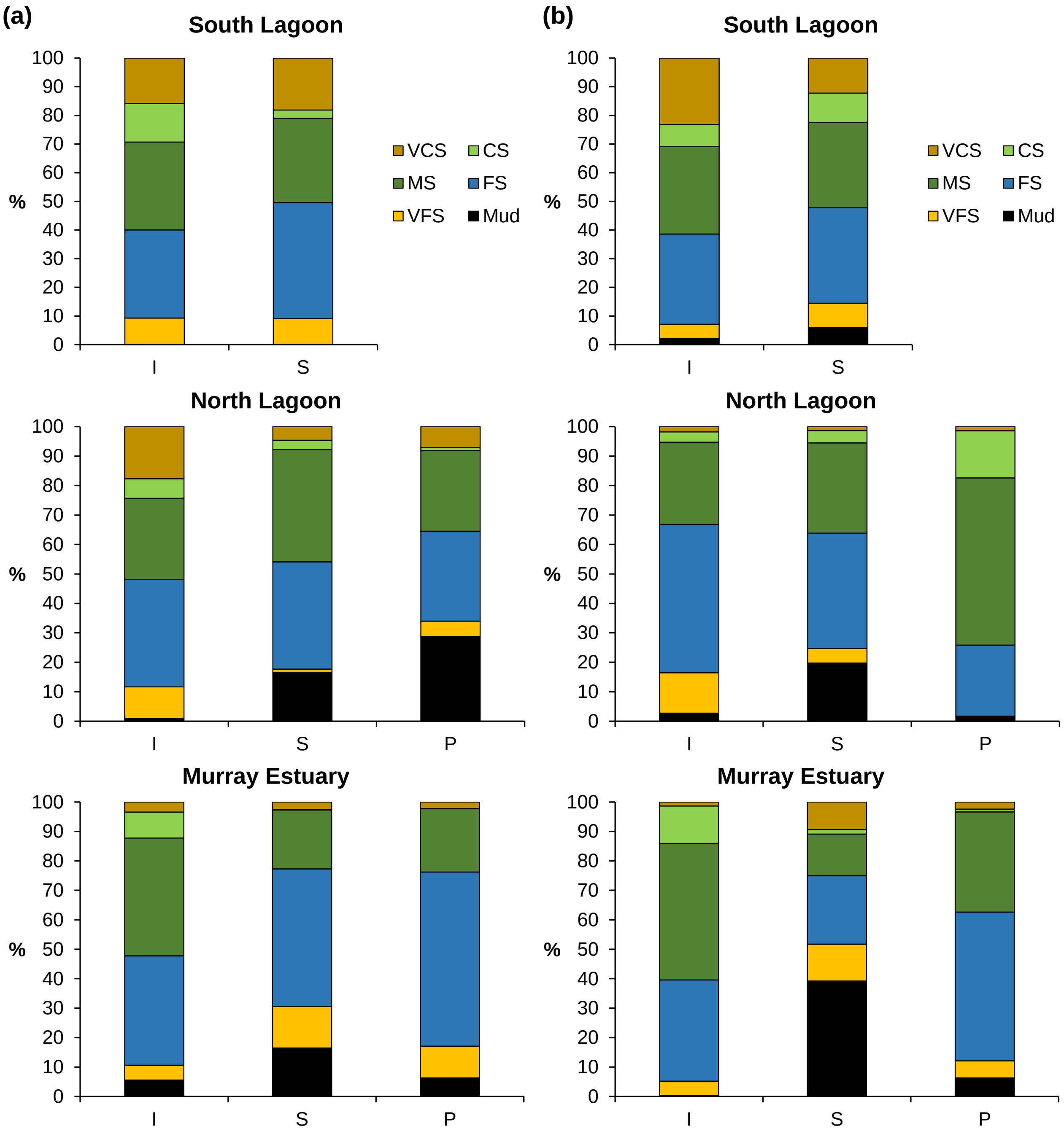


Figure A.2. Sediment grain size composition in the sampling zones (I = intertidal, S = Subtidal, P = Peninsula), for (a) December 2020 based on two sites per region of the Coorong (no sediment samples were obtained at Hells Gate), (b) June 2021 (all sites). The grain size fractions are: Mud <63 µm, VFS (very fine sand) 63-125 µm, FS (fine sand) 125-250 µm, MS (medium sand) 250-500 µm, CS (coarse sand) 500-1000 µm, VCS (very coarse sand) >1000 µm.

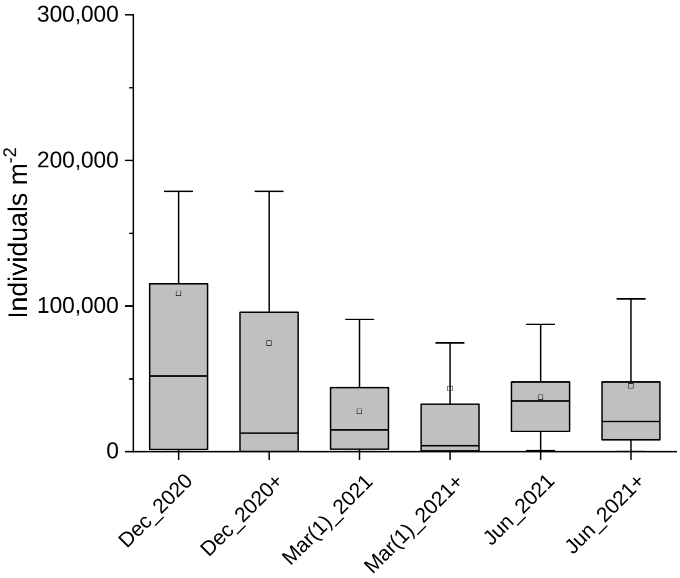


Figure A.3. Boxplots of total macroinvertebrate individual densities for the North Lagoon where additional sites were sampled in seasonal surveys from December 2020, marked with '+'. For each seasonal survey, plots are shown without and with the additional sites. The whiskers display the 1.5 interquartile range IQR.

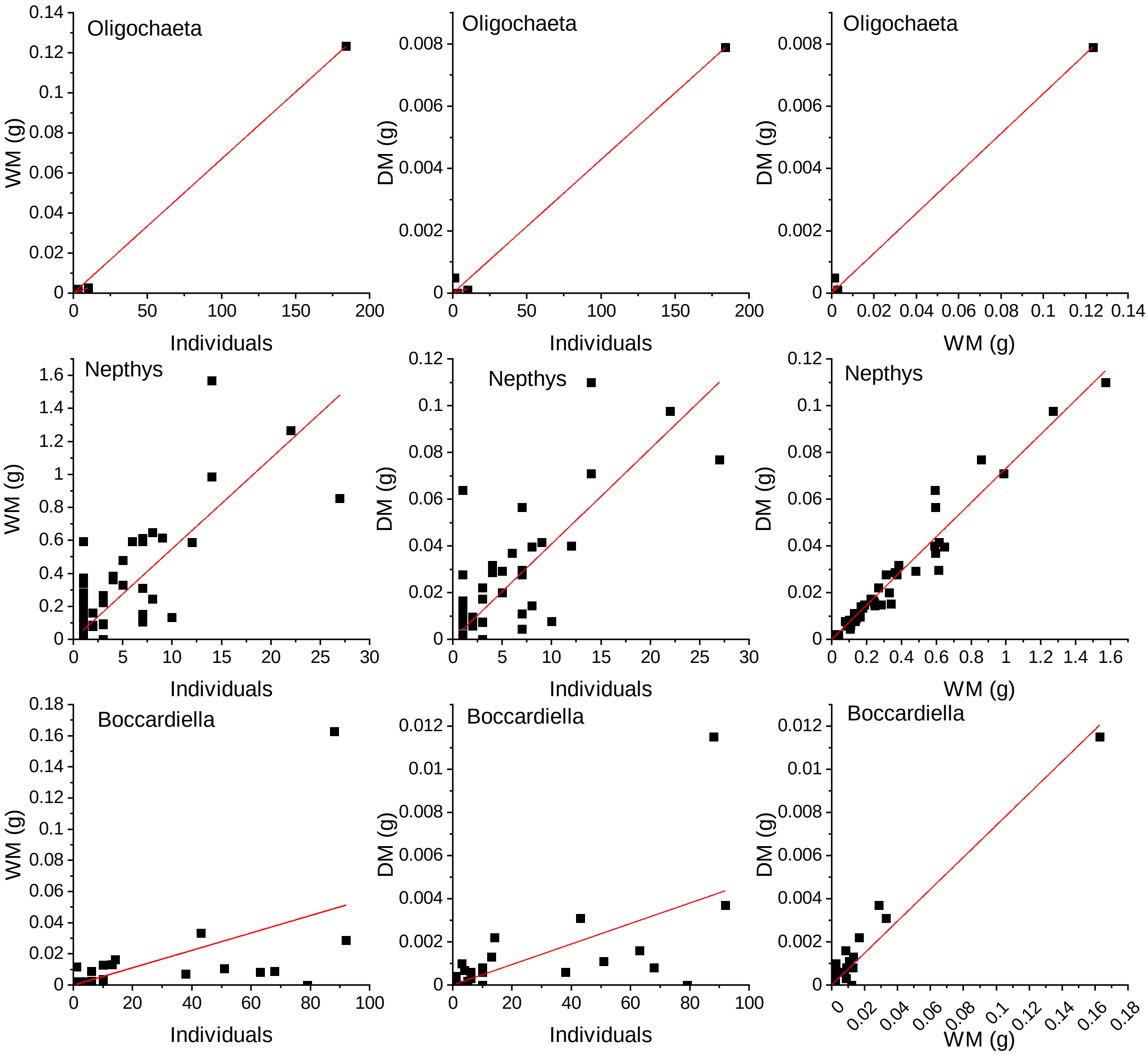


Figure A.4. Scatterplots with linear fits for three taxa of annelids (oligochaetes, *Aglaophamus (Nepthys) australiensis*, and *Boccardiella limnicola*), between individual counts, wet and dry mass of the sample, based on frozen specimens.

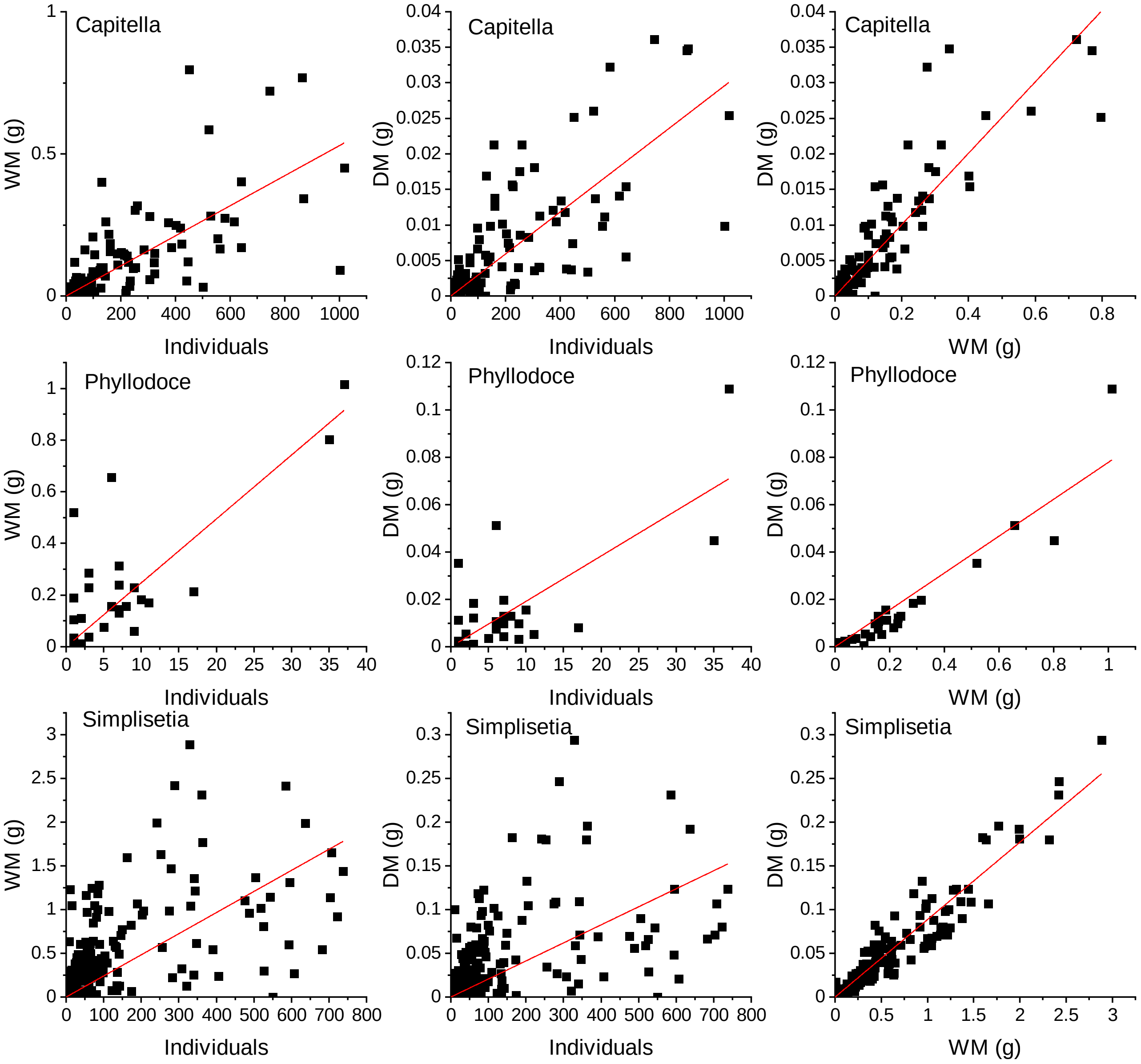


Figure A.5. Scatterplots with linear fits for three taxa of annelids (*Capitella*, *Phyllodoce novaehollandiae*, and *Simplisetia aequisetis*) between individual counts, wet and dry mass of the sample, based on frozen specimens.

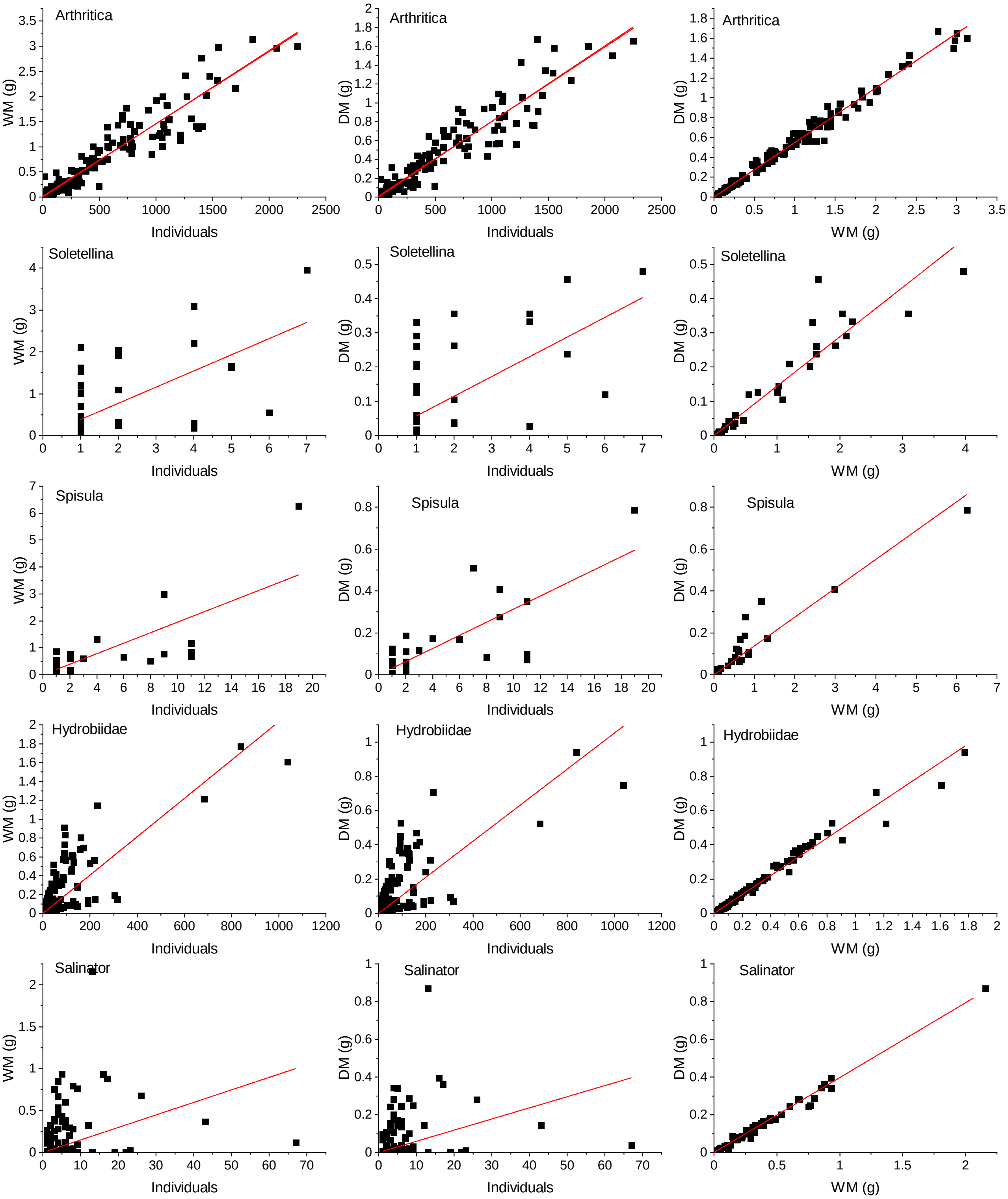


Figure A.6. Scatterplots with linear fits for five taxa of molluscs (*Arthritica semen, Hiatula (Soletellina) alba, Spisula trigonella,* hydrobiid snails and *Salinator fragilis*) between individual counts, wet and dry mass of the sample, based on frozen specimens.

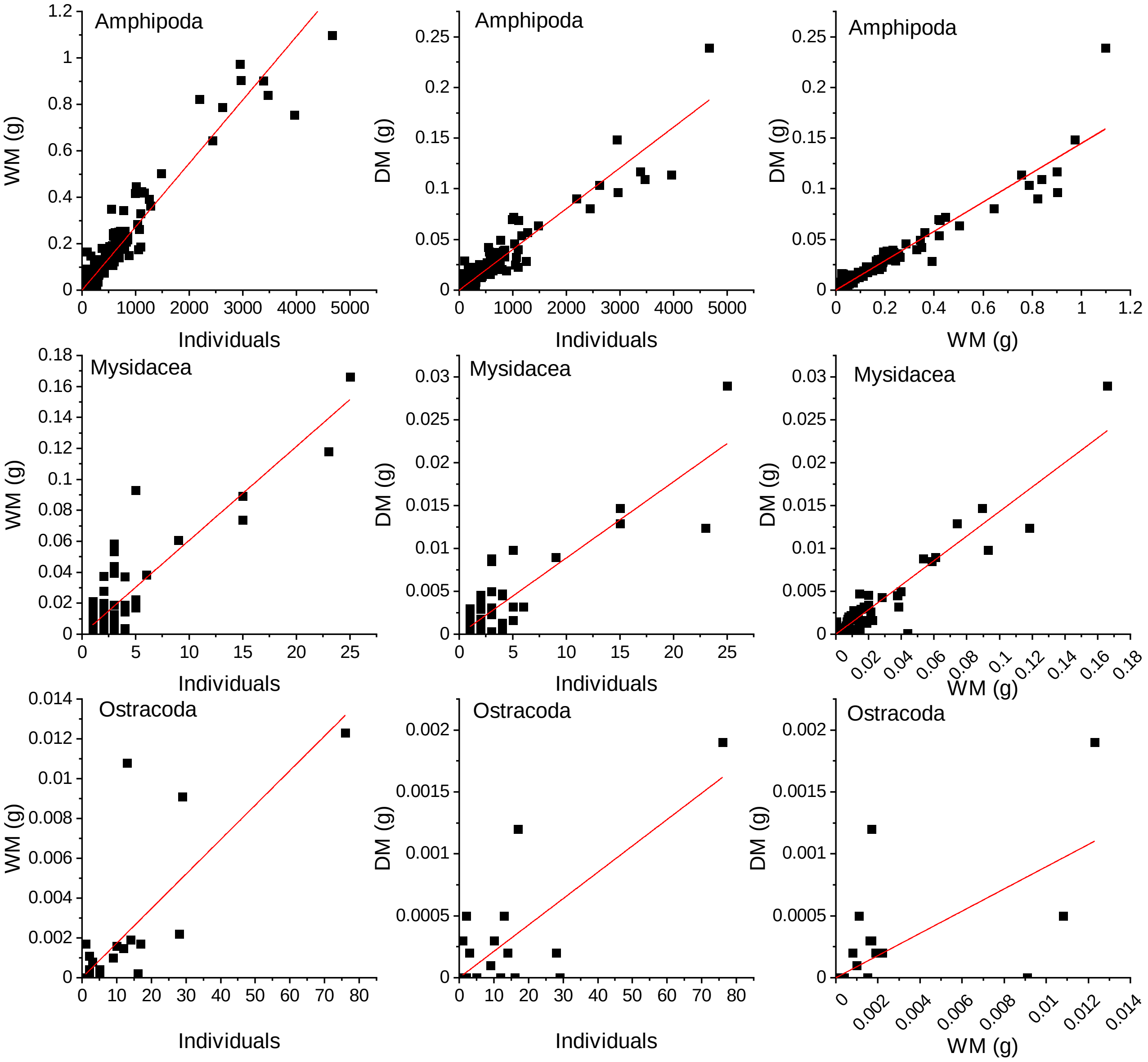


Figure A.7. Scatterplots with linear fits for three taxa of crustaceans (amphipods, mysid shrimps, and ostracods) between individual counts, wet and dry mass of the sample, based on frozen specimens.

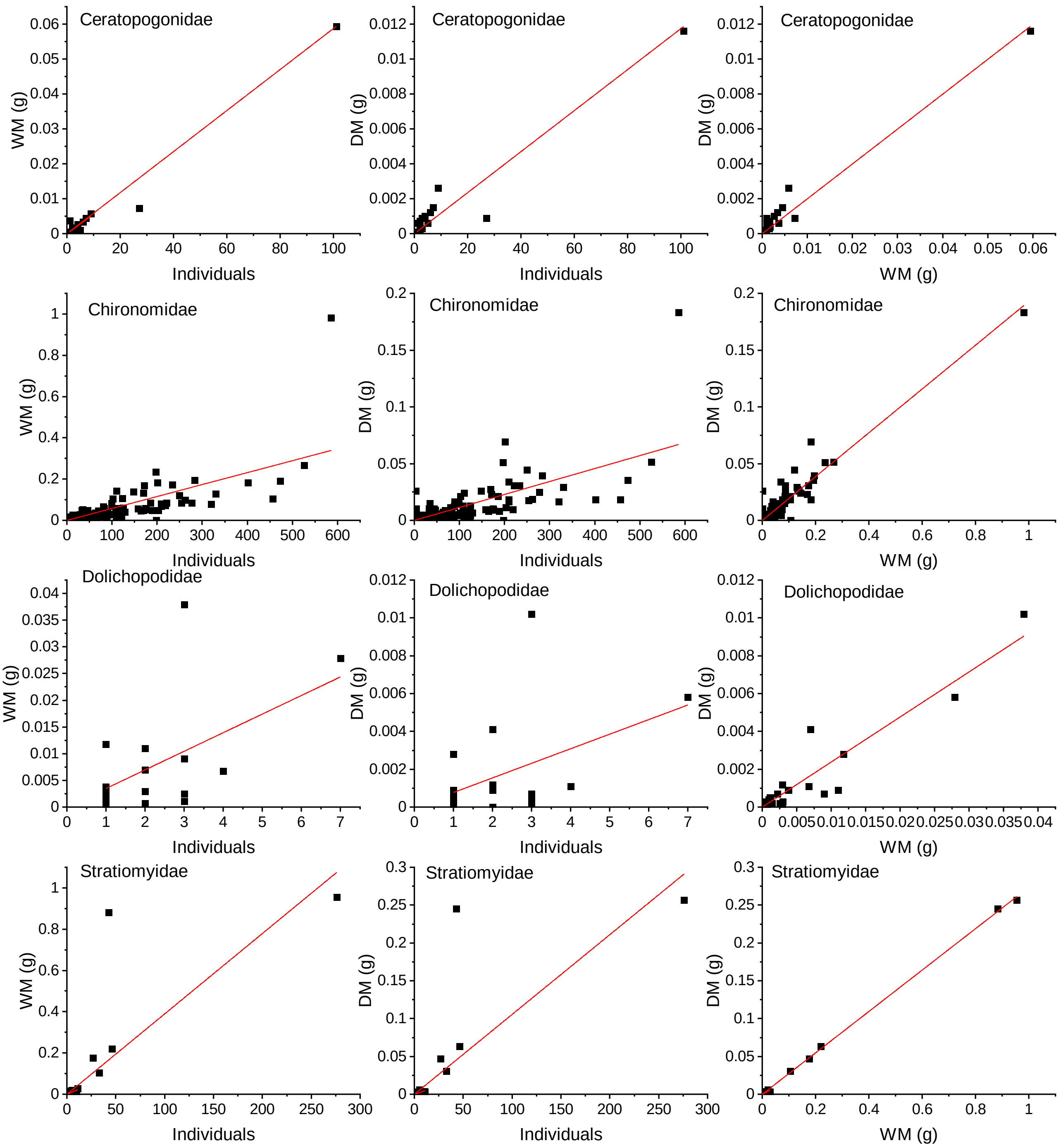


Figure A.8. Scatterplots with linear fits for four taxa of hexapods (insect larvae of Ceratopogonidae, Chironomidae, Dolichopodidae and Stratiomyidae) between individual counts, wet and dry mass of the sample, based on frozen specimens.

Appendix B – Further test results

Table B.1. Pair-wise test results from permutational ANOVA (PERMANOVA) on differences in total density of zooplankton, microcrustacean density, rotifer density and zooplankton assemblage between regions within months and between months within regions over the surveys from March 2020 to December 2021.

		TOTAL DENSITY	MICROCRUSTACEAN DENSITY	ROTIFER DENSITY	ZOOPLANKTON ASSEMBLAGE
Levels of factors	Pair-wise tests	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$
March 2020	SL, NL	0.7064	0.5572	0.4017	0.1431
	SL, ME	**0.0003**	**0.0006**	t=Denominator is 0	**0.0002**
	NL, ME	**0.0067**	**0.0071**	1	**0.0036**
June 2020	SL, NL	**0.0004**	0.3099	**0.0006**	**0.0006**
	SL, ME	0.1203	0.3392	0.0891	**0.0074**
	NL, ME	**0.0028**	0.8807	**0.0031**	**0.0045**
September 2020	SL, NL	**0.0008**	**0.0027**	**0.0015**	**0.001**
	SL, ME	**0.024**	0.15	**0.0436**	0.0585
	NL, ME	**0.0078**	**0.0111**	0.0968	**0.0164**
December 2020	SL, NL	**0.0003**	**0.0002**	**0.0002**	**0.0009**
	SL, ME	**0.0009**	0.0806	**0.0001**	**0.0021**
	NL, ME	**0.002**	**0.0024**	0.5983	**0.0023**
March 2021	SL, NL	**0.0002**	**0.0001**	**0.0027**	**0.0004**
	SL, ME	**0.0006**	**0.0085**	**0.0037**	**0.0006**
	NL, ME	**0.0021**	**0.0022**	0.1874	**0.0018**
June 2021	SL, NL	**0.0172**	**0.0003**	0.3807	**0.0005**
	SL, ME	0.417	**0.036**	0.2627	**0.0207**
	NL, ME	**0.029**	**0.0418**	0.5495	0.1026
September 2021	SL, NL	0.8601	0.1934	0.1811	**0.0061**
	SL, ME	**0.0027**	**0.0103**	**0.0259**	**0.0003**
	NL, ME	**0.0374**	**0.0038**	0.5078	**0.0018**
December 2021	SL, NL	**0.0222**	**0.0043**	0.2035	**0.0006**
	SL, ME	0.8273	0.9239	0.9455	0.0462
	NL, ME	**0.0516**	**0.0168**	0.3044	**0.0094**
South Lagoon	Mar2020, Jun2020	**0.0235**	0.7858	0.0836	0.089
	Mar2020, Sep2020	0.6342	0.7053	N/A	**0.0173**
	Mar2020, Dec2020	0.115	0.1536	1	**0.013**
	Mar2020, Mar2021	0.9638	0.8707	1	0.2111
	Mar2020, Jun2021	0.2347	0.689	0.2111	0.1828
	Mar2020, Sep2021	**0.0002**	**0.0002**	**0.003**	**0.0001**
	Mar2020, Dec2021	**0.0003**	0.134	0.0781	**0.0008**
	Jun2020, Sep2020	0.0946	0.9812	0.0824	**0.0021**
	Jun2020, Dec2020	0.73	0.3241	0.2996	**0.0119**
	Jun2020, Mar2021	0.0685	0.6688	0.2884	0.0472
	Jun2020, Jun2021	0.9095	0.9819	0.2766	0.149

Levels of factors	Pair-wise tests	TOTAL DENSITY	MICROCRUSTACEAN DENSITY	ROTIFER DENSITY	ZOOPLANKTON ASSEMBLAGE
		$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$
	Jun2020, Sep2021	**0.0002**	**0.0012**	0.0933	**0.0004**
	Jun2020, Dec2021	0.1697	0.3193	0.2996	**0.0056**
	Sep2020, Dec2020	0.2755	0.301	1	0.5319
	Sep2020, Mar2021	0.8104	0.5735	1	0.4601
	Sep2020, Jun2021	0.3053	0.9898	0.2058	0.2134
	Sep2020, Sep2021	**0.0001**	**0.0004**	**0.0023**	**0.0002**
	Sep2020, Dec2021	**0.0063**	0.3075	0.0882	**0.0254**
	Dec2020, Mar2021	0.213	0.1456	1	0.2115
	Dec2020, Jun2021	0.7322	0.3008	0.2025	0.1939
	Dec2020, Sep2021	**0.0004**	**0.0037**	**0.0089**	**0.0005**
	Dec2020, Dec2021	0.136	0.9524	0.0822	0.0961
	Mar2021, Jun2021	0.2472	0.5466	0.2022	0.3601
	Mar2021, Sep2021	**0.0002**	**0.0004**	**0.0095**	**0.0001**
	Mar2021, Dec2021	**0.0043**	0.1095	0.1381	**0.0139**
	Jun2021, Sep2021	**0.0128**	**0.0004**	0.9253	**0.0001**
	Jun2021, Dec2021	0.5438	0.3147	0.7338	0.1643
	Sep2021, Dec2021	**0.0031**	**0.0026**	0.6659	**0.0029**
North Lagoon	Mar2020, Jun2020	**0.0025**	0.0644	**0.0034**	**0.0024**
	Mar2020, Sep2020	**0.0023**	**0.0024**	**0.0425**	**0.0022**
	Mar2020, Dec2020	**0.0024**	**0.0024**	**0.0023**	**0.0021**
	Mar2020, Mar2021	**0.002**	**0.0031**	**0.0143**	**0.0018**
	Mar2020, Jun2021	**0.0024**	**0.0019**	0.5473	**0.0021**
	Mar2020, Sep2021	**0.009**	**0.0044**	0.1811	**0.0023**
	Mar2020, Dec2021	**0.0061**	**0.0045**	1	**0.0028**
	Jun2020, Sep2020	**0.0091**	**0.0064**	**0.0074**	**0.0065**
	Jun2020, Dec2020	**0.0041**	**0.0027**	**0.0357**	**0.002**
	Jun2020, Mar2021	0.2659	**0.0019**	0.0642	**0.0023**
	Jun2020, Jun2021	**0.0458**	**0.0019**	**0.0014**	**0.0024**
	Jun2020, Sep2021	0.1476	**0.0132**	0.0776	**0.0411**
	Jun2020, Dec2021	**0.0058**	**0.0042**	**0.0024**	**0.0027**
	Sep2020, Dec2020	**0.0016**	**0.0024**	0.0873	**0.002**
	Sep2020, Mar2021	**0.0047**	**0.0023**	0.3201	**0.0017**
	Sep2020, Jun2021	0.2325	**0.0017**	**0.0375**	**0.0018**
	Sep2020, Sep2021	0.4637	0.404	0.639	0.5237
	Sep2020, Dec2021	0.9981	0.0786	**0.0277**	**0.002**
	Dec2020, Mar2021	0.2465	**0.0447**	0.7327	0.2991
	Dec2020, Jun2021	**0.0024**	**0.0023**	**0.0017**	**0.0025**
	Dec2020, Sep2021	**0.0067**	**0.0018**	0.4964	**0.0021**
	Dec2020, Dec2021	**0.0026**	**0.0027**	**0.0014**	**0.0034**
	Mar2021, Jun2021	**0.0112**	**0.0237**	**0.0221**	**0.0048**

Levels of factors	Pair-wise tests	TOTAL DENSITY	MICROCRUSTACEAN DENSITY	ROTIFER DENSITY	ZOOPLANKTON ASSEMBLAGE
		$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$
	Mar2021, Sep2021	0.0653	**0.0025**	0.7442	**0.023**
	Mar2021, Dec2021	**0.0024**	**0.0028**	**0.0158**	**0.0026**
	Jun2021, Sep2021	0.9714	**0.0435**	0.1851	0.0508
	Jun2021, Dec2021	0.2544	0.1661	0.5544	**0.0029**
	Sep2021, Dec2021	0.4795	0.4116	0.196	0.0511
Murray Estuary	Mar2020, Jun2020	0.1041	**0.036**	0.0643	0.1429
	Mar2020, Sep2020	**0.0349**	0.0818	0.1822	0.1925
	Mar2020, Dec2020	0.1238	0.7184	**0.0018**	**0.0214**
	Mar2020, Mar2021	0.8884	0.2925	**0.0131**	**0.0198**
	Mar2020, Jun2021	0.261	0.5415	1	0.1043
	Mar2020, Sep2021	**0.0021**	**0.002**	**0.0182**	**0.0022**
	Mar2020, Dec2021	0.0801	0.0662	0.183	0.1196
	Jun2020, Sep2020	0.4404	0.5647	0.3712	0.9197
	Jun2020, Dec2020	**0.0123**	0.0779	**0.0135**	**0.0026**
	Jun2020, Mar2021	**0.0358**	0.1492	0.3042	**0.0049**
	Jun2020, Jun2021	0.7807	0.211	0.1068	0.1984
	Jun2020, Sep2021	**0.0024**	**0.002**	0.1049	**0.0018**
	Jun2020, Dec2021	0.605	0.9386	0.7521	0.1068
	Sep2020, Dec2020	**0.006**	0.1445	**0.0022**	**0.0084**
	Sep2020, Mar2021	**0.0076**	0.2817	0.0952	**0.0277**
	Sep2020, Jun2021	0.4869	0.3323	0.4283	0.3423
	Sep2020, Sep2021	**0.0019**	**0.0027**	0.0576	**0.0012**
	Sep2020, Dec2021	0.9296	0.7517	0.7065	0.355
	Dec2020, Mar2021	0.0813	0.4832	0.061	0.0303
	Dec2020, Jun2021	**0.0362**	0.7828	**0.0025**	**0.0062**
	Dec2020, Sep2021	**0.0068**	**0.0031**	0.626	**0.0027**
	Dec2020, Dec2021	**0.0113**	0.1156	**0.0102**	0.0541
	Mar2021, Jun2021	0.2317	0.7711	**0.0315**	**0.0179**
	Mar2021, Sep2021	**0.0026**	**0.0019**	0.1667	**0.0019**
	Mar2021, Dec2021	**0.0435**	0.2456	0.1968	**0.0265**
	Jun2021, Sep2021	**0.0022**	**0.002**	**0.0307**	**0.0023**
	Jun2021, Dec2021	0.5009	0.2527	0.3001	0.0783
	Sep2021, Dec2021	**0.002**	**0.0021**	0.0796	**0.0016**

Table B.2. Pair-wise test results from permutational ANOVA (PERMANOVA) on differences in species density based on taxa, prey types and trophic groups of macroinvertebrates between regions for each of the surveys from February 2020 to August 2021.

		Taxa	Prey types	Trophic groups
SURVEYS	Pair-wise tests	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$
February 2020	SL, NL	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**
	NL, ME	**0.004**	0.832	1.0000
March 2020	SL, NL	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**
	NL, ME	**0.0001**	0.1110	**0.006**
June 2020	SL, NL	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**
	NL, ME	**0.0001**	**0.0119**	**0.0001**
August 2020	SL, NL	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**
	NL, ME	**0.0001**	**0.0036**	**0.0005**
September 2020	SL, NL	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**
	NL, ME	**0.0001**	0.0511	**0.0001**
October 2020	SL, NL	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**
	NL, ME	**0.0001**	0.7685	**0.0195**
November 2020	SL, NL	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**
	NL, ME	**0.0001**	0.1459	**0.0003**
December 2020	SL, NL	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**
	NL, ME	**0.0001**	0.0912	**0.0002**
January 2021	SL, NL	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**
	NL, ME	**0.0001**	0.8921	**0.0184**
February 2021	SL, NL	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**
	NL, ME	**0.0002**	0.3963	**0.0012**
March (1) 2021	SL, NL	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**
	NL, ME	**0.0001**	0.0034	**0.0002**
March (4) 2021	SL, NL	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**
	NL, ME	**0.0001**	**0.0002**	**0.0001**
April 2021	SL, NL	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**

		Taxa	Prey types	Trophic groups
SURVEYS	Pair-wise tests	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$
	NL, ME	**0.0001**	**0.0005**	**0.0002**
May 2021	SL, NL	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**
	NL, ME	0.0951	0.0483	0.1351
June 2021	SL, NL	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**
	NL, ME	**0.0002**	**0.0065**	**0.0206**
August 2021	SL, NL	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**
	NL, ME	**0.0001**	0.1524	**0.0062**

Table B.3. Pair-wise test results from permutational ANOVA (PERMANOVA) on differences in species density based on taxa, prey types and trophic groups of macroinvertebrates between surveys for each region.

	Taxa			Prey types			Trophic groups		
SURVEYS	SL	NL	ME	SL	NL	ME	SL	NL	ME
	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$
Feb_2020, Mar_2020	0.8708	**0.0001**	**0.0215**	1.0000	**0.0101**	0.1765	0.7970	**0.0003**	0.2492
Feb_2020, Jun_2020	0.6260	**0.0001**	1.0000	0.7606	0.1501	0.5700	0.8224	**0.0002**	0.2421
Feb_2020, Aug_2020	**0.0124**	**0.0009**	0.9396	0.1683	0.0555	0.2418	**0.0279**	**0.0003**	1.0000
Feb_2020, Sep_2020	0.8840	**0.0003**	0.5127	0.5755	0.1469	0.8735	0.8188	**0.0002**	0.4396
Feb_2020, Oct_2020	**0.0162**	**0.0057**	1.0000	0.0978	0.5200	0.0821	**0.0066**	**0.0142**	0.7220
Feb_2020, Nov_2020	**0.0007**	**0.0002**	0.6995	**0.0238**	**0.0072**	**0.0165**	**0.0004**	**0.0009**	1.0000
Feb_2020, Dec_2020	0.6802	**0.0001**	**0.0250**	0.6960	**0.0040**	0.0530	0.7742	**0.0001**	0.0900
Feb_2020, Jan_2021	0.6722	**0.0008**	0.2940	0.7404	0.0952	**0.0309**	1.0000	**0.0040**	0.4721
Feb_2020, Feb_2021	**0.0071**	**0.0002**	0.0613	0.1414	**0.0085**	**0.0203**	0.0595	**0.0001**	0.1601
Feb_2020, Mar(1)_2021	**0.0010**	**0.0001**	**0.0001**	**0.0185**	**0.0001**	**0.0040**	**0.0046**	**0.0001**	**0.0015**
Feb_2020, Mar(4)_2021	0.2676	**0.0001**	0.4229	0.1128	**0.0001**	**0.0023**	0.0505	**0.0001**	0.8786
Feb_2020, Apr_2021	0.5628	**0.0001**	0.8405	0.2641	**0.0003**	0.5723	0.1307	**0.0004**	1.0000
Feb_2020, May_2021	**0.0252**	**0.0008**	**0.0003**	0.2243	0.7318	**0.0002**	0.1996	**0.0012**	0.0955
Feb_2020, Jun_2021	0.3824	**0.0002**	**0.0085**	0.7643	0.4410	**0.0008**	1.0000	**0.0001**	0.0723
Feb_2020, Aug_2021	**0.0074**	**0.0160**	0.9383	0.6941	0.2854	0.4194	**0.0070**	**0.0062**	0.8622
Mar_2020, Jun_2020	0.7682	0.7695	**0.0025**	0.7883	0.4390	**0.0358**	0.4048	1.0000	**0.0259**
Mar_2020, Aug_2020	**0.0149**	0.4135	**0.0077**	0.1634	0.6690	**0.0121**	**0.0052**	0.9355	0.2589
Mar_2020, Sep_2020	1.0000	0.5595	0.0633	0.6318	0.6397	0.1240	1.0000	0.8045	0.6405
Mar_2020, Oct_2020	**0.0197**	0.0814	**0.0040**	0.1034	0.1557	0.7301	**0.0002**	0.3098	0.3667
Mar_2020, Nov_2020	**0.0024**	0.7898	**0.0161**	**0.0352**	0.4615	0.4454	**0.0001**	0.6441	0.2468
Mar_2020, Dec_2020	0.3734	0.6128		0.5430	0.4235	0.5549	0.3051	0.1484	0.8207
Mar_2020, Jan_2021	0.7930	0.2327	0.1911	0.7795	0.7935	0.4142	0.8177	0.6693	0.6542
Mar_2020, Feb_2021	**0.0042**	0.6196	0.8284	0.2005	0.6925	0.3355	0.1396	0.3814	0.9129
Mar_2020, Mar(1)_2021	**0.0004**	0.1432	0.0536	**0.0236**	0.0393	0.1660	0.0126	0.0720	0.0863
Mar_2020, Mar(4)_2021	0.1516	**0.0072**	0.1288	0.1527	**0.0004**	0.1695	0.1083	**0.0018**	0.3472
Mar_2020, Apr_2021	0.4200	0.5496	**0.0308**	0.3291	0.0972	0.4973	0.2352	0.3868	0.1951
Mar_2020, May_2021	**0.0106**	0.1208	**0.0377**	0.2968	0.0802	**0.0367**	0.3362	0.5205	0.6638
Mar_2020, Jun_2021	0.4877	0.0470	0.5105	1.0000	**0.0361**	**0.0279**	0.8253	0.2693	0.5598
Mar_2020, Aug_2021	**0.0094**	**0.0235**	**0.0051**	0.5335	**0.0017**	0.8802	**0.0007**	0.2214	0.3190
Jun_2020, Aug_2020	0.0782	0.5876	0.9245	0.0803	0.7901	0.4640	0.1681	1.0000	0.3506
Jun_2020, Sep_2020	0.6985	0.8018	0.4004		0.9087	0.8626	0.5647	0.7360	**0.0237**
Jun_2020, Oct_2020	0.1144	0.1663	1.0000	0.0482	0.5263	**0.0152**	0.0862	0.3336	0.0450
Jun_2020, Nov_2020	**0.0242**	0.5513	0.5406	**0.0140**	0.1529	**0.0007**	**0.0046**	0.5627	0.1492
Jun_2020, Dec_2020	0.1999	0.4043	**0.0028**	0.2161	0.0965	**0.0084**	1.0000	0.1163	**0.0007**
Jun_2020, Jan_2021	1.0000	0.4000	0.1377	1.0000	0.7100	**0.0034**	0.6912	0.7262	**0.0368**
Jun_2020, Feb_2021	**0.0026**	0.4570	**0.0113**	0.4301	0.2057	**0.0017**	0.0630	0.3304	**0.0034**
Jun_2020, Mar(1)_2021	**0.0007**	0.0693	**0.0001**	0.1083	**0.0035**	**0.0001**	**0.0056**	0.0540	**0.0001**
Jun_2020, Mar(4)_2021	0.0775	**0.0048**	0.2540	0.3398	**0.0002**	**0.0001**	0.0489	0.0005	0.1310

	Taxa			Prey types			Trophic groups		
SURVEYS	SL	NL	ME	SL	NL	ME	SL	NL	ME
	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$
Jun_2020, Apr_2021	0.2801	0.3946	0.7494	0.6298	**0.0142**	0.1630	0.0680	0.3446	0.2094
Jun_2020, May_2021	**0.0095**	0.2270	**0.0001**	0.5870	0.3683	**0.0001**	0.1065	0.5208	**0.0025**
Jun_2020, Jun_2021	0.8201	0.1090	**0.0008**	0.7787	0.3029	**0.0002**	0.5529	0.3459	**0.0013**
Jun_2020, Aug_2021	0.0548	0.0539	0.9272	0.3383	**0.0198**	0.1375	0.0634	0.2404	0.0942
Aug_2020, Sep_2020	**0.0183**	0.8541	0.4085	0.0601	1.0000	0.3500	**0.0118**	0.7210	0.3764
Aug_2020, Oct_2020	0.8770	0.4888	1.0000	1.0000	0.4227	**0.0110**	0.6740	0.4215	0.7220
Aug_2020, Nov_2020	0.8707	0.3399	0.5752	0.5097	0.3061	**0.0007**	0.0907	0.6168	1.0000
Aug_2020, Dec_2020	**0.0001**	0.1973	**0.0067**	0.3906	0.2129	**0.0045**	**0.0303**	0.1345	0.0945
Aug_2020, Jan_2021	0.0952	0.8029	0.1827	0.0561	1.0000	**0.0033**	**0.0339**	0.7796	0.4727
Aug_2020, Feb_2021	**0.0001**	0.2745	**0.0252**	**0.0022**	0.4128	**0.0033**	**0.0001**	0.3521	0.1682
Aug_2020, Mar(1)_2021	**0.0001**	**0.0299**	**0.0001**	**0.0001**	**0.0140**	**0.0001**	**0.0001**	0.0776	**0.0007**
Aug_2020, Mar(4)_2021	**0.0004**	**0.0031**	0.3114	**0.0032**	**0.0004**	**0.0002**	**0.0002**	**0.0022**	0.8784
Aug_2020, Apr_2021	**0.0034**	0.2353	0.7588	**0.0137**	0.0519	0.0869	**0.0003**	0.3753	1.0000
Aug_2020, May_2021	**0.0001**	0.6237	**0.0002**	**0.0064**	0.2655	**0.0001**	**0.0002**	0.6215	0.0944
Aug_2020, Jun_2021	0.1332	0.4918	**0.0033**	0.0708	0.1663	**0.0001**	**0.0108**	0.4132	0.0768
Aug_2020, Aug_2021	0.6967	0.2475		0.6202	**0.0146**	0.0730	0.5547	0.3142	0.8710
Sep_2020, Oct_2020	**0.0302**	0.3073	0.4240	**0.0402**	0.4378	0.0594	**0.0023**	0.2026	0.5773
Sep_2020, Nov_2020	**0.0044**	0.4348	0.7411	**0.0062**	0.2833	**0.0160**	**0.0001**	0.8722	0.3532
Sep_2020, Dec_2020	0.4718	0.2735	0.0757	0.1735	0.1731	**0.0423**	0.4030	0.2654	0.3610
Sep_2020, Jan_2021	0.7224	0.5910	0.6533	1.0000	0.9063	**0.0240**	0.8509	0.4416	1.0000
Sep_2020, Feb_2021	**0.0118**	0.3539	0.1459	0.3381	0.3741	**0.0153**	0.1491	0.5486	0.4611
Sep_2020, Mar(1)_2021	**0.0010**	**0.0415**	**0.0002**	0.0560	**0.0119**	**0.0027**	**0.0156**	0.1443	**0.0047**
Sep_2020, Mar(4)_2021	0.2114	**0.0035**	0.8327	0.2625	**0.0014**	**0.0031**	0.1104	**0.0033**	0.5266
Sep_2020, Apr_2021	0.4817	0.2818	0.6834	0.4986	0.0526	0.4100	0.2231	0.5378	0.2519
Sep_2020, May_2021	**0.0328**	0.4312	**0.0005**	0.4692	0.3045	**0.0005**	0.3155	0.3206	0.2219
Sep_2020, Jun_2021	0.4557	0.2784	**0.0185**	0.7994	0.2445	**0.0005**	0.8479	0.1186	0.2136
Sep_2020, Aug_2021	**0.0096**	0.1273	0.4061	0.2566	**0.0249**	0.3009	**0.0024**	0.1127	0.4887
Oct_2020, Nov_2020	0.5929	0.0956	0.5839	1.0000	**0.0782**	0.8374	0.3023	0.2067	0.8008
Oct_2020, Dec_2020	**0.0003**	**0.0346**	**0.0036**	0.2311	**0.0352**	0.8858	**0.0028**	**0.0174**	0.1304
Oct_2020, Jan_2021	0.1346	0.7127	0.1760	**0.0321**	0.3837	0.7277	**0.0101**	0.6718	0.7390
Oct_2020, Feb_2021	**0.0001**	0.0693	**0.0199**	**0.0016**	0.1012	0.6087	**0.0001**	0.0911	0.2411
Oct_2020, Mar(1)_2021	**0.0001**	**0.0019**	**0.0001**	**0.0001**	**0.0008**	0.4347	**0.0001**	**0.0064**	**0.0012**
Oct_2020, Mar(4)_2021	**0.0004**	**0.0011**	0.3100	**0.0023**	**0.0002**	0.3943	**0.0001**	**0.0002**	1.0000
Oct_2020, Apr_2021	**0.0052**	0.0602	0.8043	**0.0092**	**0.0084**	0.3497	**0.0002**	0.1103	0.6134
Oct_2020, May_2021	**0.0001**	0.8394	**0.0001**	**0.0032**	0.8929	0.1562	**0.0002**	0.7762	0.1323
Oct_2020, Jun_2021	0.2194	0.7549	**0.0018**	**0.0398**	0.9040	0.1001	**0.0024**	0.6305	0.1000
Oct_2020, Aug_2021	0.5112	0.6961	1.0000	0.3772	0.1423	0.6413	1.0000	1.0000	1.0000
Nov_2020, Dec_2020	**0.0001**	0.9097	**0.0159**	0.0640	1.0000	1.0000	**0.0001**	0.4556	0.0595
Nov_2020, Jan_2021	**0.0346**	0.2153	0.4221	**0.0063**	0.4195	1.0000	**0.0004**	0.4307	0.4974

	Taxa			Prey types			Trophic groups		
SURVEYS	SL	NL	ME	SL	NL	ME	SL	NL	ME
	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$
Nov_2020, Feb_2021	**0.0001**	0.9491	0.0666	**0.0003**	0.9065	0.8445	**0.0001**	0.8032	0.1265
Nov_2020, Mar(1)_2021	**0.0001**	0.3800	**0.0001**	**0.0001**	0.4300	0.6536	**0.0001**	0.3324	**0.0003**
Nov_2020, Mar(4)_2021	**0.0001**	0.0560	0.6178	**0.0005**	**0.0271**	0.6053	**0.0001**	**0.0184**	1.0000
Nov_2020, Apr_2021	**0.0006**	0.8555	0.9373	**0.0027**	0.5406	0.1422	**0.0001**	0.7604	1.0000
Nov_2020, May_2021	**0.0001**	0.1188	**0.0003**	**0.0008**	**0.0399**	0.2180	**0.0001**	0.3093	0.0747
Nov_2020, Jun_2021	0.0602	**0.0373**	**0.0101**	**0.0104**	**0.0085**	0.1469	**0.0001**	0.1034	0.0577
Nov_2020, Aug_2021	0.8894	**0.0358**	0.5478	0.1269	**0.0015**	0.3827	0.4213	0.1319	1.0000
Dec_2020, Jan_2021	0.2376	0.1218	0.2187	0.1946	0.3203	0.8859	0.6423	0.0687	0.4344
Dec_2020, Feb_2021	**0.0022**	1.0000	0.8367	**0.0099**	0.7629	0.7643	**0.0063**	0.6950	0.9007
Dec_2020, Mar(1)_2021	**0.0005**	0.3685	0.0603	**0.0007**	0.3868	0.6458	**0.0004**	0.8084	0.1443
Dec_2020, Mar(4)_2021	0.2970	**0.0345**	0.1420	**0.0097**	**0.0126**	0.6175	**0.0047**	**0.0225**	0.1465
Dec_2020, Apr_2021	0.8720	0.9083	**0.0321**	0.0539	0.4685	0.2174	**0.0146**	0.8308	**0.0405**
Dec_2020, May_2021	**0.0112**	0.0602	**0.0422**	**0.0350**	**0.0141**	0.3211	**0.0233**	**0.0319**	0.9077
Dec_2020, Jun_2021	0.1241	**0.0096**	0.5133	0.3575	**0.0022**	0.1898	0.6529	**0.0010**	0.7534
Dec_2020, Aug_2021	**0.0001**	**0.0095**	**0.0059**		**0.0006**	0.4108	**0.0027**	**0.0076**	0.1142
Jan_2021, Feb_2021	**0.0058**	0.1757	0.3582	0.4192	0.5274	1.0000	0.1137	0.2270	0.5751
Jan_2021, Mar(1)_2021	**0.0005**	**0.0102**	**0.0029**	0.0583	**0.0310**	0.8575	**0.0116**	**0.0323**	**0.0150**
Jan_2021, Mar(4)_2021	0.1260	**0.0026**	0.8779	0.3157	**0.0015**	0.8401	0.0901	**0.0017**	0.6624
Jan_2021, Apr_2021	0.3375	0.1414	0.4146	0.6023	0.0955	0.1633	0.1891	0.2562	0.3863
Jan_2021, May_2021	**0.0151**	0.8914	**0.0018**	0.5814	0.2564	0.4420	0.2619	0.9268	0.3636
Jan_2021, Jun_2021	0.8388	0.8060	0.0804	0.7767	0.1525	0.2530		0.7735	0.3149
Jan_2021, Aug_2021	0.0533	0.4135	0.1744	0.3057	**0.0181**	0.3664	**0.0066**	0.5788	0.6244
Feb_2021, Mar(1)_2021	0.6595	0.4762	0.0460	0.4882	0.2431	1.0000	0.4976	0.5535	0.1098
Feb_2021, Mar(4)_2021	0.3759	0.0670	0.2777	1.0000	**0.0125**	1.0000	1.0000	**0.0283**	0.2556
Feb_2021, Apr_2021	0.1544	0.9493	0.0954	1.0000	0.3533	0.1214	1.0000	1.0000	0.0870
Feb_2021, May_2021	0.8080	0.0861	**0.0341**	1.0000	0.0524	0.5685	0.8065	0.1361	0.7910
Feb_2021, Jun_2021	**0.0018**	**0.0236**	0.4374	0.1947	**0.0146**	0.3160	0.0459	**0.0171**	0.6596
Feb_2021, Aug_2021	**0.0001**	**0.0237**	**0.0211**	**0.0328**	**0.0018**	0.2913	**0.0001**	0.0463	0.2042
Mar(1)_2021, Mar(4)_2021	0.1501	0.0864	**0.0018**	0.6620	**0.0151**	1.0000	0.6712	**0.0299**	**0.0025**
Mar(1)_2021, Apr_2021	**0.0380**	0.6035	**0.0006**	0.3872	0.9033	**0.0348**	0.3839	0.6296	**0.0002**
Mar(1)_2021, May_2021	0.2957	**0.0033**	0.7226	0.3571	**0.0004**	0.3815	0.2650	**0.0129**	0.2653
Mar(1)_2021, Jun_2021	**0.0001**	**0.0002**	0.3263	**0.0212**	**0.0001**	0.2865	**0.0062**	**0.0001**	0.3357
Mar(1)_2021, Aug_2021	**0.0001**	**0.0004**	**0.0001**	**0.0024**	**0.0001**	0.1359	**0.0001**	**0.0033**	**0.0010**
Mar(4)_2021, Apr_2021	0.6905	0.1049	0.5687	0.8164	0.0895	0.0281	0.8257	0.0558	0.8497
Mar(4)_2021, May_2021	0.6032	**0.0001**	**0.0025**	0.8096	**0.0001**	0.5969	0.6506	**0.0006**	0.1408
Mar(4)_2021, Jun_2021	0.0504	**0.0001**	0.0616	0.1455	**0.0001**	0.4060	**0.0358**	**0.0001**	0.1057
Mar(4)_2021, Aug_2021	**0.0004**	**0.0002**	0.3003	**0.0302**	**0.0001**	0.1444	**0.0001**	**0.0001**	
Apr_2021, May_2021	0.2870	0.0781	**0.0007**	1.0000	**0.0028**	**0.0076**	1.0000	0.1667	0.0500
Apr_2021, Jun_2021	0.1581	**0.0185**	**0.0115**	0.3177	**0.0003**	**0.0074**	0.1314	**0.0307**	0.0461

	Taxa			Prey types			Trophic groups		
SURVEYS	SL	NL	ME	SL	NL	ME	SL	NL	ME
	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$
Apr_2021, Aug_2021	**0.0028**	**0.0188**	0.7501	0.0890	**0.0002**	0.8769	**0.0001**	0.0696	0.8171
May_2021, Jun_2021	**0.0043**	1.0000	0.2227	0.2838	0.9002	0.7426	0.1824	1.0000	1.0000
May_2021, Aug_2021	**0.0001**	0.4872	**0.0001**	0.0616	0.2064	0.0578	**0.0004**	0.6794	0.1100
Jun_2021, Aug_2021	0.0726	0.3412	**0.0032**	0.3392	0.0592	**0.0304**	**0.0013**	0.5100	0.0946

Table B.4. Pair-wise test results from permutational ANOVA (PERMANOVA) on differences in species density based on taxa, prey types and trophic groups of macroinvertebrates between zones (I -= intertidal mudflat, P = peninsula mudflat, S = subtidal sediment) for each region, based on all surveys from February 2020 to August 2021. The peninsula zone was not sampled in the South Lagoon.

		Taxa	Prey types	Trophic groups
SURVEYS	Pair-wise tests	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$
South Lagoon	I, S	0.1438	**0.0323**	0.2023
North Lagoon	I, P	**0.0291**	0.8779	**0.0028**
	I, S	**0.0107**	**0.0401**	**0.0092**
	P, S	0.7954	0.0520	0.6913
Murray Estuary	I, P	**0.0046**	**0.0111**	**0.0154**
	I, S	1.0000	**0.0256**	**0.0032**
	P, S	**0.0351**	1.0000	**0.0001**

Table B.5. Pair-wise test results from permutational ANOVA (PERMANOVA) on differences in total individual densities, total biomass, and communities of macroinvertebrates and their energy density between regions for each of the surveys from February 2020 to August 2021.

		Total individual density	Total Biomass (Dry mass)	Community	Energy density
SURVEYS	Pair-wise tests	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$
February 2020	SL, NL	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	NL, ME	0.4885	**0.0001**	**0.0001**	**0.0001**
March 2020	SL, NL	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	NL, ME	0.2333	**0.0012**	**0.0001**	**0.0022**
June 2020	SL, NL	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	NL, ME	**0.0106**	**0.0001**	**0.0001**	**0.0002**
August 2020	SL, NL	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	NL, ME	**0.0008**	**0.021**	**0.0001**	0.1307
September 2020	SL, NL	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	NL, ME	**0.0222**	0.3118	**0.0001**	0.3721
October 2020	SL, NL	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	NL, ME	**0.0139**	**0.0003**	**0.0001**	**0.0004**
November 2020	SL, NL	**0.0023**	**0.0007**	**0.0001**	**0.002**
	SL, ME	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	NL, ME	**0.0001**	**0.0001**	**0.0001**	**0.0001**
December 2020	SL, NL	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	NL, ME	**0.0423**	0.1818	**0.0001**	0.1724

		Total individual density	Total Biomass (Dry mass)	Community	Energy density
SURVEYS	Pair-wise tests	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$
January 2021	SL, NL	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	NL, ME	0.147	**0.0382**	**0.0001**	**0.0409**
February 2021	SL, NL	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	NL, ME	0.4717	**0.0001**	**0.0001**	**0.0025**
March (1) 2021	SL, NL	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	NL, ME	**0.0002**	**0.0002**	**0.0001**	**0.0009**
March (4) 2021	SL, NL	**0.0015**	**0.0019**	**0.0019**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	NL, ME	**0.0001**	**0.0001**	**0.0001**	**0.0023**
April 2021	SL, NL	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	NL, ME	**0.0005**	**0.0036**	**0.0001**	**0.0037**
May 2021	SL, NL	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	NL, ME	0.4288	0.3702	**0.0001**	0.5491
June 2021	SL, NL	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	NL, ME	t negative	0.0732	**0.0001**	0.0739
August 2021	SL, NL	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	SL, ME	**0.0001**	**0.0001**	**0.0001**	**0.0001**
	NL, ME	**0.0004**	**0.0001**	**0.0001**	**0.0001**

Table B.6. Pair-wise test results from permutational ANOVA (PERMANOVA) on differences in total individual densities, total biomass, and community of macroinvertebrates between surveys for each region.

SURVEYS	Total individual density			Total Biomass (Dry mass)			Community		
	SL	NL	ME	SL	NL	ME	SL	NL	ME
	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$
Feb_2020, Mar_2020	**0.003**	**0.0077**	**0.0003**	**0.0113**	**0.0413**	**0.0014**	**0.0113**	**0.0023**	**0.0004**
Feb_2020, Jun_2020	0.2072	**0.0077**	0.2198	0.4694	**0.0327**	**0.0351**	0.075	**0.0012**	**0.0001**
Feb_2020, Aug_2020	**0.0001**	0.3181	**0.0043**	**0.0002**	0.1401	0.6103	**0.0001**	**0.0117**	**0.0001**
Feb_2020, Sep_2020	0.2829	0.4807	0.0757	0.9694	**0.021**	**0.0002**	0.187	**0.0041**	**0.0001**
Feb_2020, Oct_2020	**0.0001**	0.9656	**0.0004**	**0.0417**	0.8406	**0.0007**	**0.0001**	**0.0123**	**0.0001**
Feb_2020, Nov_2020	**0.0001**	**0.0001**	0.9259	**0.0167**	0.0762	0.4254	**0.0001**	**0.0008**	**0.0001**
Feb_2020, Dec_2020	**0.0109**	0.1095	0.8536	0.5183	0.1954	**0.0051**	0.0518	**0.001**	**0.0001**
Feb_2020, Jan_2021	0.1222	0.1109	0.4723	0.7219	0.8304	0.2279	0.1545	**0.0041**	**0.0001**
Feb_2020, Feb_2021	**0.0393**	**0.0104**	**0.0009**	**0.0001**	**0.0028**	**0.0006**	0.0839	**0.0039**	**0.0001**
Feb_2020, Mar(1)_2021	0.2441	**0.0001**	**0.0029**	**0.0212**	**0.0279**	**0.0002**	**0.0406**	**0.0003**	**0.0001**
Feb_2020, Mar(4)_2021	0.1544	**0.0001**	**0.0257**	**0.0296**	**0.0001**	0.2704	**0.016**	**0.0001**	**0.0001**
Feb_2020, Apr_2021	0.3838	**0.0003**	0.2753	0.7088	0.1359	**0.0168**	0.0819	**0.0001**	**0.0001**
Feb_2020, May_2021	0.2738	0.102	**0.0006**	0.6711	0.6838	**0.0003**	0.1887	**0.0013**	**0.0001**
Feb_2020, Jun_2021	**0.0046**	**0.0003**	**0.0001**	**0.0166**	0.1269	**0.0052**	**0.0089**	**0.0004**	**0.0001**
Feb_2020, Aug_2021	**0.0041**	**0.0017**	0.7274	**0.0001**	**0.0328**	0.2425	**0.0011**	**0.0001**	**0.0001**
Mar_2020, Jun_2020	0.1098	0.8869	0.0749	0.0868	0.9616	0.2635	0.0664	0.4774	**0.0015**
Mar_2020, Aug_2020	0.3873	0.0497	**0.0001**	**0.0207**	**0.0028**	**0.0012**	**0.0303**	0.1842	**0.0001**
Mar_2020, Sep_2020	**0.0233**	0.0558	**0.0003**	**0.0157**	0.5589	**0.0249**	0.0768	0.454	**0.0001**
Mar_2020, Oct_2020	0.286	**0.0121**	**0.0001**	0.9872	0.0655	**0.0001**	**0.0033**	0.1963	**0.0001**
Mar_2020, Nov_2020	0.2866	0.2261	**0.0036**	0.7161	0.9171	**0.0014**	**0.001**	0.5372	**0.0001**
Mar_2020, Dec_2020	0.1041	0.4566	**0.0177**	**0.0021**	0.8676	0.337	0.1051	0.404	**0.0001**
Mar_2020, Jan_2021	0.1146	0.3841	0.0588	**0.0427**	0.1438	0.1281	0.1682	0.6353	**0.0001**
Mar_2020, Feb_2021	**0.0001**	0.7855	0.9046	**0.0001**	0.4173	0.7575	**0.0003**	0.9639	**0.0027**
Mar_2020, Mar(1)_2021	**0.0001**	0.0939	0.4988	**0.0001**	0.7954	0.9045	**0.0001**	**0.0208**	**0.0007**
Mar_2020, Mar(4)_2021	**0.0001**	**0.0006**	0.31	**0.0001**	**0.0038**	0.1704	**0.0002**	**0.0001**	**0.0001**
Mar_2020, Apr_2021	**0.0002**	0.3176	0.104	**0.0082**	0.6011	0.5857	**0.0013**	**0.0001**	**0.0003**
Mar_2020, May_2021	0.051	0.1646	0.6439	0.0584	0.145	0.4705	0.0961	0.0708	**0.0001**
Mar_2020, Jun_2021	0.8366		0.2958	0.8244		0.7228	0.3111	**0.007**	**0.0027**
Mar_2020, Aug_2021	0.4257	0.7839	**0.0037**	0.226	0.7517	**0.0152**	**0.0142**	**0.0066**	**0.0001**
Jun_2020, Aug_2020	**0.0097**	0.0463	**0.0016**	**0.0007**	**0.0018**	**0.0358**	**0.0035**	0.0625	**0.0004**
Jun_2020, Sep_2020	0.6972	0.0521	**0.0144**	0.5148	0.5797	**0.0035**	0.6489	0.1033	**0.0334**
Jun_2020, Oct_2020	**0.0047**	**0.0118**	**0.0002**	0.162	0.0558	**0.0002**	**0.0123**	0.1099	**0.0002**
Jun_2020, Nov_2020	**0.0035**	0.3015	0.2747	0.0884	0.9526	**0.024**	**0.0018**	0.2872	**0.0008**
Jun_2020, Dec_2020	0.5707	0.4047	0.3299	0.215	0.8384	0.0919	0.8568	0.2052	**0.0037**
Jun_2020, Jan_2021	0.8692	0.3408	0.769	0.7859	0.1396	0.5916	0.5884	0.328	**0.0001**
Jun_2020, Feb_2021	**0.0048**	0.6897	0.0786	**0.0001**	0.4418	0.1722	**0.0349**	0.3646	**0.0028**
Jun_2020, Mar(1)_2021	**0.025**	0.1473	0.1984	**0.0063**	0.8403	0.1566	**0.0177**	0.0571	**0.0002**
Jun_2020, Mar(4)_2021	**0.0158**	**0.0006**	0.459	**0.0128**	**0.0029**	0.6335	**0.027**	**0.0002**	**0.0008**

SURVEYS	Total individual density			Total Biomass (Dry mass)			Community		
	SL	NL	ME	SL	NL	ME	SL	NL	ME
	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$
Jun_2020, Apr_2021	0.0476	0.4195	0.991	0.3384	0.5539	0.6401	0.1799	**0.0007**	**0.0056**
Jun_2020, May_2021	0.8221	0.1398	**0.0407**	0.836	0.1207	0.0889	0.3581	0.0686	**0.0001**
Jun_2020, Jun_2021	0.1516		**0.0071**	0.0918		0.1939	0.2957	**0.0132**	**0.0003**
Jun_2020, Aug_2021	0.2963	0.6765	0.3423	**0.0045**	0.7112	0.1887	0.0765	0.0579	**0.0001**
Aug_2020, Sep_2020	**0.0004**	0.9359	0.6534	**0.0002**	**0.0013**	**0.0002**	**0.0016**	0.9047	0.3833
Aug_2020, Oct_2020	0.8002	0.3938	0.5423	0.0469	0.3794	**0.03**		0.8736	**0.0039**
Aug_2020, Nov_2020	0.8453	**0.0025**	**0.0232**	0.0915	**0.0058**	0.7895	**0.0345**	**0.0186**	**0.0001**
Aug_2020, Dec_2020	**0.002**	0.3302	0.1107	**0.0001**	**0.022**	**0.0049**	**0.0167**	0.0535	**0.0097**
Aug_2020, Jan_2021	**0.0067**	0.371	**0.0117**	**0.0002**	0.201	0.1846	**0.0022**	0.251	**0.0002**
Aug_2020, Feb_2021	**0.0001**	0.0818	**0.0001**	**0.0001**	**0.0002**	**0.0011**	**0.0001**	0.3976	**0.0001**
Aug_2020, Mar(1)_2021	**0.0001**	**0.0003**	**0.0001**	**0.0001**	**0.0014**	**0.0003**	**0.0001**	**0.0009**	**0.0001**
Aug_2020, Mar(4)_2021	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	0.215	**0.0001**	**0.0001**	**0.0001**
Aug_2020, Apr_2021	**0.0001**	**0.0026**	**0.0058**	**0.0001**	**0.0095**	**0.0188**	**0.0001**	**0.0001**	**0.0001**
Aug_2020, May_2021	**0.0025**	0.505	**0.0001**	**0.0002**	0.0989	**0.0013**	**0.0007**	0.0525	**0.0001**
Aug_2020, Jun_2021	0.2711	0.0482	**0.0001**	**0.0431**	**0.0096**	**0.0042**	0.0638	**0.0007**	**0.0001**
Aug_2020, Aug_2021	0.0521	**0.0409**	**0.0046**	0.1538	**0.0007**	0.2099	0.1255	**0.0093**	**0.001**
Sep_2020, Oct_2020	**0.0005**	0.4832	0.3204	**0.0368**	**0.0283**	**0.0001**	**0.0014**	0.7617	0.1043
Sep_2020, Nov_2020	**0.0003**	**0.0041**	0.1289	**0.0157**	0.6861	**0.0002**	**0.0001**	0.0561	**0.0035**
Sep_2020, Dec_2020	0.2264	0.3151	0.237	0.5782	0.5156	0.2659	0.9642	0.2549	0.2641
Sep_2020, Jan_2021	0.5475	0.3711	0.0497	0.7171	0.0746	**0.0039**	0.6421	0.6307	**0.0007**
Sep_2020, Feb_2021	**0.0046**	0.1071	**0.0003**	**0.0002**	0.8985	0.054	**0.026**	0.6939	**0.0007**
Sep_2020, Mar(1)_2021	**0.0227**	**0.0005**	**0.0004**	**0.0391**	0.7194	**0.0192**	**0.015**	**0.0012**	**0.0001**
Sep_2020, Mar(4)_2021	**0.0175**	**0.0001**	**0.004**	0.0674	**0.0366**	**0.0048**	**0.0098**	**0.0001**	**0.0003**
Sep_2020, Apr_2021	0.0619	**0.0055**	**0.0322**	0.7591	0.3026	**0.0183**	0.1196	**0.0001**	**0.0118**
Sep_2020, May_2021	0.8922	0.527	**0.0003**	0.6606	0.0654	0.1143	0.5901	0.1546	**0.0003**
Sep_2020, Jun_2021	**0.0363**	0.3489	**0.0001**	**0.0137**		0.0554	0.1904	**0.0007**	**0.0006**
Sep_2020, Aug_2021	0.0915	0.078	0.0655	**0.0007**	0.3826	**0.0006**	**0.0189**	**0.0197**	**0.0079**
Oct_2020, Nov_2020	0.9432	**0.0008**	**0.0053**	0.7673	0.1003	0.0621	0.163	**0.0211**	0.0481
Oct_2020, Dec_2020	**0.0004**	0.1159	**0.0367**	**0.0092**	0.1726	**0.0001**	**0.0077**	0.0955	0.0964
Oct_2020, Jan_2021	**0.0045**	0.141	**0.0028**	0.1009	0.7313	**0.0024**	**0.0014**	0.3753	**0.001**
Oct_2020, Feb_2021	**0.0001**	**0.0248**	**0.0001**	**0.0001**	**0.0139**	**0.0001**	**0.0001**	0.3762	**0.0001**
Oct_2020, Mar(1)_2021	**0.0001**	**0.0001**	**0.0001**	**0.0002**	**0.0411**	**0.0001**	**0.0001**	**0.0009**	**0.0001**
Oct_2020, Mar(4)_2021	**0.0001**	**0.0001**	**0.0002**	**0.0003**	**0.0001**	**0.0054**	**0.0001**	**0.0001**	**0.0001**
Oct_2020, Apr_2021	**0.0001**	**0.0007**	**0.0009**	**0.0292**	0.1758	**0.0001**	**0.0001**	**0.0001**	**0.0014**
Oct_2020, May_2021	**0.001**	0.1698	**0.0001**	0.1114	0.6114	**0.0001**	**0.0003**	0.2303	**0.0001**
Oct_2020, Jun_2021	0.1856	**0.0226**	**0.0001**	0.8585		**0.0001**	**0.0301**	**0.0044**	**0.0001**
Oct_2020, Aug_2021	**0.0302**	**0.0144**	**0.0006**	0.3378	0.0922	**0.0003**	0.7415	0.0516	**0.0079**
Nov_2020, Dec_2020	**0.0005**	0.0831	0.8984	**0.0032**	0.8218	**0.0043**	**0.0003**	0.3832	0.1443
Nov_2020, Jan_2021	**0.0024**	0.0605	0.5041	0.0497	0.1868	0.1295	**0.0015**	0.4561	0.2461
Nov_2020, Feb_2021	**0.0001**	0.1503	**0.0041**	**0.0001**	0.5717	**0.0006**	**0.0001**	0.7388	**0.0027**

SURVEYS	Total individual density			Total Biomass (Dry mass)			Community		
	SL	NL	ME	SL	NL	ME	SL	NL	ME
	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$
Nov_2020, Mar(1)_2021	**0.0001**	0.7875	**0.0108**	**0.0002**	0.9054	**0.0002**	**0.0001**	0.3339	**0.0003**
Nov_2020, Mar(4)_2021	**0.0001**	**0.0157**	0.0704	**0.0003**	**0.0173**	0.1584	**0.0001**	**0.0037**	**0.0174**
Nov_2020, Apr_2021	**0.0001**	0.7531	0.3315	**0.0104**	0.5984	**0.0145**	**0.0001**	**0.0014**	**0.0395**
Nov_2020, May_2021	**0.0011**	**0.0109**	**0.0016**	0.057	0.1762	**0.0007**	**0.0001**	**0.0266**	**0.0001**
Nov_2020, Jun_2021	0.1927	0.5055	**0.0006**	0.8788		**0.0039**	**0.0002**	**0.0034**	**0.0002**
Nov_2020, Aug_2021	**0.022**	0.1023	0.754	0.5338	0.7228	0.1358	0.1879	**0.0031**	**0.0204**
Dec_2020, Jan_2021	0.7051	0.9185	0.5202	0.3591	0.3063	0.0615	0.304	0.5075	0.0752
Dec_2020, Feb_2021	**0.0001**	0.6387	**0.019**	**0.0003**	0.4409	0.4868	**0.0008**	0.4933	**0.0133**
Dec_2020, Mar(1)_2021	**0.0003**	**0.029**	**0.0415**	0.1047	0.7107	0.3367	**0.0009**	0.0451	**0.0006**
Dec_2020, Mar(4)_2021	**0.0001**	**0.0001**	0.1365	0.1748	**0.0192**	0.0733	**0.0011**	**0.0001**	**0.0447**
Dec_2020, Apr_2021	**0.0003**	0.1175	0.3743	0.8217	0.8061	0.207	**0.0283**	**0.0003**	0.0798
Dec_2020, May_2021	0.3465	0.6512	**0.0118**	0.3164	0.3147	0.7017	0.149	0.0725	**0.0011**
Dec_2020, Jun_2021	0.1632		**0.0014**	**0.0031**		0.5039		**0.0005**	**0.0165**
Dec_2020, Aug_2021	0.408	0.6128	0.7486	**0.0001**	0.9533	**0.0195**	0.084	**0.013**	0.0973
Jan_2021, Feb_2021	**0.0007**	0.5462	**0.0616**	**0.0001**	**0.0402**	0.0841	**0.0137**	0.964	0.0501
Jan_2021, Mar(1)_2021	**0.0096**	**0.017**	0.1393	**0.0158**	0.0999	0.0625	**0.0069**	**0.0411**	**0.0011**
Jan_2021, Mar(4)_2021	**0.0052**	**0.0002**	0.3515	**0.03**	**0.0002**	0.9762	**0.012**	**0.0003**	0.0717
Jan_2021, Apr_2021	**0.0192**	0.0766	0.7967	0.5082	0.3414	0.368	0.048	**0.0007**	0.2364
Jan_2021, May_2021	0.6653	0.7157	**0.033**	0.9425	0.9082	0.0529	0.2468	0.3678	**0.0005**
Jan_2021, Jun_2021	0.1661		**0.0062**	**0.0444**		0.1146	0.135	**0.0162**	**0.0012**
Jan_2021, Aug_2021	0.3518	0.5016	0.611	**0.002**	0.2146	0.6034	0.0849	0.0501	0.0287
Feb_2021, Mar(1)_2021	0.6445	0.052	0.4453	**0.034**	0.5891	0.8008	0.6235	0.0295	0.1634
Feb_2021, Mar(4)_2021	0.6851	**0.0002**	0.2889	**0.0192**	**0.0195**	0.1225	0.1327	**0.0001**	0.919
Feb_2021, Apr_2021	0.2872	0.2029	0.1045	**0.0002**	0.1848	0.4166	0.1916	**0.0004**	0.8821
Feb_2021, May_2021	**0.0068**	0.2714	0.7305	**0.0001**	**0.0239**	0.6711	0.0744	0.1028	**0.0131**
Feb_2021, Jun_2021	**0.0001**		0.3806	**0.0001**	0.0763	0.9368	**0.0005**	**0.0031**	0.2066
Feb_2021, Aug_2021	**0.0001**	0.9804	**0.003**	**0.0001**	0.2169	**0.0048**	**0.0001**	**0.0157**	0.0735
Mar(1)_2021, Mar(4)_2021	0.9099	**0.0108**	0.6352	0.8717	**0.0088**	0.0959	0.1785	**0.0096**	**0.023**
Mar(1)_2021, Apr_2021	0.6697	0.5116	0.2368	0.0836	0.4452	0.4576	0.1462	0.1144	0.0909
Mar(1)_2021, May_2021	0.0325	**0.0013**	0.2592	0.0144	0.0902	0.4673	0.0763	**0.0146**	**0.0001**
Mar(1)_2021, Jun_2021	**0.0001**	0.0755	0.0804	**0.0001**		0.7675	**0.0003**	**0.0073**	**0.0008**
Mar(1)_2021, Aug_2021	**0.0006**	0.0343	**0.0112**	**0.0001**	0.5784	**0.0019**	**0.0001**	**0.0076**	**0.0011**
Mar(4)_2021, Apr_2021	0.53	**0.0037**	0.5019	0.1396	**0.001**	0.4221	0.3059	**0.01**	0.736
Mar(4)_2021, May_2021	0.0212	**0.0001**	0.1575	**0.0267**	**0.0001**	0.0685	**0.0296**	**0.0001**	**0.0027**
Mar(4)_2021, Jun_2021	**0.0002**	**0.0001**	0.0542	**0.0001**	**0.0001**	0.1376	**0.0003**	**0.0001**	**0.0416**
Mar(4)_2021, Aug_2021	**0.0001**	**0.0002**	0.0628	**0.0001**	**0.0002**	0.6056	**0.0001**	**0.0001**	0.2761
Apr_2021, May_2021	0.0632	**0.0122**	0.0597	0.4793	0.3307	0.2489	0.1068	**0.0011**	**0.0032**
Apr_2021, Jun_2021	**0.0005**	0.4207	**0.0136**	**0.009**		0.4361	**0.0047**	**0.0014**	**0.0365**
Apr_2021, Aug_2021	**0.0006**	0.1519	0.4011	**0.0004**	0.7901	0.0919	**0.0003**	**0.0006**	0.1442
May_2021, Jun_2021	0.0731	0.4997	0.5946	0.0577		0.7578	0.1059	0.1848	0.2273

SURVEYS	Total individual density			Total Biomass (Dry mass)			Community		
	SL	NL	ME	SL	NL	ME	SL	NL	ME
	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$	$P_{(perm)}$
May_2021, Aug_2021	0.1623	0.1872	**0.001**	**0.0031**	0.1881	**0.0039**	**0.0071**	0.4769	**0.0002**
Jun_2021, Aug_2021	0.561		**0.0001**	0.3915		**0.0268**	0.0687	0.086	**0.0065**

Table B.7. Test results from distance-based redundancy analysis (DISTLM) using environmental variables as predictor for macroinvertebrate community data from February 2020 to August 2021. Marginal tests show how much each variable explains when taken alone, while sequential tests are conditional on variables added sequentially based on how much they add to the explanation of variability. The percent values give the proportion of the variability in macroinvertebrate community data that is explained by the respective environmental variable. Only variables adding with significant *P*-values are shown for sequential tests. ns = non significant.

VARIABLE	P	%
Marginal tests		
Dissolved oxygen (%)	ns	0.54
Dissolved oxygen (mg/L)	ns	1.81
Salinity	**0.001**	59.15
Temperature (°C)	ns	1.63
Barrage Flow (GL)	ns	0.61
Salt Creek Flow GL	ns	0.33
Water level	ns	5.37
Sequential tests		
Salinity	**0.001**	55.70

Table B.8. Test results from distance-based redundancy analysis (DISTLM) using environmental variables as predictor for macroinvertebrate community data for December 2020 and June 2021. Note that Hells Gate was not included in the analysis for December 2020 as no samples were taken for sediment properties. Only variables adding with significant *P*-values are shown for sequential tests. ns = non significant. See Table B.7 caption for more detail on DISTLM tests.

VARIABLE	P	%
Marginal tests		
Dissolved oxygen (%)	ns	2.62
Dissolved oxygen (mg/L)	**0.0199**	9.57
Salinity	**0.0001**	48.93
Sediment organic matter	ns	4.03
Median grain size	**0.0047**	13.57
Sediment sorting	ns	5.06
Barrage Flow	ns	1.73
Salt Creek Flow	ns	1.73
Water level	ns	2.89
Sequential tests		
Dissolved oxygen (mg/L)	**0.0020**	18.63
Salinity	**0.0001**	54.18
Sediment organic matter	**0.0332**	58.08
Median grain size	**0.0360**	63.99

Table B.9. Test results from distance-based redundancy analysis (DISTLM) using zooplankton and macroinvertebrate prey as predictor for fish community data for seasonal surveys from Autumn 2020 to Winter 2021. Only variables adding with significant *P*-values are shown for sequential tests. ns = non significant. See Table B.7 caption for more detail on DISTLM tests. D-L = Deep-Large, E-L = Epifauna-Large, S-L = Surface-Large, S-M = Surface-Medium, S-S = Surface-Small.

VARIABLE	P	%
Marginal tests		
Rotifers	**0.0167**	8.61
Microcrustaceans	**0.0007**	14.44
Meroplankton	**0.0034**	11.71
Hyperbenthos	ns	1.51
S-M_benthos	**0.0001**	25.93
S-S_benthos	**0.0001**	31.04
E-L_benthos	**0.0001**	21.81
D-L_benthos	**0.0001**	44.57
S-L_benthos	**0.0001**	23.29
Sequential tests		
Rotifers	**0.0197**	8.61
Microcrustaceans	**0.0266**	7.27
Meroplankton	**0.0139**	7.56
Hyperbenthos	**0.0425**	5.28
S-M_benthos	**0.0003**	10.89
S-S_benthos	**0.0001**	9.81
D-L_benthos	**0.0003**	7.19

Table B.10. Pair-wise test results from permutational ANOVA (PERMANOVA) on differences in total energy density for fish between regions within months over the surveys from March 2020 to December 2021.

		Fish energy density
Levels of factors	Pair-wise tests	$P_{(perm)}$
March 2020	SL, NL	0.0501
	SL, ME	0.8237
	NL, ME	**0.0365**
June 2020	SL, NL	**0.0450**
	SL, ME	**0.0136**
	NL, ME	**0.0027**
September 2020	SL, NL	**0.0072**
	SL, ME	0.2402
	NL, ME	0.3458
December 2020	SL, NL	0.7809
	SL, ME	0.7056
	NL, ME	0.4916

Levels of factors	Pair-wise tests	Fish energy density $P_{(perm)}$
March 2021	SL, NL	**0.0015**
	SL, ME	**0.0057**
	NL, ME	0.9055
June 2021	SL, NL	0.3655
	SL, ME	0.9817
	NL, ME	0.2812
September 2021	SL, NL	0.4605
	SL, ME	**0.0046**
	NL, ME	0.0586
December 2021	SL, NL	**0.0044**
	SL, ME	0.9971
	NL, ME	**0.0049**

Table B.11. Test results from permutational ANOVA (PERMANOVA) on differences in crude protein content of smallmouth hardyhead and Sandy sprat between regions and surveys (winter and summer).

	SMALLMOUTH HARDYHEAD				SANDY SPRAT			
MAIN TEST	df	MS	PSEUDO-F	$P_{(PERM)}$	df	MS	PSEUDO-F	$P_{(PERM)}$
Region (Re)	2	44.69	23.38	**0.0001**	1	0.06	0.06	0.8133
Season (Se)	1	43.50	22.76	**0.0004**	1	107.77	110.60	**0.0002**
Re x Se	2	73.52	38.46	**0.0001**	1	11.35	11.65	**0.0072**
Residual	18	1.91			12	0.97		

Table B.12. Pair-wise test results from permutational ANOVA (PERMANOVA) on differences in crude protein content of smallmouth hardyhead between regions (SL = South Lagoon, NL = North Lagoon, ME = Murray Estuary) and two seasons.

Levels of factors	Pair-wise tests	Crude protein content $P_{(perm)}$
Summer	SL, NL	**0.0299**
	SL, ME	**0.0260**
	NL, ME	0.4284
Winter	SL, NL	0.1401
	SL, ME	0.8601
	NL, ME	0.1715
South Lagoon	Summer, Winter	**0.0292**
North Lagoon	Summer, Winter	**0.0287**
Murray Estuary	Summer, Winter	0.5493

Appendix C – Additional tables and figures for production and bioenergetics

Table C.1. Energy content (mean ± standard error SE) in kJ/g dry mass for detritus, plankton, plant (*Ruppia* and filamentous algae), macroinvertebrates and fish from samples in the Coorong, and differentiated by region. See Table 3 for number of samples per region.

		ENERGY CONTENT (kJ / g DRY MASS)											
		ALL			SOUTH LAGOON			NORTH LAGOON			MURRAY ESTUARY		
PREY TYPE	SPECIES/TAXA	MEAN		SE	MEAN		SE	MEAN		SE	MEAN		SE
Detritus		2.90											
Plankton		6.06	±	1.12	2.83	±	0.81	5.16	±	1.13	10.33	±	2.42
Plant	*Ruppia*	10.09	±	0.77	10.25	±	1.27						
	Filamentous algae	4.50	±	0.32	9.86	±	0.67						
Macroinvertebrates	*Aglaophamus (Nephtys) australiensis*	15.69	±	0.37				16.68	±		15.64	±	0.38
	Amarinus laevis	11.08	±	0.26							11.08	±	0.26
	Amphipoda	12.12	±	0.36				12.34	±	0.55	11.95	±	0.49
	Arenicolidae	9.35	±	1.98				6.15	±	0.47	14.16	±	0.51
	Australonereis ehlersi	15.75	±	1.47				15.75	±	1.47			
	Capitella capitata	12.79	±	0.52				12.67	±	0.59	13.55	±	0.99
	Ceratopogonidae	9.82			9.82								
	Chironomidae	10.81	±	0.76	12.81	±	0.58	8.66	±	1.80	7.61	±	1.16
	Ficopomatus enigmaticus	14.31	±	1.12				17.18	±	0.46	11.44		0.34
	Hiatula (Soletellina) alba	11.97	±	0.41				11.72	±	0.26	12.10	±	0.60
	Mysidae	15.23	±	0.55				15.23	±	0.55			
	Paragrapsus gaimardii	9.42	±	0.39				9.73	±	0.73	9.16	±	0.39
	Phyllodoce novaehollandiae	15.24	±	1.54				20.29	±		14.23	±	1.42
	Salinator fragilis	8.82	±	0.46							8.82	±	0.46
	Simplisetia aequisetis	11.80	±	0.32				11.79	±	0.45	11.82	±	0.45
	Spisula trigonella	11.14	±	0.73				10.23	±	1.13	12.04	±	0.91
	Stratiomyidae	13.38	±	0.55	13.38	±	0.55						
Fish	*Acanthopagrus butcheri*	22.11	±	0.11									
	Afurcagobius tamarensis	18.52	±	0.25	16.32	±		18.90	±	0.06	18.62	±	0.26
	Aldrichetta forsteri	19.37	±	0.25				19.53	±	0.39	19.24	±	0.32
	Ammotretis rostratus	17.47									17.47		
	Argyrosomus japonicus	19.08	±	0.69				20.17			18.81	±	0.83
	Arripis truttaceaus	18.95	±	0.20				19.06	±	0.23	18.87	±	0.31
	Atherinosoma microstoma	18.64	±	0.11	18.75	±	0.18	18.60	±	0.24	18.56	±	0.12

		ENERGY CONTENT (KJ / G DRY MASS)											
		ALL			SOUTH LAGOON			NORTH LAGOON			MURRAY ESTUARY		
prey type	species/taxa	mean		SE	mean		SE	mean		SE	mean		SE
	Hyperlophus vittatus	18.68	±	0.16				18.93	±	0.16	18.50	±	0.24
	Hyporhamphus regularis	19.04	±	0.31				18.96	±	0.48	19.15	±	0.38
	Pseudaphritis urvillii	20.13	±	0.23	20.49	±	0.67	19.87	±	0.28	20.23	±	0.40
	Rhombosolea tapirina	18.63	±	0.16				18.54	±	0.22	18.72	±	0.25
	Tasmanogobius lasti	18.02	±	0.60				18.58	±	0.37	17.03	±	1.50

Table C.2. Energy content (mean ± standard error SE) in kJ/g wet mass for detritus, plankton, plant (*Ruppia* and filamentous algae), macroinvertebrates and fish from samples in the Coorong, and differentiated by region. See Table 3 for number of samples per region.

		ENERGY DENSITY (kJ / g WET MASS)											
		ALL			SOUTH LAGOON			NORTH LAGOON			MURRAY ESTUARY		
PREY TYPE	SPECIES/TAXA	MEAN		SE	MEAN		SE	MEAN		SE	MEAN		SE
Detritus		1.49											
Plankton		1.75	±	0.32	0.82	±	0.23	1.49	±	0.33	2.98	±	0.70
Plant	*Ruppia*	2.26	±	0.17	2.30	±	0.28	2.21	±	0.15			
	Filamentous algae	0.84	±	0.06									
Macroinvertebrates	*Aglaophamus (Nephtys) australiensis*	1.07	±	0.03				1.14		--	1.07	±	0.03
	Amarinus laevis	2.13	±	0.05							2.13	±	0.05
	Amphipoda	1.95	±	0.06				1.99	±	0.09	1.92	±	0.08
	Arenicolidae	0.76	±	0.16				0.50	±	0.04	1.15	±	0.04
	Australonereis ehlersi	1.28	±	0.12				1.28	±	0.12		±	
	Capitella capitata	1.27	±	0.05				1.26	±	0.06	1.35	±	0.10
	Ceratopogonidae	3.20		--	3.20								
	Chironomidae	2.22	±	0.16	2.63	±	0.12	1.77	±	0.37	1.56	±	0.24
	Ficopomatus enigmaticus	1.45	±	0.11				1.75	±	0.05	1.16	±	0.03
	Hiatula (Soltellina) alba	1.77	±	0.06				1.73	±	0.04	1.78	±	0.09
	Mysidae	2.20	±	0.08				2.20	±	0.08			
	Paragrapsus gaimardii	3.77	±	0.16				3.90	±	0.29	3.67	±	0.16
	Phyllodoce novaehollandiae	0.83	±	0.08				1.10		--	0.77	±	0.08
	Salinator fragilis	3.02		0.16							3.02	±	0.16
	Simplisetia aequisetis	1.04	±	0.03				1.04	±	0.04	1.05	±	0.04
	Spisula trigonella	2.18	±	0.14				2.00	±	0.22	2.36	±	0.18
	Stratiomyidae	3.89	±	0.16	3.89	±	0.16						
Fish	*Acanthopagrus butcheri*	5.88	±	0.03									
	Afurcagobius tamarensis	5.01	±	0.07	4.42			5.11	±	0.02	5.04	±	0.07
	Aldrichetta forsteri	6.11	±	0.13				6.21	±	0.20	6.03	±	0.17
	Ammotretis rostratus	4.76									4.76		
	Argyrosomus japonicus	5.54	±	0.20				5.86			5.46	±	0.24
	Arripis truttaceaus	5.91	±	0.06				5.94	±	0.07	5.88	±	0.10
	Atherinosoma microstoma	5.32	±	0.03	5.36	±	0.05	5.31	±	0.07	5.30	±	0.03
	Hyperlophus vittatus	4.63	±	0.04				4.69	±	0.04	4.58	±	0.06
	Hyporhamphus regularis	5.81	±	0.09				5.78	±	0.15	5.84	±	0.12
	Pseudaphritis urvillii	6.36	±	0.07	6.48	±	0.21	6.28	±	0.09	6.39	±	0.13

		ENERGY DENSITY (KJ / G WET MASS)											
		ALL			SOUTH LAGOON			NORTH LAGOON			MURRAY ESTUARY		
PREY TYPE	SPECIES/TAXA	MEAN		SE	MEAN		SE	MEAN		SE	MEAN		SE
	Rhombosolea tapirina	4.97	±	0.04				4.94	±	0.06	4.99	±	0.07
	Tasmanogobius lasti	5.52	±	0.18				5.69	±	0.11	5.22	±	0.46

Table C.3. Energy content values (kJ/dry mass, DM) for macroinvertebrates from marine and estuarine sediments based on data from this study (set in bold), and literature. Taxa names with an asterisk* indicate where values for energy content were used in this study for energy density calculations, as we could not obtain calorific content from samples in the Coorong.

		c		
TAXA	(MEAN ± SE OR MEDIAN)	MIN-MAX RANGE, 95% CONFIDENCE INTERVAL LOWER, UPPER LIMIT)	REGION	SOURCE
Crustacea	15.31	14.63, 16.55	Europe	Brey et al. 1988
Amphipoda	**12.12 ± 0.36**	**5.76 – 15.14**	**South Australia**	**this study**
Amphipoda	16.12 ± 3.17			Brey et al. 2010
Amphipoda	15.05		Arctic	Wacasey & Atkinson 1987
Amphipoda	20.30		France	Dauvin & Joncourt 1989
Corophium volutator	15.41	13.27 - 16.85	Europe	Rumohr et al. 1987
***Gammarus* spp.**	16.11	10.23 - 19.66	Europe	Rumohr et al. 1987
Isopoda	14.77 ± 0.82			Brey et al. 2010
Isopoda	12.96		Arctic	Wacasey & Atkinson 1987
***Idothea* spp. (Isopoda)**		6.7 - 24.87	Europe	Rumohr et al. 1987
Ostracoda*	5.74 ± 1.15			Brey et al. 2010
Mysidae	**15.23 ± 0.55**	**14.68 – 15.78**	**South Australia**	**this study**
Mysidae	19.46 ± 3.17			Brey et al. 2010
Mysidacea		13.54 - 30.47	Europe	Rumohr et al. 1987
Decapoda	16.26		Arctic	Wacasey & Atkinson 1987
Australian ghost shrimp	12.72 ± 0.25		Victoria	Dann 2014
Paragrapsus gaimardii	**9.42 ± 0.39**	**6.63 – 14.37**	**South Australia**	**this study**
Amarinus laevis	**11.08 ± 0.26**	**9.96 – 11.89**	**South Australia**	**This study**
Brachynotus spinosus	12.97 ± 0.13		Victoria	Dann 2014
Bivalvia	18.85	18.35, 19.33	Europe	Brey et al. 1988
Spisula trigonella	**11.14 ± 0.73**	**3.85 – 18.82**	**South Australia**	**this study**
Spisula elliptica	18.65		France	Dauvin & Joncourt 1989
Hiatula* (*Soletellina*) *alba	**11.97 ± 0.41**	**7.79 – 17.14**	**South Australia**	**this study**
Abra alba	18.8	17.02 - 20.26	Europe	Rumohr et al. 1987
Veneridae	17.46 ± 2.80			Brey et al. 2010
Tellinidae*	18.38 ± 0.81			Brey et al. 2010
***Tellina* spp.**	17.30		France	Dauvin & Joncourt 1989
Macoma balthica	17.79	16.12 - 19.05	Europe	Rumohr et al. 1987
Tellina deltoidalis	7.58		Victoria	Dann 2014
Gastropoda	18.24	17.01, 19.06	Europe	Brey et al. 1988
Gastropoda	18.77		Arctic	Wacasey & Atkinson 1987
Salinator fragilis	**8.82 ± 0.46**	**7.39 – 10.21**	**South Australia**	**this study**
***Littorina* spp.**	17.53 ± 0.85			Brey et al. 2010
Littorina littorea	19.76	18.70 - 21.41	Europe	Rumohr et al. 1987
Littorina saxatilis	18.13		Arctic	Wacasey & Atkinson 1987
***Hydrobia* spp.**	24.61		Europe	Rumohr et al. 1987
Hydrobiidae (with shell)*	5.67			Brey et al. 2010

	ENERGY CONTENT (kJ/g DM)			
TAXA	(MEAN ± SE OR MEDIAN)	MIN-MAX RANGE, 95% CONFIDENCE INTERVAL LOWER, UPPER LIMIT)	REGION	SOURCE
Polychaeta	16.79	15.29, 17.5	Europe	Brey et al. 1988
Polychaeta	16.10		Arctic	Wacasey & Atkinson 1987
Polychaeta errantia	17.5	16.67, 20.34	Europe	Brey et al. 1988
Polychaeta sedentaria	14.19	11.14, 17.2	Europe	Brey et al. 1988
Nephtys (Aglaophamus) australiensis	**15.69 ± 0.37**	**9.54 – 18.78**	**South Australia**	**this study**
***Nephtys* spp.**	17.52	15.50 - 19.75	Europe	Rumohr et al. 1987
***Nephtys* spp.**	18.44 ± 1.96			Brey et al. 2010
***Nephtys* spp.**	20.25		France	Dauvin & Joncourt 1989
Nephtys ciliata	16.66		Arctic	Wacasey & Atkinson 1987
Simplisetia aequisetis	**11.80 ± 0.32**	**6.66 – 17.23**	**South Australia**	**this study**
Australonereis ehlersi	**15.75 ± 1.47**	**14.28 – 17.22**	**South Australia**	**this study**
Nereididae	20.36 ± 2.62			Brey et al. 2010
Nematonereis	19.74 ± 0.43		France	Dauvin & Joncourt 1989
***Nereis* spp.**	20.76 ± 3.05			Brey et al. 2010
Nereis diversicolor	18.04	16.48 - 19.70	Europe	Rumohr et al. 1987
***Lumbrinereis* sp.**	13.39 ± 0.08		Victoria	Dann 2014
Phyllodoce novaehollandiae	**15.24 ± 1.54**	**12.24 – 20.29**	**South Australia**	**this study**
***Phyllodoce* spp.**	18.27 ± 2.10			Brey et al. 2010
***Phyllodoce* spp.**	19.93		France	Dauvin & Joncourt 1989
Phyllodoce groenlandica	16.78		Arctic	Wacasey & Atkinson 1987
Ficopomatus enigmaticus	**14.31 ± 1.12**	**10.62 – 18.26**	**South Australia**	**this study**
Sabella peicillum	19.79		Sweden	Norbbin & Bamstedt 1984
Sabella pavonina	20.50 ± 0.75		France	Dauvin & Joncourt 1989
Mediomastus	15.78 ± 0.75		France	Dauvin & Joncourt 1989
Polydora pulchra*	20.31 ± 0.72		France	Dauvin & Joncourt 1989
Spio decoratus	19.09 ± 0.25		France	Dauvin & Joncourt 1989
Tharyx marioni	17.80 ± 0.71		France	Dauvin & Joncourt 1989
Arenicolidae	**9.35 ± 1.98**	**5.22 – 14.67**	**South Australia**	**this study**
Capitella cf capitata	**12.79 ± 0.52**	**6.95 – 14.99**	**South Australia**	**this study**
Capitellidae	16.10 ± 0.45			Brey et al. 2010
Oligochaeta	22.36	21.51, 22.79	Europe	Brey et al. 1988
Oligochaeta*	14.19 ± 9.53			Brey et al. 2010
Nemertea*	20.94 ± 2.99			Brey et al. 2010
Nemertea	17.84		Arctic	Wacasey & Atkinson 1987
Nemertea	20.93		Sweden	Norbbin & Bamstedt 1984
Cnidaria				
Edwardsia*	14.80 ± 0.42		France	Dauvin & Joncourt 1989
Insect larvae	22.44	21.99, 22.88	Europe	Brey et al. 1988
Chironomidae	**10.81 ± 0.76**	**4.55 – 17.30**	**South Australia**	**this study**

TAXA	ENERGY CONTENT (kJ/g DM) (MEAN ± SE OR MEDIAN)	MIN-MAX RANGE, 95% CONFIDENCE INTERVAL LOWER, UPPER LIMIT)	REGION	SOURCE
Chironomidae	22.3		Europe	Rumohr et al. 1987
Chironomidae	15.37	14.86 - 15.98	Europe	Bertoli et al. 2018
Ceratopogonidae	**9.82**		**South Australia**	**this study**
Stratiomyidae	**13.38 ± 0.55**	**10.73 – 16.25**	**South Australia**	**this study**

Appendix C4: Energy content values (wet mass, WM) for estuarine fish based on data from this study (set in bold), and literature.

		ENERGY CONTENT (kJ/g WM)			
TAXA	COMMON NAME	MEAN ± SE	VARIATION (MIN-MAX RANGE)	REGION	SOURCE
Arripidae					
Arripis truttaceaus	**Australian salmon**	**5.91 ± 0.06**	**5.12–6.45**	**South Australia**	**this study**
Arripis truttaceaus	Australian salmon	7.12		Western Australia	McCluskey et al. 2016
Arripis georgianus	Australian herring	6.62		Western Australia	McCluskey et al. 2016
Atherinidae					
Atherinosoma microstoma	**Smallmouth hardyhead**	**5.32 ± 0.03**	**4.90–5.98**	**South Australia**	**this study**
Leptatherina presbyteroides	Elongate hardyhead	4.23		Western Australia	McCluskey et al. 2016
Bovichtidae					
Pseudaphritis urvilii	**Congolli**	**6.36 ± 0.07**	**5.23–7.54**	**South Australia**	**this study**
Clupeidae					
Hyperlophus vittatus	**Sandy Sprat**	**4.63 ± 0.04**	**3.97–4.94**	**South Australia**	**this study**
Hyperlophus vittatus	Sandy Sprat	6.59		Western Australia	McCluskey et al. 2016
Hyperlophus vittatus	Sandy Sprat	4.24		New South Wales	Lawson et al. 2018
Brevoortia tyrannus	Atlantic menhaden	6.76		USA	Thayer et al. 1973
Gobiidae		4.26		Scotland	Healy 1972, cited in Lawson et al. 2018
Afurcagobius tamarensis	**Tamar goby**	**5.01 ± 0.07**	**4.41–5.52**	**South Australia**	**this study**
Tasmanigobius lasti	**Lagoon goby**	**5.52 ± 0.18**	**3.89–6.00**	**South Australia**	**this study**
Gobiosoma bosci	Naked goby	6.40		USA	Thayer et al. 1973
Hemiramphidae					
Hyporhamphus regularis	**River garfish**	**5.81 ± 0.09**	**5.29–6.63**	**South Australia**	**this study**
Mugiligae					
Aldrichetta fosteri	**Yelloweye mullet**	**6.11 ± 0.13**	**4.73–8.20**	**South Australia**	**this study**
Aldrichetta fosteri	Yelloweye mullet	4.58		Western Australia	McCluskey et al. 2016
Mugil cephalus	Sea mullet	5.30		Western Australia	McCluskey et al. 2016
Mugil cephalus	Sea mullet	5.31		USA	Thayer et al. 1973
Pleuronectidae					
Rhombosolea tapirina	**Greenback flounder**	**4.97 ± 0.04**	**4.46–5.24**	**South Australia**	**this study**
Ammotretis rostratus	**Longsnout flounder**	**4.76**		**South Australia**	**this study**
Paralichthyidae					
Paralichthys dentatus	Summer flounder	4.80		USA	Thayer et al. 1973
Paralichthys dentatus	Summer flounder	4.14	2.72–5.31	USA	Schloesser & Fabrizio 2017
Sciaenidae					
Argyrosomus japonicus	**Mulloway**	**5.54 ± 0.20**	**5.03–5.98**	**South Australia**	**this study**
Leiostomus xanthurus	Spot	4.86		USA	Thayer et al. 1973
Micropogon undulatus	Atlantic croaker	4.60		USA	Thayer et al. 1973

TAXA	COMMON NAME	ENERGY CONTENT (kJ/g WM) MEAN ± SE	VARIATION (MIN-MAX RANGE)	REGION	SOURCE
Micropogon undulatus	Atlantic croaker	4.70	2.99–7.53	USA	Schloesser & Fabrizio 2017
Sparidae					
Acanthopagrus butcheri	**Black Bream**	**5.88 ± 0.03**	**5.81–5.95**	**South Australia**	**this study**
Rhabdosargus sarba	Tarwhine	4.97		Western Australia	McCluskey et al. 2016
Lagodon rhomboides	Pinfish	4.86		USA	Thayer et al. 1973

Appendix C.5: Energy content values (dry mass, DM) for plankton, plants, algae, and detritus from marine and estuarine environments based on data from this study (set in bold), and literature.

	ENERGY CONTENT (kJ/g DM)			
TAXA	(MEAN ± SE OR MEDIAN)	MIN-MAX RANGE, 95% CONFIDENCE INTERVAL LOWER, UPPER LIMIT)	REGION	SOURCE
Plankton	**6.06 ± 1.12**	**1.00–18.17**	**South Australia**	**this study**
Copepoda	20.88 ± 0.58			Brey et al. 2010
Ostracoda	10.47 ± 2.10			Brey et al. 2010
Artemia	19.56 ± 0.78			Brey et al. 2010
Plants				
Ruppia	**10.09 ± 0.077**	**6.17 – 15.35**	**South Australia**	**this study**
Alismatales	14.84 ± 0.77			Brey et al. 2010
Zostera	13.40 ± 1.33			Brey et al. 2010
Posidonia	15.14			Brey et al. 2010
Algae				
Filamentous algae	**4.50 ± 0.32**	**3.07 – 5.95**	**South Australia**	**this study**
Cladophora	11.37 ± 1.19			Brey et al. 2010
Rhizoclonium	8.13			Brey et al. 2010
Ulva	13.11 ± 0.58			Brey et al. 2010
Detritus	**2.90**		**South Australia**	**this study**
Detritus	4.25–5.50			Palavesam et al. 2005
Detritus (various sources)	13.41 ± 0.67	6.91–19.35	Laboratory	Tenore 1983
Detritus (*Gracilaria & Spartina*)		~13–17	Laboratory	Tenore et al. 1984

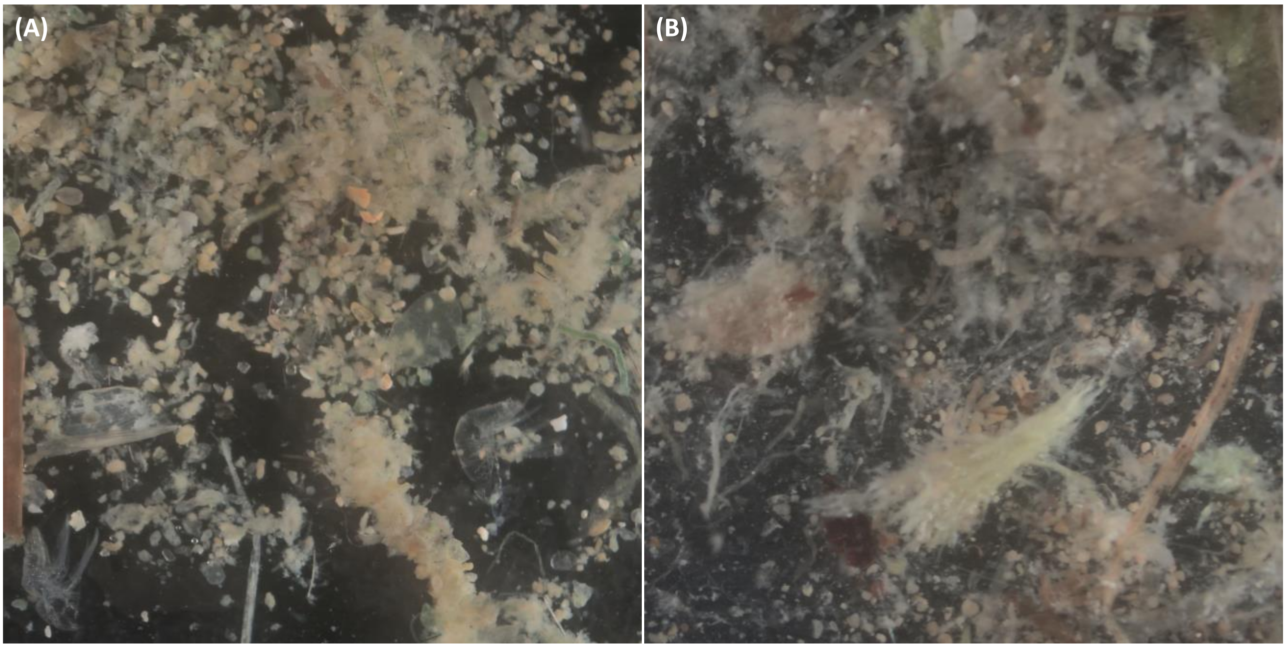


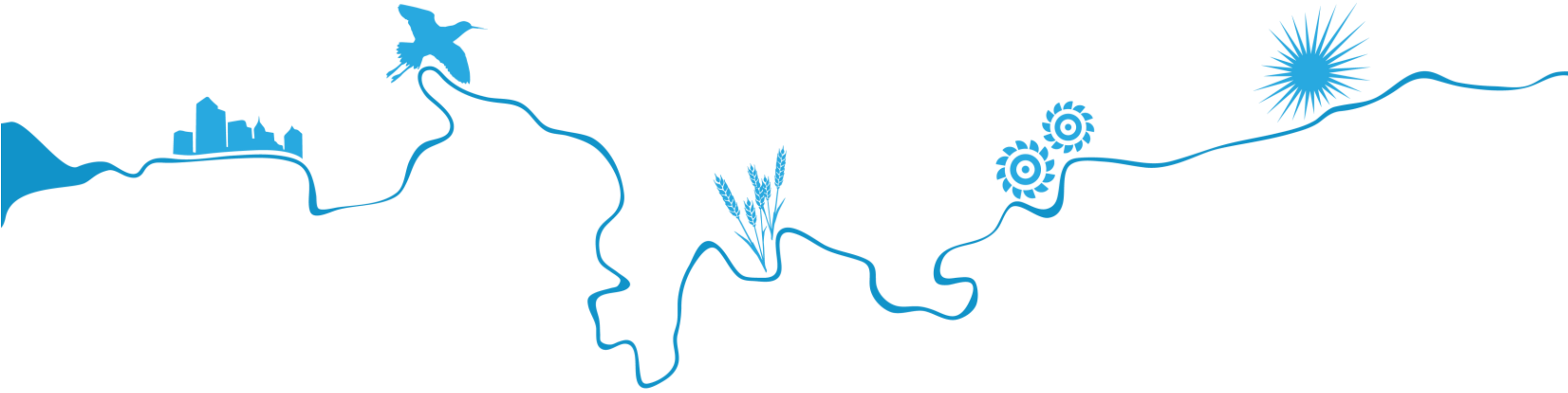
Figure C.1. Microscope images from detrital material collected from meiofauna samples in the Murray Estuary (A) and South Lagoon (B).

Appendix C.6: Estimated production and Production/Biomass (P:B) ratios for macroinvertebrates from the Coorong (this study), in comparison with values from the literature for the same or related species and based on using a variety of methods.

TAXA	PRODUCTION	P:B	METHOD/S	SYSTEM	REFERENCE
Arthritica semen	**102.65 g AFDM/m^2/year**	**6.16**	**Empirical (Edgar)**	**Coorong**	**This study**
Arthritica semen	4.1-6.7 g DM/m^2/year	3.9	increment summation	Peel Inlet, Peel-Harvey Estuary, Western Australia	Wells & Threlfall (1982)
Corbula trigona	9.8-24.3 g DM/m^2/year	1.7-3.8	Removal-Summation	Lake Aheme - West Africa, coastal lagoon	Maslin & Pattee (1989)
Corbula trigona	12.1-26.6 g DM/m^2/year	2.2-3.9	Size-frequency	Lake Aheme - West Africa, coastal lagoon	Maslin & Pattee (1989)
Mercenaria mercenaria	4-14 g AFDM/m^2	0.2-0.5	increment summation	Southhampton Water - coastal plain estuary, intertidal mud flat, England	Hibbert (1976)
Cerastoderma edule	29-71 g AFDM/m^2	1.1-2.6	increment summation	Southhampton Water - coastal plain estuary, intertidal mud flat, England	Hibbert (1976)
Theora lubrica	21.1 g DM/m^2/year			Seto Inland Sea, Japan	Imabayashi & Wakabayashi (1992)
Mya arenaria	11.6 g (flesh)DM/m^2/year	2.5	increment summation or removal summation	Petpeswick Inlet - narrow, shallow estuary, Cananda	Burke & Mann (1974)
Macoma balthica	1.93 g (flesh)DM/m^2/year	1.53			Burke & Mann (1974)
Ensis directus	to > 100 g AFDM/m^2/year	to ~6	increment summation	Wadden Sea - tidal flat	Dekker & Beukema (2012)
Hiatula alba	**0.73 g AFDM/m^2/year**	**1.99**	**Empirical (Edgar)**	**Coorong**	**This study**
Spisula	**2.00 g AFDM/m^2/year**	**2.85**	**Empirical (Edgar)**	**Coorong**	**This study**
Spisula subtruncata	16.99-42.13 gAFDM/m^2/year	3.82	increment summation	Po River Delta (5 m depth), Italy	Ambrogi & Ambrogi (1985)
Spisula solidissima	0.0006-0.87 gAFDM/m^2/year	1.5-5.7	increment summation	Delaware Bay, USA	Howe et al. (1988)
Hydrobiidae	**10.01 g AFDM/m^2/year**	**6.54**	**Empirical (Edgar)**	**Coorong**	**This study**
Hydrobia sp.	4.5-83.7 g DM/m^2/year		Empirical (Banse & Mosher)	Berg River estuary, South Africa	Kalejta & Hockey (1991)
Hydrobia ulvae	3.64-10.41 g AFDM/m^2/year	1.98-5.80	Removal-Summation	Bidasoa estuary, Spain	Sola (1996)
Hydrobia ulvae	7.23-12.79 g AFDM/m^2/year	1.24-1.78	increment summation	Grevelingen estuary, The Netherlands	Wolff & de Wolf (1977)
Hydrobia ulvae	15.2-93.7 g AFDM/m^2/year	1.3-4.5	Allen Curve	Mondego estuary, Portugal - eutrophication gradient, seagrass meadows	Lillebø et al. (1999)
Hydrobia ulvae	<0.01 g AFDM/m^2/year	6.58	Empirical (Banse & Mosher)	mussel bed in the northern Wadden Sea	Asmus (1987)
Hydrococcus brazieri	0.5-7.6 g DM/m^2/year	2.2	increment summation	Peel Inlet, Peel-Harvey Estuary, Western Australia	Wells & Threlfall (1982)

Taxa	Production	P:B	Method/s	System	Reference
Salinator fragilis	**5.72 g AFDM/m^2/year**	**3.39**	**Empirical (Edgar)**	**Coorong**	**This study**
Littorina littorea	9.69+/-4.20 g AFDM/m^2/year	0.48	Winberg (1971)	mussel bed in the northern Wadden Sea	Asmus (1987)
Littorina obtusata	0.09 g AFDM/m^2/year	2.88	Empirical (Banse & Mosher)	mussel bed in the northern Wadden Sea	Asmus (1987)
Simplisetia aequisetis	**9.66 g AFDM/m^2/year**	**6.75**	**Empirical (Edgar)**	**Coorong**	**This study**
Simplisetia aequisetis	8.74 g DM/m^2/year	3.4	increment summation	Swan River Estuary, Western Australia	De Roach (2007)
Simplisetia aequisetis	92 g AFDM/m^2/year	2.94	increment summation	Port Phillip Bay, Victoria (near wastewater)	Dorsey (1981)
Ceratonereis (Simplisetia) erythraeensis	14.42 g DM/m^2/year	1.9	increment summation	Berg River estuary, South Africa	Kalejta (1992)
Australonereis	**0.04 g AFDM/m^2/year**	**2.68**	**Empirical (Edgar)**	**Coorong**	**This study**
Australonereis ehlersi	12.5 g DM/m^2/year	3.2	increment summation	Swan River Estuary, Western Australia	De Roach (2007)
Nephtyidae	**1.36 g AFDM/m^2/year**	**3.66**	**Empirical (Edgar)**	**Coorong**	**This study**
Nephtys spp.	0.09-4.32 g AFDM/m^2/year; 0.29-7.34 gDM/m^2/year	0.38-2.9	varied	Multiple systems	Medernach et al. (2000) and references therin
Phyllodoce	**0.07 g AFDM/m^2/year**	**3.07**	**Empirical (Edgar)**	**Coorong**	**This study**
Phyllodoce linneata	0.016-0.020 g AFDM/m^2/year	4.16-5.26	Empirical (Tumbiolo & Downing)	Sacca di Goro - brackish lagoon, Italy	Mistri et al. (2001)
Boccardiella	**0.34 g AFDM/m^2/year**	**8.33**	**Empirical (Edgar)**	**Coorong**	**This study**
Prionospio caspersi	8.06 g AFDM/m^2/year	4.09	Size-frequency	Po River Delta, Italy	Ambrogi (1990)
Streblospio	3.0-15.65 g DM/m^2/year	4.4-5.4	increment summation; size-frequency	Salt marsh, USA; muddy bay, Spain	Sardá & Martin (1993)
Arenicolidae	**0.67 g AFDM/m^2/year**	**3.27**	**Empirical (Edgar)**	**Coorong**	**This study**
Capitella capitata	**13.91 g AFDM/m^2/year**	**7.98**	**Empirical (Edgar)**	**Coorong**	**This study**
Capitella capitata	47-270 g M/m^2/year	23-36	increment summation	littoral zone off coast of Spain (near wastewater)	Méndez et al. (1997)
Capitella capitata	0.23 g AFDM/m^2/year	1.96	Size-frequency	Rio de la Plata estuary, Argentina	Martin & Bastida (2006)
Capitella capitata	1.43 g AFDM/m^2/year	3.78	Empirical (Banse & Mosher)	mussel bed in the northern Wadden Sea	Asmus (1987)
Oligochaeta	**0.14 g AFDM/m^2/year**	**8.9**	**Empirical (Edgar)**	**Coorong**	**This study**
Oligochaeta	0.12-0.98 g AFDM/m^2/year	5.63-6.15	Empirical (Tumbiolo & Downing)	Sacca di Goro - brackish lagoon, Italy	Mistri et al. (2001)

Taxa	Production	P:B	Method/s	System	Reference
Oligochaeta	0.0001-0.0212 g AFDM/m^2/year	0.2-2.47	Empirical (Sprung)	Ria Formosa - lagoon (intertidal), Portugal	Sprung (1994)
Oligochaeta	3.26 g AFDM/m^2/year	17	Empirical (Banse & Mosher)	Columbia River estuary (mudflat), USA	Jones (1983)
Amphipoda	**36.79 g AFDM/m^2/year**	**8.61**	**Empirical (Edgar)**	**Coorong**	**This study**
Amphipoda (multiple species)	0.2-47 g DM/m^2/year	0.9-23.6	varied	multiple systems, mostly Europe and North America	Vetter (1996) and references therein
Microdeutopus gryllotalpa	13.49 g AFDM/m^2/year	11.7	Size-frequency	Shallow coastal (warm temperate) lagoon, Spain	Drake & Arias (1995a)
Corophium urdaibaiense	2.93-5.85 g AFDM/m^2/year	4.7-9.4	Size-frequency	Urdaibai estuary, Spain - intertidal flat	Pérez et al. (2007)
Mysidacea	**0.37 g AFDM/m^2/year**	**5.15**	**Empirical (Edgar)**	**Coorong**	**This study**
Mysidacea	1.32-2.27 g DM/m^2/year	6.8-13.1	Size-frequency	Kaikorai Lagoon - small intermittently closed estuary, New Zealand	Lill et al. (2012)
Mysidacea	0.031-0.050 gAFDM/m^2/year	8.5-13.7	Size frequency, Empirical (Brey; Morin & Bourassa)	Seagrass meadows, western Mediterranean Sea	Barberá et al. (2013)
Mysidacea		2.57	Size-frequency	Mondego estuary - warm-temperate estuary, Portugal	Azeiteiro et al. (1999)
Stratiomyidae	**0.11 g AFDM/m^2/year**	**5.67**	**Empirical (Edgar)**	**Coorong**	**This study**
Chironomidae	**3.09 g AFDM/m^2/year**	**8.38**	**Empirical (Edgar)**	**Coorong**	**This study**
Tanytarsus barbitarsis	66 g DM/m^2/year			Lake Werowrap, western Victoria	Paterson & Walker (1974)
Chironomus salinarius	0.07-3.52 g AFDM/m^2/year	5.48-6.18	Empirical (Tumbiolo & Downing)	Sacca di Goro - brackish lagoon, Italy	Mistri et al. (2001)
Chironomus salinarius	16.8 (0.1-72.2) g DM/m^2/year	12.7	Size-frequency	semi-natural lagoon in the Bay of Cadiz, Spain - used for fish aquaculture	Drake & Arias (1995b)
Chironomidae (multiple species)	3.2 (middle reaches) -108 (lower reaches) g DM/m^2/year	52-53	Multiplied biomass by instantaneous daily growth rate, equations from Golubkov (2000)	Bolshaya Samoroda River - saline river, Russia	Golovatyuk et al. (2020)
Chironomidae (multiple species)	0.019 - 49.2 g DM/m^2/year	'4-95			Golovatyuk et al. (2020)
Tanytarsus kharaensis	0.019 (middle reaches) - 15.47 (lower reaches) g DM/m^2/year	35-95			Golovatyuk et al. (2020)
Cricotopus sylvestris	5.8 g DM/m^2/year	21	Size-frequency	Hudson River estuary, USA	Menzie (1981)



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