A Review of Critical Entrainment Thresholds for Riverine Microinvertebrates and Experimental Designs for the Lower River Murray

T. N. Dornan, C. M. Bice, D. Furst, J. D. Brookes and Q. Ye

Government of South Australia
Department of Primary Industries and Regions

Government of South Australia
Department for Environment and Water

SARDI
R&D
SOUTH AUSTRALIAN RESEARCH AND DEVELOPMENT INSTITUTE

A Review of Critical Entrainment Thresholds for Riverine Microinvertebrates and Experimental Designs for the Lower River Murray

Report for the Department for Environment and Water

T. N. Dornan, C. M. Bice, D. Furst, J. D. Brookes and Q. Ye

January 2024

DISCLAIMER

© 2024 SARDI

ALL ENQUIRIES

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

GLOSSARY

Biofilm: An assemblage of microorganisms adhering to a solid surface that may provide habitat for microinvertebrates.

Boundary layer: A transitional region in the water column between slow-flowing water at the surface of substrates and the free-flowing water layers higher in the water column.

Cladoceran: A superorder of microcrustaceans predominantly found in freshwater.

Collimators: Devices used to narrow and align the flow of water, ensuring a more uniform and parallel stream.

Copepod: A class of microcrustaceans common in most aquatic environments.

Diapause: A dormant state that allows organisms to survive adverse environmental conditions by significantly reducing metabolic activities.

Diel vertical migration: The daily movement of organisms from deeper waters during the day to near-surface waters during the night, primarily for feeding and predator avoidance.

Drift: The passive movement of microinvertebrates carried along by the flow of water.

Entrainment: The process by which microinvertebrates are captured and transported by river currents.

Flow refugia: Zones within river systems where water flow characteristics (e.g. flow velocity and depth) provide shelter for aquatic organisms.

Flume: A human-made channel, often used in scientific research and engineering, designed to direct, measure, and analyze water flow under controlled conditions.

Froude number: A dimensionless value for measuring how fast water flows in relation to its wave-making and gravity effects, used to determine if flow is laminar or turbulent.

Lentic habitat: Still or slow flowing freshwater habitat.

Littoral zone: The habitat of a river close to the banks of the river.

Lorica: A protective outer casing or shell that envelops certain microorganisms, including some types of microinvertebrates, providing structural support and defence against predators.

Lotic habitat: Fast flowing freshwater habitat, characterised by shallow water and slower flows.

Microflagellate: A small, typically single-celled organism equipped with one or more whip-like structures called flagella.

Microinvertebrate: Planktonic organisms, including rotifers, cladocerans, copepods, and ostracods.

Microcrustacean: Small, planktonic crustaceans including cladocerans, copepods, and ostracods.

Ostracod: A class of microcrustaceans characterised by a bivalve-like shell and found in various aquatic environments.

Parthenogenesis: A form of asexual reproduction where an embryo develops from unfertilised eggs.

Pedal glands: Specialised excretory glands or adhesive structures located in the foot region of some rotifers, used primarily for attachment to substrates.

Pelagic zone: The open waters of a river, away from the banks or streambed, characterised by deep water and higher flows.

Reynolds number: A dimensionless value that helps predict flow patterns (i.e. laminar or turbulent) by comparing the relative effects of inertia and viscosity.

Rheotaxis: The behavioural response to water currents, guiding their movement either towards or away from the flow direction.

Rotifer: A diverse Phylum of microscopic microinvertebrates, typically much smaller than microcrustaceans**.**

Slackwaters: Areas where the water flow is considerably reduced, often serving as habitat zones for various organisms, including microinvertebrates.

Viscous sublayer: A region of reduced water velocity adjacent to solid substrates.

Water flow rate: The volume of water passing through a habitat or stream over time (e.g. L s^{-1}).

Water Residence Time (WRT): The duration of time water spends in a specific habitat.

Water velocity: The speed (e.g. m s^{-1}) of flowing water.

ACKNOWLEDGEMENTS

EXECUTIVE SUMMARY

Microinvertebrates (specifically cladocerans, copepods, ostracods, and rotifers) show a high diversity in life history, behaviour, and morphology. Together, these animals form an essential component of food webs in aquatic ecosystems. The primary dispersal vector for microinvertebrates in aquatic ecosystems is 'drift', whereby microinvertebrates are transported downstream with the current. Drift, the downstream transport of microinvertebrates with the current is one of the most important transport phenomena in stream ecology. Drift enhances dispersal, allowing microinvertebrates to colonise new habitats, escape predators and maintain species and genetic diversity (Hayes et al., 2018; Hoover, 1994; Perić et al., 2014). However, relatively little is known about what velocities entrain microinvertebrates from substrates and how this threshold interacts with other biological and physical variables, making it challenging to achieve optimal outcomes through environmental water delivery or infrastructure management. The objectives of this project were to: (1) conduct a literature review to detail what factors may influence microinvertebrate drift and highlight previous attempts to experimentally derive critical entrainment thresholds for microinvertebrates in flowing water; and (2) summarise the available methods and experimental designs capable of investigating the mechanism of entrainment and inferring critical entrainment thresholds. Additionally, Part 2 proposes a series of costed experimental designs that can be implemented to test mechanisms of entrainment, thresholds of entrainment in the lower River Murray.

Microinvertebrate swimming ability and behaviour is tied to their size and morphology, which can considerably influence their drift dynamics (Lagergren et al., 2001; Palmer 1992; Sidler 2018b). By orienting their body and actively swimming downwards, microcrustaceans (cladocerans, copepods, ostracods) can increase their settling rate, thereby reducing drift distance. Interestingly, rotifers, which are typically far smaller than microcrustaceans, rarely exhibit significant control over their sinking rate (Palmer 1990; Palmer 1992). Once settled on substrates, evidence suggests microcrustaceans and rotifers can display selective entry into the drift (Karabin & Ejsmont-Karabin, 2005; Palmer 1992). The presence of flow refugia (i.e., zones that provide shelter from high-flow) also impacts microinvertebrate drift. Microhabitat structure on riverbanks (i.e., littoral zone) can reduce water velocities to levels such that microinvertebrates with sufficient swimming ability can more easily avoid being washed out and entrained within the drift (Gibbs et al., 2020; Richardson, 1992). Other sources of flow refugia, such as the hyporheic zone and the viscous sublayer, are thought to reduce entrainment of drifting individuals, though this is largely speculative and evidence is scarce, particularly for the lower River Murray.

Previous methods to derive microinvertebrate critical entrainment thresholds have varied, as have the results. Microinvertebrate entrainment and swimming ability have been directly investigated using flumes, flow chambers, and video tracking. Alternatively, inferences in entrainment thresholds have been made in streams by monitoring how drift density is influenced by water velocity. Generally, microinvertebrate drift rapidly increases when water velocities exceed 10 cm s^{-1}, though evidence suggests some taxa, particularly larger copepods, may have higher entrainment thresholds of approximately 15 cm s^{-1} (Gibbs et al., 2020; Palmer 1992). Following entrainment within the drift, the swimming ability of most taxa rarely allows microinvertebrates to maintain their horizontal position when flows exceed 2.5–3.5 cm s^{-1} (Richardson 1992).

Three approaches are recommended to test critical entrainment thresholds of lower River Murray microinvertebrates, each with distinct strengths and limitations. The first approach involves a field experiment in a channel or creek, approximately 1–2 km in length, featuring minimal inlets. This channel or creek will possess hydrological structures capable of regulating downstream water velocity. The primary focus of this experiment is to determine how microinvertebrate communities throughout the water column respond to changes in water velocity. By sampling microinvertebrate communities at progressively increasing distances downstream, the experiment aims to inform the relationship between microinvertebrate community assemblage and abundance, and hydraulic conditions such as water velocity and depth. This field approach allows researchers to capture natural hydraulic conditions and microinvertebrate communities within the lower River Murray, generating 'real-life' results at a scale relevant to managers. However, while this approach is well-suited to measuring how microinvertebrates are transported and dropped from the drift, the complex environment of a natural setting makes it difficult to discern precise thresholds for microinvertebrate entrainment.

The second approach is a laboratory-based flume experiment that will investigate fine-scale entrainment thresholds of microinvertebrates. Microinvertebrates introduced to the flume will be transported downstream under increasing flow velocities and captured by a net for analysis. This experimental flume approach will provide a controlled environment to precisely measure velocities at which certain taxa begin to become entrained from sediments. However, size constraints in laboratory settings will limit research on settling rates, drift distances, and drift re-entry, all of which impact drift magnitude in natural streams. Additionally, the sourcing of microinvertebrates for laboratory experiments remains a logistical dilemma that is not present for in situ studies. Therefore, the combined results of the laboratory flume and field study will complement each other, providing a more comprehensive understanding of microinvertebrate entrainment dynamics.

The third recommended approach is a desk-based study that will carry out a meta-analysis of past research concerning microinvertebrate communities. Microinvertebrate data has been collected from over 80 sites across the lower River Murray, representing a rich repository of data that can be used to investigate the relationship between microinvertebrate communities and hydrological variables. These are readily available in situ data however, further exploration, analyses and modelling will be required to address specific questions of microinvertebrate entrainment.

The above recommended approaches, or a combination of them, could be implemented during the next stage of this project to help derive specific velocity thresholds for microinvertebrate entrainment (including entering and dropping out from drift) for lower River Murray communities. The findings will inform environmental water delivery and river operations, including infrastructure management to achieve the best ecological outcomes in the lower River Murray.

Keywords: Rotifer, microcrustacean, entrainment, velocity, River Murray.

1. INTRODUCTION

1.1. Background

The Murray-Darling Basin (MDB) is primarily formed by the River Murray and the Darling River. The MDB is Australia's largest river system, spanning approximately 14% (1.07 million km^2) of Australia's total land area and providing habitat for a range of native biota (Murray–Darling Basin Authority, 2020). The Basin supplies water to 3.6 million people (Murray–Darling Basin Authority, 2021a) and represents half (48%) of all irrigated water use in the country (Australian Bureau of Statistics, 2021). The Basin exhibits a high degree of biophysical (e.g., climate, habitat, and biodiversity) variability with generally low runoff and high evaporation (Davies et al., 2010).

The River Murray is the longest river in Australia, running from the Australian Alps in New South Wales to the Southern Ocean at Goolwa, South Australia, spanning approximately 2,500 km. It is among the world's most regulated rivers (Nilsson et al., 2005). Two major headwater dams capture and store water, a series of 16 main channel locks, and five tidal barrages regulate flow and water levels within the channel. Additionally, many smaller regulators and levees control lateral connectivity among river, anabranch, and floodplain/wetland habitats. In addition to this regulation, various competing demands for freshwater resources have led to substantial upstream diversion, considerably altering the hydraulics of the system.

To address these competing demands, water users of the MDB subscribe to a sophisticated water-trading scheme called the Murray-Darling Basin Plan, which allots water based on availability. The Basin Plan ensures a volume of water is allocated to the environment ('water for the environment' or 'environmental water') to achieve environmental outcomes. Allocation of environmental water has been partially accomplished through the Commonwealth Environmental Water Holder (CEWH) purchasing water entitlements from irrigators.

Environmental watering aims to mitigate, and where possible reverse, the negative impacts of river regulation on the environment through the restoration of aspects of the river's natural flow regime, particularly flow volumes, lotic channel conditions and inundation extents. The river can be influenced through the delivery of in-channel flow pulses and by the control of water levels through the operation of floodplain regulators and/or weir pool manipulations. In-channel flow pulses aim to promote lotic conditions, connectivity and water level variability, nutrient mobilisation, and improved productivity (Rees et al., 2021). Flow pulses also aim to promote spawning of certain fishes (e.g., golden perch, *Macquaria ambigua*) and enhance transport of fish larvae and other planktonic organisms (DEW, 2020; DEW, 2021). The

manipulation of water levels with floodplain regulators and main channel locks involves raising or lowering water levels from normal pool levels to promote inundation or hydraulic outcomes in floodplains and channels. Increasing flow and manipulating water levels through engineering actions have differential influences on instream hydraulics (e.g., water velocities and turbulence) and, thus, the transport of riverine biota.

To best inform river ecosystem management, a more comprehensive understanding of the impact of altered flow regimes and riverine hydraulics on key biota is critical. One such group is riverine microinvertebrates (e.g., rotifers, cladocerans, copepods, ostracods). For example, inundation of off-channel river habitats promotes high microinvertebrate productivity. Microinvertebrates are transported to the main river channel when water flows through floodplains or water levels are decreasing (lateral hydrological connectivity). Subsequently, microinvertebrates are transported downstream when velocity and turbulence are high and locks have reduced in-channel impact (longitudinal hydrological connectivity; see section 2.1.2), where microinvertebrates serve as important food resources for many larval and juvenile fishes. There is limited understanding of the relationship between microinvertebrates and river hydraulics. Indeed, the Weir Pool Monitoring Strategy led by the Department of Environment for Environment and Water (DEW) has identified key knowledge gaps regarding the entrainment velocities and rates of loss of microinvertebrates from the river drift. Research on microinvertebrate communities has focused on reservoirs and lakes due to the opinion that flowing rivers are inherently unsuitable environments for them. In fact, certain microinvertebrate taxa can remain abundant in the main channel of large rivers (Pourriot et al., 1997), particularly those with slow flows (Lair, 2005) and plentiful flow refugia (see section 2.2). Through a better understanding of the hydraulic mechanisms that entrain and transport microinvertebrates, environmental water and water level management may be used (to a degree) to promote these taxa at critical times and locations. This will have considerable consequences for the metabolism and aquatic food web of the River Murray, as microinvertebrates are primary consumers and are critical for the transfer of energy to higher trophic organisms (Kobayashi et al., 1996; Medeiros & Arthington, 2008).

1.2. Objectives

This project aimed to conduct a literature review and to develop and recommend appropriate experimental designs to assess the velocity thresholds at which key littoral rotifer and microcrustacean species are entrained and maintained within the drift. The experimental design should inform the rates at which microinvertebrates can enter or exit the drift at different velocities specific to the context of the lower River Murray. Therefore, the overarching aims can be summarised as: (1) conduct a literature review to detail what factors may influence

microinvertebrate drift and present previous attempts at inferring critical entrainment thresholds (section 2); and (2) summarise the available methods and experimental designs capable of investigating the mechanism of entrainment and inferring critical entrainment thresholds, resulting in costed experimental designs that can be implemented in the lower River Murray (Section 3).

1.3. Study site

The area of interest for this review is the lower River Murray. For this review, the lower River Murray will be used to describe the river from Wentworth to the Southern Ocean. The lower River Murray begins at the confluence of the Murray and Darling Rivers (Figure 1), flowing through a semi-arid region and comprising 9% of the MDB's catchment area (Murray–Darling Basin Authority, 2021b). Large headwater storages and increased water diversions have drastically impacted flow regimes and hydraulic conditions (i.e., water level and velocity) in the river to the detriment of ecosystem structure and function (Bunn & Arthington, 2002). The lower River Murray lacks any significant tributaries and, as such, its hydrological behaviour is primarily determined by flows from the Darling River and middle and upper River Murray (Walker, 2006).

Ten low-level locks (situated 29–88 km apart) have fragmented the channel in the lower River Murray, turning the 830 km stretch of lotic river into a series of cascading, predominantly lentic weir pools (Bice et al., 2017; Walker, 2006). Furthermore, upstream diversion has reduced the frequency, magnitude and duration of high flows and floods, disrupting longitudinal and lateral connectivity, which was widespread, co-occurring and integrated during natural river conditions (Walker, 2006). Changes to the hydraulic nature, flooding frequency and connectivity of the lower River Murray have been associated with declines in various native biota (Mallen-Cooper & Zampatti, 2018; Walker, 1993). The mean and median annual flows into South Australia are 5,300 and 3,700 GL, respectively (observed data, 1/7/1977–30/06/2022; DEW, 2022). In contrast, mean and median flow into South Australia modelled under natural conditions were 12,800 and 11,600 GL, respectively (Bice et al., 2017; Murray–Darling Basin Authority, 2012).
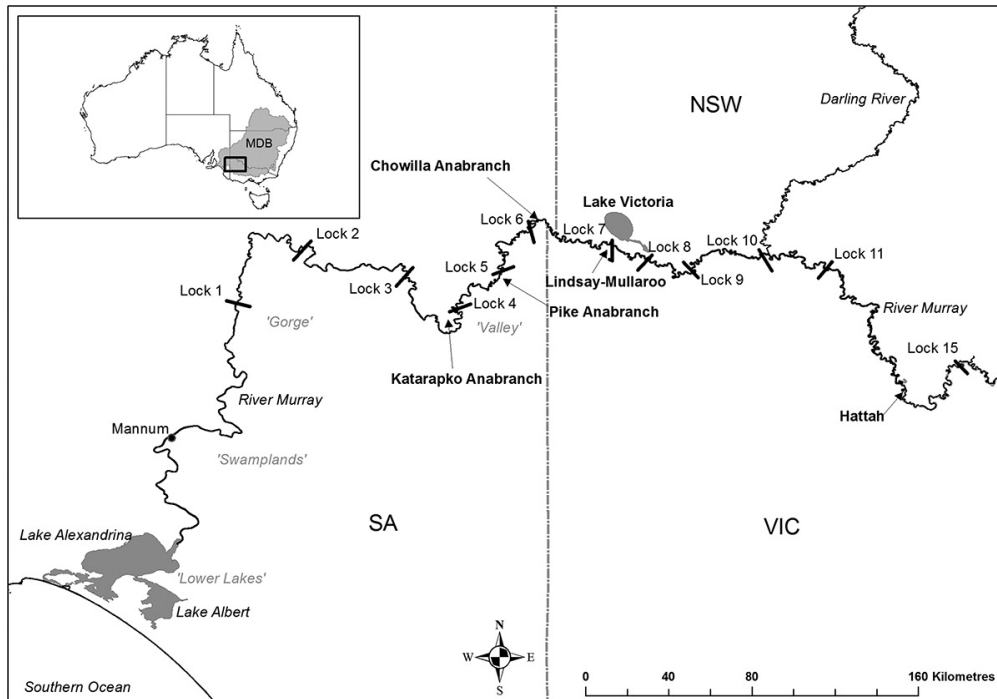
Figure 1. The River Murray from Lock 15 to its terminus at the Southern Ocean, detailing Locks 1–15 and the major anabranch systems, namely Lindsay–Mullaroo, Chowilla, Pike and Katarapko (Bice et al., 2017).

2. LITERATURE REVIEW ON MICROINVERTEBRATE ENTRAINMENT

2.1. Microinvertebrates of the lower River Murray

2.1.1. Abundance and diversity

Microinvertebrates of the MDB are highly diverse, comprising multiple kingdoms and phyla. This report focuses on metazoan microinvertebrates, specifically rotifers and microcrustaceans. Rotifers (phylum Rotifera) typically range from 0.1–0.5 mm in length, though they can be 0.05–2 mm long (Wallace & Smith, 2009). In contrast, microcrustaceans such as cladocerans, copepods and ostracods generally measure 1–2 mm, but sizes can vary significantly among species (García-Comas et al., 2016; Rizo et al., 2019). Metazoan microinvertebrate groups are highly responsive to a range of abiotic variables, including hydraulics, inundation, and water quality (see Table 1 for more information). Therefore, restructuring of a microinvertebrate community can occur within days of sediment inundation and emergence from diapause eggs. Furthermore, changes in temperature or salinity can influence the swimming abilities of microinvertebrates and decrease emergence rates from sediments (Armonies, 1988; Nielsen et al., 2007; Seuront, 2006; Sidler et al., 2018b). Given the high degree of habitat variability in the MDB, including the lower River Murray, and rapid responses of microinvertebrates, considerable spatio-temporal variability in species richness and abundance is observed, with densities ranging from <100 individuals per litre (Ind.L^{-1}) to >4,000 Ind.L^{-1} (Dornan et al., 2021; Furst et al., 2020; Shiel et al., 1982; Shiel, 1985).

Table 1. Known influences of environmental variables on microinvertebrate communities and behaviour in relation to entrainment and downstream transportation.

Variable	Influence on microinvertebrates	Source
Temperature	Decreasing temperatures from 20 to 14 °C substantially lowered the counter-current swimming effort of the freshwater copepod *Eucyclops serrulatus* in a flume experiment. Raising temperatures from 11 to 16 °C had no clear effect on swimming behaviour.	Sidler et al., 2018b
	The drift of harpacticoid copepods increased most intensely when temperatures were decreased from ~18–14 °C in flume experiments.	Bruno et al., 2012
	Warmer temperatures increased the upward migration velocities of microinvertebrates in a lake.	Simoncelli et al., 2019
	Increased temperatures raised the metabolic rate (oxygen uptake, ammonia excretion, phosphate excretion) of marine microinvertebrates.	Ikeda, 1985

	Greater water viscosity associated with decreased water temperatures considerably lowered the ingestion rates of two freshwater cladocerans.	Loiterton et al., 2004
	Temperatures lower than seasonally occurring in the field (5°C) strongly decreased copepod and ostracod emigration from sediment.	Armonies, 1988
Salinity	Increasing salinity from 6 mg Cl$^-$.L^{-1} to 350 mg Cl$^-$.L^{-1} in a freshwater mesocosm experiment decreased the total abundance of microinvertebrates from ~150 Ind.L^{-1} to 90 Ind.L^{-1}	Sun & Arnott, 2022
	Freshwater *Daphnia* were sensitive to chloride concentrations, with decreased reproduction and increased mortality between 5 and 40 mg Cl$^-$ L^{-1}.	Arnott et al., 2020
	Salinity is a major environmental factor influencing microinvertebrate community composition and population growth rates in freshwater environments. NaCl concetrations negatively affect freshwater zooplankton growth rates from $\geq$ 1.5–3.0 g L^{-1}.	Modenutti, 1998; Sarma et al., 2006
	Raising salinity increased the overall swimming ability of the estuarine calanoid copepod *Eurytemora affinis*. Swimming speed of males increased from ~1 to ~3.25 mm s^{-1}.	Seuront, 2006
	Increasing salinity from 5 to 15–20 psu modified the resting period of the estuarine copepod *Pseudodiaptomus annandalei,* increasing its average swimming speed from 1.8 mm s^{-1} to 2.1 mm s^{-1}. Increasing salinity to 25 psu decreased swimming speed to 1.7 mm s^{-1}.	Michalec et al., 2012
	Prolonged exposure to high salinity (5,000 mg.L^{-1}) decreased the abundance and richness of microinvertebrates emerging from sediment. Though, brief pulses of high salinity may have a positive influence on emergence.	Nielsen et al., 2007
	Overlying water salinities of 4% significantly lowered the emergence of copepods and ostracods from the sediment.	Armonies, 1988
pH	There was no detectable change in the swimming activity of the calanoid copepod *Pseudocalanus acuspes* in response to ocean acidification.	Almén et al., 2017
	Short-term exposure to a pH of 4–5 was lethal to 50% or more of *Daphnia* species (9ladocera). Sub-lethal impacts on Na flux, reproduction and heart rate were observed in the same pH range. The cladoceran *Bosmina longirostris* had a mere 6% mortality at pH 5.0, with surviving individuals showing normal behaviour.	Locke, 1991

	An in situ mesocosm experiment found lowering pH from 8.8 to 4.5 over 23 days resulted in the elimination of acid-sensitive species. Only two small cladocerans (*Bosmina longirostris* and *Chydorus sphaericus*) were acid tolerant.	Havens & Heath, 1989
Light	The reaction of microinvertebrates to changes in light intensity is thought to be the primary physiological mechanism controlling diel vertical migration.	Burks et al., 2002; Cottier et al., 2006; Ringelberg, 1999
	Microcrustaceans (copepods and ostracods) emergence from the sediment is negatively correlated with light intensity.	Armonies, 1988
	DO concentration influenced microinvertebrate community composition. Large cladocerans were dominant in lakes with oxic conditions, whereas rotifers and small cladocerans were dominant in lakes with large oxygen depletion.	Karpowicz et al., 2020
Dissolved oxygen (DO)	Decreasing DO concentrations from 8.9 to 1.2 mg.L^{-1} increased the mean time spent swimming from 5.4 to 13% for the cladoceran *Moina micrura*. Decreasing DO below 1.2 mg.L^{-1} to sub-lethal levels reduced mean swimming time to 6.1%.	Svetlichny & Hubareva, 2002
	Under anoxic conditions, most microinvertebrate taxa were predominantly found in the epilimnion during the day and night and did not exhibit diel vertical migration.	Doubek et al., 2018
	Oxygen concentrations <1 mg.L^{-1} resulted in reduced survival of the copepods *Acartia tonsa* and *Oithona colcarva* and inhibited the hatching of *A. tonsa* eggs. CopepodsCopepods were in low abundance or absent in the bottom waters where oxygen was at its lowest.	Roman et al., 1993
	Critical values of DO have been observed to decrease egg development, egg hatching, filtering, survival and abundance in microcrustaceans (copepods and ostracods).	Ekau et al., 2009 and the references therein

In the lower River Murray, the most abundant microinvertebrates are often the rotifer genera *Trichocerca*, *Keratella*, *Synchaeta* and *Brachionus*. These genera have been found in the guts of larval Murray cod (*Maccullochella peelii*) or Golden perch (*Macquaria ambigua*) (Bice et al., 2023; Ye et al., 2020). Of the rotifer genera, the littoral genus *Trichocerca* has repeatedly dominated the lower River Murray, often peaking in abundance from October–November (Furst et al., 2018, 2019a, 2020). The species *Trichocerca pusilla* is believed to consume the high-quality diatom *Aulacoseira*, which contains high concentrations of long-chain polyunsaturated fatty acids (LC-PUFA). Several international studies have identified *Trichocerca* as an important prey item for copepods (Williamson, 1983), flatworms (Núñez-Ortiz et al., 2022), macroinvertebrate larvae (Chimney et al., 1981), shrimps (Haskell & Stanford, 2006), and fish (Sampson et al., 2009). *Trichocerca* was recently found, through molecular analyses, to be an important component of Murray cod larvae diets in the lower River Murray (Bice et al., 2023). As invertebrates have a limited ability to synthesise some LC-PUFAs, this suggests *T. pusilla* and others that consume *Aulacoseira* are high-quality food sources for higher-level consumers.

The invasive pelagic rotifer *Keratella americana*, first recorded in Australia in 2015 (Ye et al., 2020), has subsequently been detected at high densities in the lower River Murray on multiple occasions (Dornan et al., 2021; Furst et al., 2019b). For example, *K. americana* accounted for approximately a quarter of all microinvertebrates in the lower River Murray in December 2020, reaching densities of 1,100 Ind.L^{-1} in the littoral zone of Lock 5 (Dornan et al., 2021). Dominance of *K. americana* may have considerable trophic consequences in the lower River Murray. Relative to other common rotifers of the same genus (e.g., *K. cochlearis, K. procurva, K. tecta and K. tropica*), *K. americana* is characterised by harder loricae (protective shells) and longer posterior spines, likely making it difficult to ingest and digest (Garza-Mouriño et al., 2005; Gilbert & Stemberger, 1984; Williamson, 1987). Both *Keratella* spp. and *Brachionus* spp. belong to the family Brachionidae and possess hard lorica. Loricate species are suggested to grow in turbulent currents of 20 cm s^{-1} and are therefore better adapted to riverine conditions (Czerniawski & Sługocki, 2017; Furst et al., 2019b; Lair, 2005 and the references therein; Sluss et al., 2008).

The cladoceran *Bosmina meridionalis* is often identified as the most abundant microcrustacean in the lower River Murray. During spring, *B. meridionalis* density is typically between 20 and 60 Ind.L^{-1} (Shiel et al., 1982, Furst et al., 2020), though it has been recorded as high as 220 Ind.L^{-1} during October 2020 (Dornan et al., 2021). *Bosmina merdionalis* is an important food resource for a diversity of animals, including Murray cod, golden perch, and freshwater catfish (*Tandanus tandanus*; Ye et al., 2020). Despite being found in the gut content of Murray cod larvae, *B. meridionalis* was not positively selected for relative to other

microinvertebrates (Bice, et al., 2023). Other common microcrustaceans that form part of numerous fish species diets in the lower River Murray include the cladoceran genera *Daphnia* and *Ceriodaphnia* and both calanoid (e.g., *Boeckella*) and cyclopoid (*Australocyclops*) copepods (Gibbs et al., 2020; Ye et al., 2020). *Daphnia* and *Ceriodaphnia* typically occur in low densities of approximately 10 Ind.L^{-1} or less (Dornan et al., 2021; Furst et al., 2020; Shiel et al., 1982). Similarly, *Boeckella* species occur in densities lower than 10 Ind.L^{-1} (Dornan et al., 2021), though they were observed as high as 27 Ind.L^{-1} at Mannum in 1977 (Shiel et al., 1982).

2.1.2.   Microinvertebrate habitat preference

Microinvertebrate assemblages can be structured by habitat zones. Within rivers, littoral, pelagic and benthic habitat zones are commonly used to group microinvertebrate assemblages. Littoral microinvertebrates are adapted to living on or near the surface of plants. Pelagic microinvertebrates are associated with lentic, open water, whereas benthic microinvertebrates are adapted to occupying the benthos. Given the dynamic conditions in a river, some intermingling of microinvertebrates between the different habitat types occurs. For instance, littoral microinvertebrates may be flushed into the pelagic zone during high flows, and pelagic microinvertebrates may be found in the littoral zone if given enough open water. Of the numerically dominant microinvertebrate genera in the lower River Murray, a majority prefer pelagic habitats, with *Trichocerca* spp. being the only taxon with a littoral preference (see Appendix 1 for habitat preferences). Similarly, numerous sub-adult copepods, principally the naupliar and copepodite stages of cyclopoid and harpacticoid copepods, are considered to have a littoral preference and are subject to being flushed into mainstream flows (Shiel, 1984).

Within rivers throughout the world, including the MDB, rotifers tend to dominate microinvertebrate communities (Furst et al., 2020; Lair, 2006; Shiel, 1984; Shiel & Walker, 1984; Ye et al., 2020). Rotifers are typically more suited to persisting in riverine habitats as they have faster development times and parthenogenesis, allowing them to take advantage of shorter water residence times (WRT). Additionally, small rotifers are less likely to be targeted by planktivorous fish than microcrustaceans (Pourriot et al., 1997 & the references therein). Mesocosm experiments have shown that rotifer populations are less disadvantaged in turbulent waters than microcrustaceans (Sluss et al., 2008; Zhou et al., 2016). Rotifers have been suggested to avoid some of the negative impacts of turbulence as they are smaller than the diameter of turbulent eddies, though research on this topic is scarce and responses are mixed (Horppila et al., 2019; Lair, 2006; Zhou et al., 2016). In contrast, larger microcrustaceans are directly impacted by turbulence via reduced prey detection, prey capture

rates, injuries (Visser & Stips, 2002) and longer development times. Therefore, low turbulence environments with longer WRTs, such as littoral zones, floodplains and slackwaters, favour the development of microcrustaceans over rotifers.

Although longer WRTs tend to favour microcrustaceans, they also have a strong positive relationship with overall microinvertebrate productivity, including rotifers. Therefore, slow-flowing, off-channel habitats represent a major source of microcrustaceans and rotifers in the Basin (Baranyi et al., 2002; Burdis & Hirsch 2016; Obertegger et al., 2007). During high flows, large quantities of microinvertebrates can be washed out of slow-flowing (lentic) habitats and transported downstream into faster-flowing (lotic) riverine habitats, seeding downstream populations (Furst et al., 2014; Furst et al., 2019a; Górski et al., 2013). The existence of littoral and off-channel habitats and the transport of microinvertebrates from lentic to lotic habitats is vital for riverine ecosystems, as the reproduction of microinvertebrates is believed to be limited in water velocities exceeding 40 cm s^{-1} (Rzoska, 1987).

2.2. Microinvertebrate drift dynamics

The primary vectors of long-distance (i.e., over multiple kilometres) microinvertebrate dispersal in riverine systems include wind, animals (e.g. waterfowl) and entrainment in flowing water (i.e., 'drift'). Few studies have investigated the importance of these vectors in riverine environments. Michels et al. (2001) revealed genetic distances between *Daphnia ambigua* populations were more influenced by stream corridors (i.e., continuous aquatic pathways) than geographic distance, suggesting flowing water was the primary dispersal vector. The mechanism that entrains microinvertebrates in water also entrains sediments (Gordon et al., 1992). When water flows around a solid object, a combination of forces (i.e., lift, drag and the acceleration reaction) act upon the object until a critical force is reached and the object is swept away with the currents (Denny, 1988; Hart & Finelli, 1999). Drift is one of the most important transport phenomena in stream ecology, as it allows microinvertebrates (and other biotas with a planktonic stage) to escape predators, colonise new habitats, maintain species and genetic diversity and distribute invertebrates to planktivorous predators (Hayes et al., 2018; Hoover, 1994; Perić et al., 2014). Although drift has been studied in adult and larval macroinvertebrates (e.g., Brittain & Eikeland, 1988; Kennedy et al., 2013; Naman et al., 2016), little research has been conducted on microinvertebrate drift due to the complexity of the topic. The small size of microinvertebrates makes direct observations difficult, particularly for microscopic rotifers. Additionally, variations in the behaviour, size, and habitat of microinvertebrates all have considerable impacts on the likelihood of entrainment, making it challenging to derive critical entrainment thresholds experimentally.

Given microinvertebrate's role as primary consumers and prey for higher trophic organisms, their dispersal in freshwater ecosystems has considerable consequences on river and lake food web dynamics. The maximum dispersal distance of microinvertebrates via flowing water is difficult to predict as several factors may influence drift distance, including organism sinking rates and the degree of turbulent mixing (Hart & Finelli, 1999). *Daphnia lumholtzi* survived a 50 km journey through a pipeline (Eisenbacher & Havel pers. comm. as cited in Havel & Shurin, 2004), though the conditions were unlikely to be representative of natural riverine conditions. During the 20th century, the dispersal of microinvertebrates in flowing water was considered a purely passive process, with microinvertebrate distributions (or 'patchiness') ultimately being a product of physical processes. Undoubtedly, physical processes greatly influence microinvertebrate communities, with some authors emphasising water velocity and substrates overwhelmingly affect their distribution patterns (Palmer et al., 1996; Richardson, 1992; Robertson et al., 1997; Whitman & Clark, 1984). By the turn of the 21st century, viewpoints shifted to acknowledge biological processes (e.g., swimming behaviour) as major contributors to microinvertebrate distributions in aquatic and marine ecosystems (Flierl et al., 1999; Folt & Burns, 1999). Thus, an understanding of the coupled biological-physical interactions of microinvertebrate drift is needed to gain a complete framework of their dispersal. The influence of microinvertebrate swimming behaviour and flow refugia (i.e., areas of reduced water velocity) on drift are often overshadowed by the more straightforward metric of current velocity. Therefore, the following three sections aim to highlight how variations in current velocity impact entrainment rates, and how flow refugia and microinvertebrate behaviour can interact to influence microinvertebrate entrainment.

2.2.1. Microinvertebrate swimming behaviour and entrainment

In isolation, the swimming ability of the most motile microinvertebrate may appear insignificant in the grand scheme of dispersal. However, the accumulated efforts of microinvertebrate swimming can significantly impact sinking rates and, therefore, the distance travelled due to entrainment within the drift. A number of studies have measured the swimming rate of specific microinvertebrate taxa, primarily from the genus *Daphnia*. *Daphnia* typically swim at an average speed of 0.4–0.8 cm s^{-1} (Dodson et al., 1995; Noss et al., 2013). However, *Daphnia pulex* were observed swimming at 2.2 cm s^{-1} over at least one second (O'Keefe et al., 1998) and *D. magna* have an average swimming speed of 1.6 cm s^{-1}, with some individuals exceeding 3.0 cm s^{-1} for 15 seconds (Larsson & Kleiven, 1996). Research has shown sustained swimming by microinvertebrates can result in an increase (Allan & Feifarek, 1995; Ciborowski, 1983; Hart & Finelli, 1999) or decrease (Allan & Feifarek, 1995; Campbell, 1985) in microinvertebrate drift distance. However, relatively little research has been conducted on microinvertebrate entrainment.

Microinvertebrate entrainment can occur passively or actively. Passive entrainment occurs when water velocity or turbulence values exceed critical entrainment thresholds, dislodging microinvertebrates from the surfaces of substrates and causing them to enter the water column (Sidler et al., 2018a). Alternatively, active entrainment is the process whereby organisms intentionally enter the water column in response to environmental cues. Numerous studies have identified greater dispersal distances by organisms during the night (e.g., Karabin & Ejsmont-Karabin, 2005; Lampert, 1993; Rinke & Petzoldt, 2008). For example, drift of copepods and rotifers in a stream increased at night relative to the day (titled 'diel vertical migration'; DVM), providing evidence they have some control over drift entry (i.e., active entrainment) (Palmer, 1992). Increased drift at night is likely a strategy for predator avoidance and resource acquisition, though DVM may also be a behaviour that regulates drift distance. Computer simulations by Pasour and Ellner (2010) suggest DVM can increase the retention time of microinvertebrates under slow-flow conditions, reducing their downstream transport. Similarly, calanoid and cyclopoid microcrustaceans in the St. Lawrence River, USA, drifted significantly more at night, although the increase in nocturnal drifting of cladocerans was not significant (Casper & Thorp, 2007). Interestingly, the potential for microinvertebrates to intentionally enter the drift suggests they possess the ability to avoid entrainment within the drift.

Certain microinvertebrates possess behaviours or morphological traits that could assist in avoiding entrainment or increase their sinking rate through the water column, thereby reducing their drift distance. For instance, differences in the morphology of two similarly sized cladocerans resulted in a 20–45% difference in drag, translating to a 14–16% slower swimming speed for the species with greater drag (Lagergren et al., 2001). Some microinvertebrates regulate drift by employing rheotaxis and swimming with or against the current (Richardson, 1992; Shang et al., 2008; Williamson, 1987). Rheotaxis is the directional movement of an organism in response to a current of water or air. Positive rheotaxis is when organisms orient to face the direction of the oncoming current (Shang et al., 2008), while negative rheotaxis is when they face away from the oncoming current (Richardson, 1992). Positive rheotaxis allows microcrustaceans to actively swim against the current as they sink downward and settle on the sediment, thereby reducing their drift distance. This is seen in the copepod *Eucyclops serrulatus,* which increased its counter-current swimming effort, substantially decreasing its downstream transport in response to increasing water velocity above 4 cm s^{-1} (Sidler 2018b). Similarly, live copepods had significantly shorter drift distances and significantly faster sinking rates than dead copepods when exposed to a flow velocity of 25 cm s^{-1} (Palmer, 1992). In contrast, no significant differences in sinking rates or drift distances were exhibited between live and dead rotifers, suggesting largely passive drifting

behaviour, likely due to their poor swimming ability. For example, the rotifers *Brachionus calyciflorus*, *Keratella cochlearis* and *Synchaeta pectinata* have average swimming speeds of 0.61, 0.5 and 0.817 mm s^{-1}, respectively (Stemberger & Gilbert, 1987), whereas copepods swimming speeds typically reach approximately 5 mm s^{-1} or faster (Svetlichny et al., 2020).

2.2.2. Advective losses of microinvertebrates in drift

Swimming effort and sinking/settling rates can have a major influence on advective losses of microinvertebrates in the drift. Palmer (1990) reported sinking rates of live and anaesthetised copepods to be 2.0 and 1.4 mm s^{-1}, respectively, demonstrating copepods have some control over their vertical distribution. In contrast, live and anaesthetised rotifers exhibited no significant difference in sinking rates, indicating rotifer dispersal is passive. Carcasses of the copepod *Acartia tonsa* revealed an average sinking rate of 1 mm s^{-1} (range ~0.3 to 1.3 mm s^{-1}), with larger individuals sinking faster in a shallow estuary (Elliott et al., 2010). Modelled carcass sinking rates of several microcrustacean taxa in a lake ranged from 0.5 to 1.4 mm s^{-1}, depending on taxa morphology (Kirillin et al., 2012). Using Palmer's (1990) sinking rates, a live copepod would drift approximately 225 m before reaching sediments in the lower River Murray, assuming a constant depth of 3 m and a constant current velocity of 15 cm s^{-1}. However, Palmer's estimates are based on sinking rates in still water and may not be suitable in turbulent riverine environments, particularly for copepods that increase their swimming effort with increasing flow rates. Additionally, estimates may not account for microinvertebrate behaviour, given some may voluntarily re-enter the drift.

In situ trials conducted in Eriksson (2001) observed microinvertebrate biomass and body length decreased as the distance from lake outlets increased. For instance, in one stream with a mean current velocity of 63 cm s^{-1}, microinvertebrate biomass decreased by 74% over 140 m. On the other hand, a separate stream with a mean current velocity of 58 cm s^{-1} only showed a similar decrease in biomass (76%) over a distance of 9 km (Eriksson, 2001). An *in situ* study by Sandlund (1982) found microinvertebrate density decreased by 45% approximately 200 m from a lake outlet, though some were detected 3.4 km downstream; microinvertebrate form and size greatly influenced drift distance. Similarly, the reduction in drifting microinvertebrates per 100 m ranged from 3.4% for *Keratella hiemalis* to 9.4% for *Daphnia longispina*, though these estimates could be heavily influenced by stream morphology, flow refugia and current velocity (Sandlund, 1982). These findings suggest a considerable proportion of drifting microinvertebrates, particularly large-bodied microcrustaceans, settle on substrates within the first several hundred metres of entering a river. However, the ultimate fate of microinvertebrates (e.g., consumed by planktivores, remaining settled on substrates, colonisation of slackwaters or re-entry into the drift) remains largely unquantified.

2.2.3. Flow refugia impacts on microinvertebrate entrainment

Flow refugia in rivers are characterised by low water velocity and turbulence (e.g., littoral zones) and are created when water flowing over the sides and beds of channels generates friction, producing unequal flows across channel cross-sections (Reynolds, 2000). In slow-flowing rivers, water velocity near riverbanks may be negligible. In the lower River Murray, for example, water velocities of 26 cm s^{-1} occur in the middle of the channel while they are ≤3 cm s^{-1} in shallow littoral zones (Gibbs et al., 2020). Microinvertebrates capable of counter-current swimming, such as cladocerans *Daphnia* and *Ceriodaphnia* (Richardson, 1992), could rapidly sink to sediments and resist velocities in flow refuges, thereby avoiding entrainment into the water column (Walks, 2007). The importance of flow refugia for microinvertebrate persistence has been demonstrated by Nielsen et al. (2010), who found significantly greater richness and density of benthic microcrustaceans in artificial slackwaters than in flowing environments in a lowland river of the MDB. Therefore, the occurrence of flow refugia may influence the colonisation, development, persistence, and magnitude of drift of microinvertebrates in a river (Battauz et al., 2017; Debastiani-Júnior et al., 2016; Palmer et al., 1996). However, for the vast majority of microinvertebrate taxa, the water velocity thresholds they can resist in the River Murray are unknown.

Flow refugia often contain physical habitat (i.e., woody debris, rocks, macrophytes, algae) which provide additional refuge against flow and predators. Primary habitats in littoral zones of lowland rivers are large woody debris and emergent macrophytes. Microinvertebrates in dense macrophyte beds have been observed at nine times the density of those in open water in a fluvial lake, indicating macrophyte beds can offer ideal habitat for riverine microinvertebrates (Basu et al., 2000; Bolduc et al., 2016). Epilithic biofilms have been suggested to provide refuge for sediment-dwelling microinvertebrates (Majdi et al., 2012).

After settling on sediments, some microinvertebrates are suggested to reside in the viscous sublayer where turbulence and velocity are considerably reduced or eliminated (Gordon et al., 1992; Silvester & Sleigh, 1985). The viscous sublayer is thickest when water currents are low and streambeds are smooth (i.e., small grain size diameter; Davies, 1986), which is more likely to occur in high-order, lowland streams (Davies & Barmuta, 1989). At current velocities of 5, 10 and 50 cm s^{-1}, the sublayer thickness in a theoretical stream was estimated to be 5.4, 2.7 and 0.54 mm, respectively (Smith, 1975 as cited in Gordon, 1992). Richardson (1992) estimated a flow velocity of <8 cm s^{-1} would generate a viscous sublayer with a width of 0.15–0.20 mm over a smooth surface. Given the thinness of the sublayer, it is unlikely to provide sufficient flow protection for larger invertebrates but may provide refuge for rotifers and small cladocerans and copepods under optimal conditions (e.g., where current velocity is ≤10 cm

s^{-1} within the margin of a river channel). While the viscous sublayer's influence on microinvertebrate entrainment is largely unquantified, it should be considered when investigating velocity thresholds. Additionally, it has been hypothesised that microinvertebrates may move into the interstitial spaces of sediments, using the space as refugium from hydraulic disturbances (Dole-Olivier et al., 1997; Palmer et al., 1992; Stubbington, 2012), though research on this phenomenon is scarce and largely speculative, particular in Australia (Cooling & Boulton, 1993).

2.3. Microinvertebrate critical entrainment thresholds

Relatively few studies have attempted to quantify critical entrainment velocities of microinvertebrates (see Table 2 for a summary). Some of the earliest laboratory experiments investigating critical entrainment thresholds of microinvertebrates were conducted in the 1990s (Palmer, 1992; Richardson, 1992). Richardson (1992) evaluated the ability of microcrustaceans to maintain their horizontal position at several water velocities (2.5, 5, 7.5 and 10 cm s^{-1}) by placing them in a 20 cm gravity-fed transparent flow chamber and measuring the time taken for them to wash out (i.e., caught in drift). Most taxa maintained their position at a water velocity of 2.5 cm s^{-1}, though none withstood 10 cm s^{1} and drifted similarly to a passive particle (Table 2). Cladocerans such as *Daphnia pulex*, *Ceriodaphnia quadrangula*, and *Moina brachiata* were some of the least competent swimmers, withstanding velocities of 2.5 cm s^{-1} for a short time but behaving like passive particles at 5 cm s^{-1}. In contrast, copepods were generally more competent swimmers. *Eucyclops agilis*, a cyclopoid copepod with the greatest swimming ability, withstood velocities of 7.5 cm s^{-1} for a time, but experienced complete washout at 10 cm s^{-1}. In addition, *E. agilis* exhibited active entry into the drift, as individuals allowed themselves to drift at velocities below 2.5 cm s^{-1} and only initiated counter-current swimming at higher velocities (Richardson, 1992). A follow-up in situ experiment found taxa with the weakest swimming ability were most common in low velocity (2 cm s^{-1}) areas, supporting taxon-specific washout velocities (Richardson, 1992). Field experiments corroborated a washout velocity of 2.5 cm s^{-1} for *Bosmina longispina* (Kariesalo & Penttilä, 1990, as cited in Palmer, 1992).

Although Richardson's flow experiment provided valuable information on critical entrainment thresholds of microinvertebrate species, its applicability to natural environments is limited. The 3 cm wide, gravity-fed flow chamber is unrepresentative of non-linear and turbulent flows that dominate in rivers. Furthermore, the lack of complex substrates in the flow chamber is not representative of those found in streambeds. The simple surface may impact the flow resistance of taxa resting on the surface of the flow chamber (e.g., ostracods, *Eucyclops agilis* and *Scapholeberis kingi*). Nevertheless, Richardson's (1992) results were corroborated by

Czerniawski (2012) in an agricultural stream and Czerniawski and Sługocki (2017) in constructed ditches.

Czerniawski (2012) sampled microinvertebrate communities along a small, fishless stream and its tributaries and found *Daphnia pulex* could resist flows of 1 cm s^{-1}, with the highest densities found in current velocities between 1.7–2.7 cm s^{-1}. No *D. pulex* were found in the main channel where the current velocity was 3.5 cm s^{-1}, indicating an inability to resist and persist in higher velocities. In contrast, adult copepods were found in velocities ranging from 1.6–8.1 cm s^{-1} and juvenile copepods were abundant at all sites, indicating they were reproducing. Czerniawski and Sługocki's (2017) use of artificial ditches found microinvertebrate abundance decreased considerably when current velocities exceeded 10 cm s^{-1} (Figure 2; Table 2). Some taxa (*Daphnia*, *Scapholeberis*, cyclopoids) studied by Richardson (1992) were observed in low abundances in ditches with current velocities exceeding 10 cm s^{-1}. The authors posit that the availability of flow refugia, flow avoidance behaviour and use of benthic habitat may explain their ability to avoid being completely washed out of the ditch.
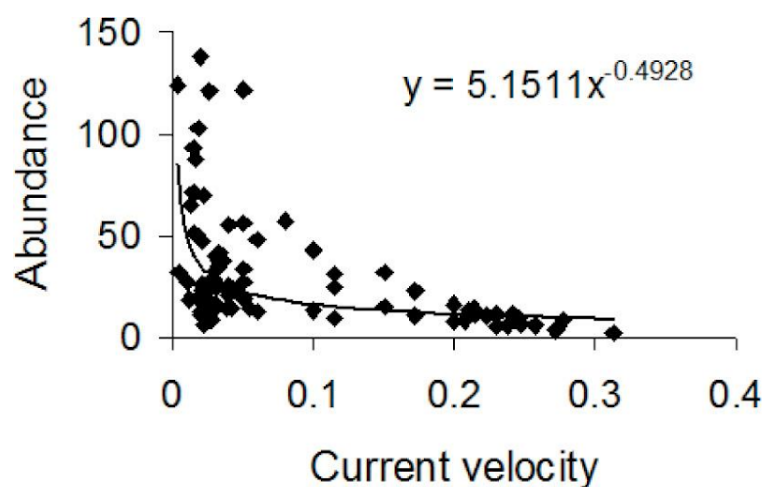
Figure 2. Relationship between current velocity (m s^{-1}) and abundance of microinvertebrates (Ind.L^{-1}). From Czerniawski and Sługocki (2017), licensed under CC BY-NC-ND 4.0.

Palmer (1992) estimated critical entrainment thresholds of live and dead microinvertebrates by exposing box cores of fresh stream sand and microinvertebrate communities of unknown composition to increasing flows (0–20 cm s^{-1}) in a flume over two minutes. Critical entrainment thresholds were visually approximated as the velocity where the number of drifting individuals "rapidly" increased (Figure 3). All live and dead taxa used in the study (rotifers, copepods, chironomids, oligochaetes) had an average critical entrainment velocity between 9–13 cm s^{-1} (Table 2). Live and dead copepods had an approximate mean entrainment threshold of 11.5

cm s^{-1} and 9.5 cm s^{-1}, respectively (Figure 3). Interestingly, rotifers had a higher entrainment threshold than copepods, averaging approximately 12.8 cm s^{-1} and 10.5 cm s^{-1} for live and dead individuals, respectively. The considerably higher thresholds than those reported by Richardson's (1992) flow chamber experiment, are likely due to the different methods used. The hydrodynamic environment (e.g., turbulence) likely differed between the two studies due to the different apparatus (flume versus flow chamber), substrates (sand versus plastic) or approaches to generating flow (pump-driven versus gravity-fed).
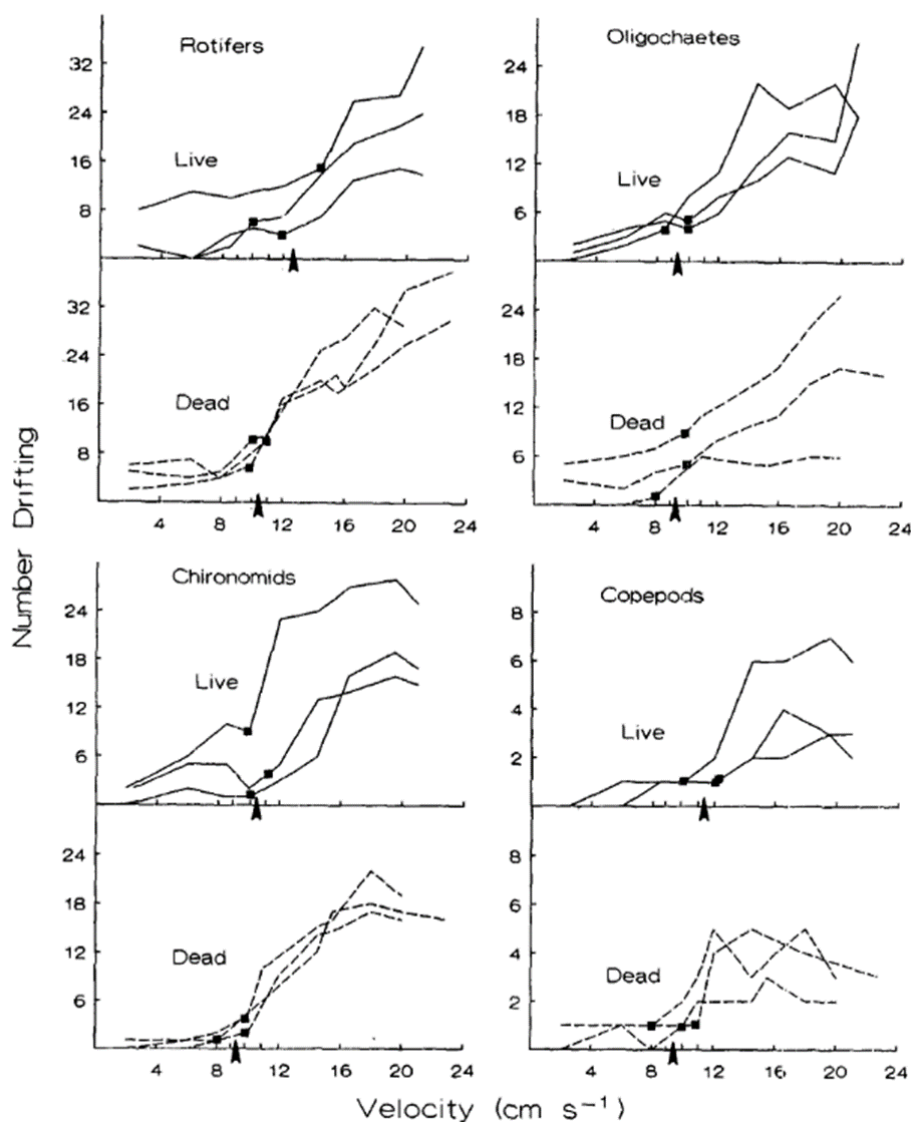
Figure 3. Number of drifting live (top) and dead (bottom) meiofauna (rotifers, copepods, oligochaetes and chironomids) captured from the drift after exposing three replicate box core sediments to various current velocities (cm s^{-1}). Critical entrainment velocities (black square) were visually estimated as the velocity at which drift magnitude began to increase most dramatically. Arrowheads on the x axis represent the mean entrainment velocity for all replicates (Palmer, 1992). Used with permission from John Wiley and Sons © 1992, by the Association for the Sciences of Limnology and Oceanography, Inc.

Majdi et al. (2012) sampled the density of rotifers dwelling in in situ epilithic biofilms under various current velocities (4–62 cm s^{-1}; Figure 4) to visually estimate a critical entrainment threshold of approximately 30 cm s^{-1}, considerably higher than the 9–13 cm s^{-1} reported by Palmer (1992). In velocities beyond 30 cm s^{-1}, rotifer densities reduced to on average 60.6% of that found below 30 cm s^{-1}. Most rotifers in their study (*Bdelloidea* and *Proales* spp.) possessed adhesive pedal glands that secrete cement, allowing temporary attachment onto substrates which may have assisted in resisting flows. This suggests biofilms are important refugia for some drifting microinvertebrates and may represent a critical source of colonising microinvertebrates. While a high velocity may prohibit microinvertebrates from remaining on sediment surfaces, it does not necessarily prevent certain microinvertebrates from colonising environments in sediments. For example, microinvertebrates were able to rapidly colonise the top 10 cm of substrate in artificial streams at current velocities of 11–12 cm s^{-1} (Smith & Brown, 2006), with the fastest flowing streams had some of the highest densities of meiofauna (including microinvertebrates) of all artificial and reference streams.
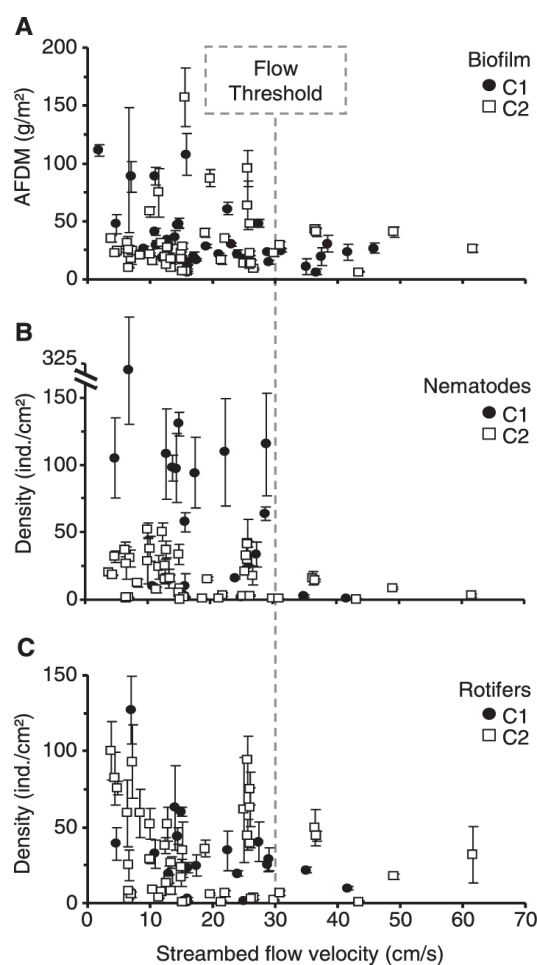
Figure 4. Mean ash-free dry mass (AFDM) of (A) epilithic biofilm, (B) mean density of biofilm-dwelling nematodes and (C) rotifers relative to streambed flow velocity during two sampling campaigns (C1 and C2). Vertical dashed line indicates the visually approximated critical entrainment threshold (Majdi et al., 2012). Used with permission from University of Chicago Press - Journals © 2012.

These studies arbitrarily estimated critical entrainment thresholds by visually approximating "rapid" changes in the magnitude of drifting microinvertebrates. In contrast, Gibbs et al. (2020) sampled microinvertebrates in the lower River Murray during an in-channel flow pulse and created a statistical relationship between hydrological/hydraulic variables and the density of *Trichocerca* spp., a genus of littoral rotifer. When the littoral zone was engaged by the rising limb of the in-channel flow pulse, the best-fit water velocity (>20 cm s^{-1}) explained 37% of the variation in *Trichocerca* density. The channel water level was a slightly better predictor, explaining 55% of the variation in density. The inundation of previously dry sediments and subsequent hatching of individuals from the egg-bank likely explains the superior predictive power of water height. However, when there was little to no engagement of the littoral zone, (representative of weir pool lowering), best-fit water velocity (>15 cm s^{-1}) explained 67% of the variation in *Trichocerca* density, whereas water level explained 23% of the variation. Regardless of littoral zone engagement, a combination of water velocity and height consistently increased predictive power, explaining as much as 75% of *Trichocerca* density during the rising limb of the in-channel pulse. While no single entrainment threshold was obtained, this study shows engaging the littoral zone through increased water levels and maintaining an average cross-sectional current velocity of 15–20 cm s^{-1} is beneficial to the entrainment and downstream transport of *Trichocerca* spp. In the lower River Murray.

Table 2. Observed or inferred critical entrainment velocities for various microinvertebrate taxa using various methods.

Taxa	Entrainment velocities	Method	Source
Rotifer spp.	~12.8 cm s^{-1}	Flume with sand substrate	Palmer, 1992
Rotifer spp.	~30 cm s^{-1}	Biofilm-dwelling in situ	Majdi et al., 2012
Trichocerca spp. (rotifer)	15–20 cm s^{-1}	Derived statistically from in situ measurements	Gibbs et al., 2020
Total microinvertebrates	10 cm s^{-1}	In situ *d*rifting microinvertebrates in man-mad ditches	Czerniawski, 2012
Copepod spp.	~11.5 cm s^{-1}	Flume with sand substrate	Palmer, 1992
Eucyclops agilis (cyclopoid copepod)	>7.75 cm s^{-1}	Flow chamber with no substrate	Richardson, 1992
Diaptomus sp. (calanoid copepod)	>2.5 cm s^{-1}	Flow chamber with no substrate	Richardson, 1992
Daphnia pulex (cladocera)	>2.5 cm s^{-1}	Flow chamber with no substrate	Richardson, 1992
Daphnia pulex (cladocera)	≤3.5 cm s^{-1}	Man-made ditch in situ	Czerniawski and Sługocki, 2017
Ceriodaphnia quadrangula (cladoceran)	>2.5 cm s^{-1}	Flow chamber with no substrate	Richardson, 1992
Scapholeberis (cladoceran)	>3.2 cm s^{-1}	Flow chamber with no substrate	Richardson, 1992
Moina brachiata (cladoceran)	2.5 cm s^{-1}*	Flow chamber with no substrate	Richardson, 1992
Diaphanosoma brachyurum (cladoceran)	2.5 cm s^{-1}*	Flow chamber with no substrate	Richardson, 1992
Bosmina longispina (cladoceran)	2.5 cm s^{-1}	–	Kariesalo and Penttilä, 1990, as cited in Palmer, 1992
Ostracod spp.	>2.5 cm s^{-1}	Flow chamber with no substrate	Richardson, 1992

*Individuals exhibited washout times almost as slow as passive particles.

2.4. Conclusion

The critical entrainment velocities of the microinvertebrate taxonomic groups presented here range from 2.5 cm s^{-1} for cladocerans in a flow chamber with no substrate to 30 cm s^{-1} for rotifers within biofilms. Entrainment velocities of microinvertebrates are greatly influenced by species-specific swimming ability, behaviour, body size, substrate, flow refugia and the physicochemical parameters of water. Therefore, in deriving critical entrainment thresholds, it is critical that the selected methodological approaches accurately represent or account for the above factors in the context of the target ecosystem. The following section (Section 3) considers these requirements and presents a series of experimental designs appropriate for examining critical entrainment thresholds for microinvertebrates in the lower River Murray.

3. METHODS REVIEW AND EXPERIMENTAL DESIGNS

3.1. Background

For over two centuries, the study of microinvertebrates has been a steadily evolving discipline (Bandara et al., 2021). As our understanding of hydrodynamics and technology has advanced, so too have the techniques employed to investigate the dynamics of microinvertebrate communities. Microinvertebrate density (or abundance) has perhaps been the most studied variable in microinvertebrate research. However, research into critical entrainment thresholds of microinvertebrates remains notably sparse. Thanks to technological advancements, novel methods for monitoring microinvertebrates and their interactions with hydraulics have emerged. These include the use of flumes (Palmer, 1992), laser diffraction (Szeligowska et al., 2020), and acoustic tracking (Genin et al., 2005). Yet, these innovative approaches are often tailored to the specific needs of individual studies. In contrast, traditional methods of monitoring microinvertebrate density (i.e., manual enumeration via microscopy) may remain the most robust, albeit time-consuming, methodology in some cases. Therefore, the aim of this review is to (1) showcase the array of potential methodologies for estimating the critical entrainment thresholds of microinvertebrates in both laboratory and natural stream settings; (2) discuss the strengths and limitations of each method, and finally; (3) develop costed experimental designs appropriate for the study area and purpose.

3.2. Field experiments and monitoring

Monitoring microinvertebrates in natural streams offers several advantages over laboratory experiments, the most notable being the hydraulics and substrate represent a natural stream. Unlike laboratory experiments, the data gained from an *in situ* experiment are at a scale relevant to water managers, making it easier to apply the results in the lower River Murray. Field experiments remove the need to source and culture microinvertebrates, potentially saving a great deal of time and effort. However, the impact of upstream effects and uncontrollable environmental variables can limit field sampling. The number of entrained microinvertebrates at a location is not wholly dependent on the hydraulics in the immediate vicinity; hydraulic conditions upstream may have dislodged microinvertebrates hundreds of metres away from the sampling site. In addition, water quality, microinvertebrate reproduction and food availability may influence the density of microinvertebrates in a natural river, introducing scatter into the data. Subsequent sections will discuss the strengths and limitations of portable flumes and direct water column monitoring.

3.2.1. Portable flumes

Laboratory flumes that control the current velocity are excellent resources for investigating fundamental hydraulic research questions, though applying research outcomes to natural environments can be difficult. Portable flumes can modify current velocity over a natural section of streambed by constriction or expansion. Gibbins et al. (2016) used a portable flume to increase hydraulic forces over a stretch of riverbed by expanding a set of hinged doors upstream of the flume and funnelling water through a gap to create a high-velocity jet over the streambed. Water velocity in the flume was measured and a net at the downstream end of the flume captured entrained macroinvertebrates. However, alongside the macroinvertebrates entrained from the sediment below the flume, the water entering the flume mouth will inevitably contain drifting macroinvertebrates. To account for drifting macroinvertebrates, a drift net is placed as close to the upstream end of the flume (2 m) as possible without reducing the water velocity in the mouth of the flume. The number of macroinvertebrates captured upstream is subtracted from the total number of macroinvertebrates captured at the exit of the flume and used to estimate the number of macroinvertebrates entrained in the flume streambed. Shear stress and mean column velocity explained the most deviance in drifting macroinvertebrates (32.1% and 31%, respectively) (Gibbins et al., 2016). In contrast, the same portable flume used in similar hydraulic conditions found shear stress ($N\ m^{-2}$) explained 73% of the variation in drifting macroinvertebrates (Gibbins et al., 2010). Variations between the time of sampling (day vs night) and sampling location (different streams) are likely the primary explanations for the different magnitude in drift response between the two studies.

Portable flumes must compromise between practicality and achieving ideal hydrodynamics. For instance, the studies using portable flumes do not quantify the number of macroinvertebrates residing on the streambed before modifying flows. Furthermore, the drift net 2 m upstream of the flume, while intended to estimate the number of macroinvertebrates entering the flume, may reduce the macroinvertebrates that reach the flume, overestimating the number of entrained macroinvertebrates. Gibbins et al. (2007) found after releasing macroinvertebrates 10 cm above the streambed, 66% settled on the bed within 1 m of transport, suggesting a drift net 2 m upstream would not significantly impact the macroinvertebrates entering the flume under their specific hydraulic circumstances. However, this assumption likely doesn't apply to microinvertebrates which may drift considerably farther than macroinvertebrates. Finally, research on a portable flume modified from Schanz et al. (2002) found flow manipulations via constriction or expansion likely produce secondary flows (Jonsson et al., 2006). Secondary flows impact turbulence experienced by the benthos and may be responsible for the lack of a developed boundary layer. However, portable flumes used in shallow tidal environments may have naturally deviated from logarithmic velocity

profiles due to unsteady or oscillatory flow (Jonsson et al., 2006). Nevertheless, the limitations of portable flumes may be a suitable compromise for the advantages gained from sampling a natural stream.

3.2.2. Water column monitoring: Traps, pumps, acoustics, and optics

A simpler approach to investigating entrainment thresholds involves directly sampling microinvertebrates entrained in the water column and establishing a statistical relationship between river hydraulics and the magnitude of microinvertebrate entrainment. Currently, no standard methods for sampling microinvertebrates in rivers exist, though Wiebe and Benfield (2003) detail 164 different microinvertebrate sampling systems. Some of the most common sampling approaches for aquatic systems include drift nets, Haney traps, and pumps. Drift nets can be towed by a boat or fixed in position by stakes (Field-Dodgson, 1985), buoys or anchors (Reichard & Janáč, 2016). Flow meters attached to nets measure the volume of water filtered through. Towed nets should be avoided because the fine mesh nets make the volume of water filtered difficult to estimate, and the number of microinvertebrates captured may be excessively high (Sluss et al., 2014). Similarly, drift nets deployed for hours can capture exceptionally large numbers of microinvertebrates, which takes considerable effort to quantify, particularly when taking multiple samples. Mesh size and stream condition must be carefully considered to strike a balance between capturing the smallest microinvertebrates of interest and avoiding clogging the net. Palmer (1992) observed that, relative to a drift net with a mesh size of 44 μm, a finer mesh size of 20 μm quickly clogged and did not capture significantly more microinvertebrates. Haney traps are commonly used to investigate the microinvertebrate communities of the lower River Murray and associated floodplains (e.g., Furst et al., 2019c; Ye et al., 2016). They are containers (typically ~4 L) with hinged doors that are manually closed after being lowered into water, allowing selective sampling of the water column. Powered pumps, another sampling technique, collect a predetermined volume of water throughout the water column (e.g., Nielsen et al., 2010). The pumped water passes through a fine net (typically 44–63 μm mesh) which is rinsed to concentrate the sample, and the volume of filtered water is automatically measured or pumped into a calibrated container. Pumps exceed traps and nets in terms of microinvertebrate sampling abundance and replicability (Appel et al., 2019). Sluss et al. (2014) advised manual bilge or battery-powered diaphragm pumps should be used rather than impeller pumps which may damage microinvertebrates, making taxonomic identification difficult.

Once microinvertebrates are identified and enumerated, their abundance can be modelled against hydraulic conditions at the time of sampling to infer critical entrainment thresholds. Hydraulic conditions can be directly measured in the field alongside microinvertebrate

sampling or can be later estimated using hydraulic models. For instance, Gibbs et al. (2020) explained 75% of the variation in drift densities of the littoral rotifer *Trichocerca* (sampled using 4 L Haney traps) by modelling upstream hydraulic conditions. However, obtaining similar estimates of upstream hydraulics through direct in situ measurements could be prohibitively laborious if performed over several kilometres.

Optical Plankton Counters (OPCs) or Laser-Optical Plankton Counters (LOPCs) offer an alternative to directly sampling microinvertebrates with nets or traps. The counters measure microinvertebrates when they pass in front and occlude a beam of light, allowing their cross-sectional area to be measured. OPCs have monitored microinvertebrate communities in marine environments, though in situ use in turbid riverine environments is limited (Moore & Suthers, 2006). The capability of OPCs to gather high spatial and temporal resolution data on microinvertebrates is promising for laboratory applications such as racetrack flumes. However, due to their large size OPCs would influence the hydrodynamics in racetrack channels, though their impact on microinvertebrate entrainment can be minimised if placed downstream of a test area. Modern LOPCs detect small particles from 0.075–1.920 mm equivalent spherical diameter (Scofield et al., 2020), allowing measurement of small rotifers. When using LOPCs, microinvertebrate concentration should be carefully considered due to the risk of two particles occluding the laser beam simultaneously, resulting in a single measurement. OPCs are highly specialised and expensive while offering little advantage over classical methods (e.g., pumps and manual enumeration) in river and laboratory settings.

The movement of microinvertebrate populations can be measured acoustically using Acoustic Doppler Current Profilers (ADCP), which are primarily used to measure current velocities. ADCPs use transducers to transmit sound waves into the water column. The sound wave is reflected off particles back to the transducer. The shift in sound frequency due to the Doppler effect is proportional to the current velocity along the path of the sound wave. This feature allows ADCPs to be used in bioacoustics, as the magnitude of acoustic backscatter is proportional to the concentration of microinvertebrates in the water column. To interpret backscatter, the ADCP must be calibrated against known abundances of microinvertebrates, achieved by sampling the water column using classical methods (i.e., traps and pumps). To discern the taxonomy and size of microinvertebrates, multiple frequencies (typically between 150–614 kHz) must be calibrated, which can be laborious in highly diverse microinvertebrate communities.

Many studies have investigated diel vertical migration (DVM) of microinvertebrates in marine and coastal environments (e.g., Cisewski et al., 2010; Record & de Young, 2006; Smeti et al., 2016) and freshwater lakes (e.g., Lorke et al., 2004; Rinke et al., 2009) using ADCPs. There

is a distinct absence of DVM studies in rivers due to concerns about instrument accuracy. In marine environments, unless there is a high suspended sediment load, strong turbulence, or extreme salinity gradients, it can be assumed backscatter is due to microinvertebrates (Sindlinger et al., 2005). In the River Murray, however, where turbulence and high loads of suspended sediments at times characterise the water column, this assumption cannot confidently be made, limiting the effectiveness of the bioacoustic capability of ADCPs. Additionally, the use of ADCPs in laboratory settings is limited because the number of microinvertebrates needed to generate backscatter may be prohibitively large. For example, Palmer's (1992) flume entrainment study had a maximum of 34 rotifers and seven copepods drifting at any time, representing an extremely small volume of microinvertebrates to generate backscatter. Therefore, acoustic methods are currently limited in the study of critical entrainment thresholds of microinvertebrates in the flowing waters of the lower River Murray.

3.3. Laboratory experiments

The measurement of microinvertebrate entrainment thresholds can take many forms in a laboratory setting. All approaches can be simplified into two distinct parts: (1) the generation of a water current and (2) the measurement of microinvertebrates entrained in the water column, sampled via nets or pumps downstream of the test area. Using a laboratory approach allows for easy control of environmental conditions and the elimination of upstream impacts that may influence microinvertebrate entrainment. Furthermore, it allows for relatively easy replication and the possibility of studying a single taxon in isolation. Unlike in situ experiments, laboratory experiments are inherently less representative of the natural environment and require the use of specialised flow apparatuses. The selection of the most appropriate flow apparatus should be of primary concern, as it will dictate the flow characteristics of the water and how microinvertebrate density can be measured. One of the most established techniques of generating flow in the laboratory involves using flumes. A standard flume design does not exist, with specifications varying depending on the research aims.

3.3.1. Straight flumes

Straight flumes are inclined channels in which water flows to a downstream test area under the influence of gravity and/or pumps to a downstream test area (e.g., Figure 5). A flume can be used to create and investigate specific water velocities or reproduce a river channel's more complex form and function in a scaled-down laboratory setting. Flumes designed to imitate the complex nature of a river channel may reproduce both the Reynolds number (determining behaviour and characteristics of viscous flows) and Froude number (representing free-surface effects in systems where gravity influences flow) of the environment of interest (Gomez, 1978). Reproducing both the Froude and Reynolds numbers of the lower River Murray (e.g., as

measured by Bice et al., 2016) would allow a more accurate simulation of natural bottom and near-bottom flow conditions under a range of flow velocities. However, the hydrodynamic character of the lower River Murray varies along its length, and careful consideration should be given to what section of the river should be replicated in a flume experiment. Furthermore, the flume must be sufficiently long to develop a turbulent boundary layer that is representative of natural riverine environments. The boundary layer is a transitional zone between slow-flowing water at the surface of substrates and the free-flowing water layers higher in the water column. Jonsson et al. (2006) reported a straight flume of 170 cm was sufficient for a boundary layer to develop.

Flumes are well-established in the study of hydrodynamics and benthic ecology. For instance, flumes have been employed to study sediment transport (Bouma et al., 2007), the response of macroinvertebrates to flow disturbances (Lancaster et al., 2006), the dislodgement of micro- and macroinvertebrates from sediments (Blanckaert et al., 2013; Palmer, 1992) and substrate selection of invertebrate larvae (Olivier et al., 1996). Artificial habitat (i.e., wood & cobbles) has been used in straight flumes to determine how dispersal and habitat impact macroinvertebrate community structure (Brown et al., 2018). Flumes vary in design, depending on the hypotheses being tested or financial or engineering constraints. Typically, straight flumes come in two designs: (1) flow-through (water is not reused after exiting the channel) (e.g., Childers & Day, 1988) or (2) recirculating (water can be pumped back into the flume; e.g. Aberle, et al., 2003; Scheingross & Lamb, 2016). Flow-through flumes are simpler to construct but require a far larger volume of water to operate than recirculating flumes. The two most important design considerations for both flume types are the entry and exit conditions for the water (see Nowell & Jumars 1987 for more detail). In brief, water pumped at the inlet of the flume has large-scale turbulence that is not representative of natural flows. Baffle elements/collimators (e.g., diffusers, honeycomb structures and perforated grids) can be placed after the inlet to dissipate large-scale turbulence while permitting small-scale turbulence (Muschenheim et al., 1989). The exit conditions (and supply rate) will determine the depth of flow, which can be controlled by installing a weir at the outlet of the flume channel or by the degree of flume incline. Given these conditions can be easily modified, the simulation of natural flows in flumes can be easier than other laboratory methods, explaining the prevalence of flume experiments in the testing of biological-hydrodynamic interactions.
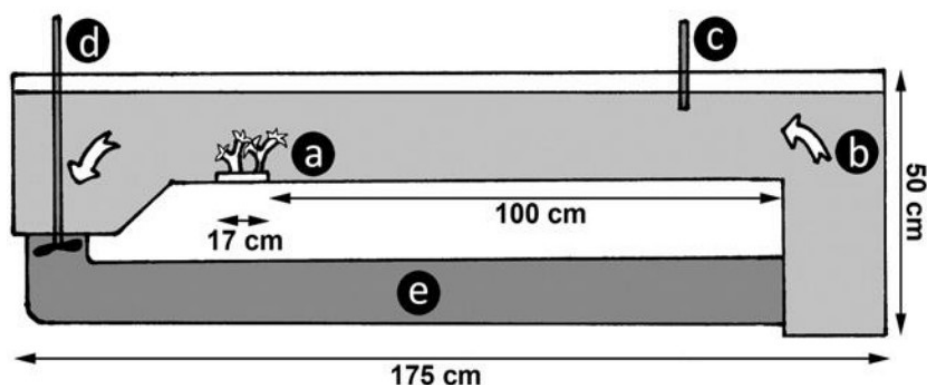
Figure 5. Example of a recirculating straight flume, showing (a) the test section with target organism (coral), (b) direction of circulation, (c) food delivery point, (d) motor propellor to generate flow and (e) a plastic return pipe (Mueller et al., 2014). Licensed under CC BY 3.0.

Straight flumes have been used to test benthic microinvertebrate entrainment thresholds. For example, Palmer (1992) used a plexiglass flume (550 cm long, 35 cm wide, 6 cm water depth) with a box core insert for sediment samples to test microinvertebrate entrainment thresholds. Box cores of fresh stream sand were inserted 450 cm downstream of the flume entrance (far enough to experience undisturbed flow) and exposed to increasing water velocities (0–20 cm s^{-1} in 2 cm s^{-1} intervals). Azoic sand was placed upstream and around the box cores. Drift nets (44 µm) at the exit of the flume captured drifting microinvertebrates entrained from the box core. Entrainment thresholds were visually estimated as the velocity whereby the number of drifting microinvertebrates "rapidly" increased. The construction of the flume was not described in detail (i.e., presence of baffle elements), nor were Reynolds or Froude numbers calculated. The exclusion of this information decreases reproducibility and makes it difficult to apply the results to the natural environment. Nevertheless, the design used by Palmer (1992) represents a simple and economical approach to determining entrainment thresholds.

To video track the counter-current swimming of copepods over a range of velocities (1.2– 6.7 cm s^{-1}) Sidler et al. (2017; 2018a) used a small (200 cm long, 27 cm wide) recirculating acrylic glass flume. Discharge was regulated via a valve and flow metre, with uniform flow conditions achieved through a combination of bricks, voluminous meshes and perforated plates at the inlet and outlet of the flume. Flow velocity, and Reynolds and Froude numbers could be calculated, and the investigation volume was located sufficiently downstream of the inlet and outlet for a defined logarithmic velocity profile (i.e., boundary layer) to develop – a feature representative of natural rivers. Although this study aimed to investigate the swimming behaviour of copepods, the design could be adapted to quantify entrainment thresholds.

To summarise, straight flumes are a well-established, relatively cheap, and an easily customised technique to replicate specific aspects of natural stream hydrodynamics.

3.3.2. Racetrack flumes

Racetrack flumes are an alteration of the straight flume design discussed in Section 3.3.1. Racetrack flumes are typically recirculating, with two straight channels joined at each end by semicircular curves, allowing for the continuous flow of water (Figure 6). Current is generated in one straight channel (typically by a belt drive, paddle, or pump; Jaeger et al., 2021) while a section in the opposite channel (i.e., the working channel) is designated as the 'test area'. Like straight flumes, there are established experimental designs for racetrack flumes, having been used to investigate larval dispersal and settlement (Glas et al., 2017; Tamburri et al., 1996), sediment deposition and resuspension (Beaulieu et al., 2005), availability and clearance rate of suspended food particles (Finelli & Sumerel, 2014; González-Ortiz et al., 2014) and copepod behaviour (Robinson et al., 2007). Racetrack flumes have been designed with sloped and vertical walls to create gradients in water current and depth, mimicking the morphology of natural rivers (Zens et al., 2017).
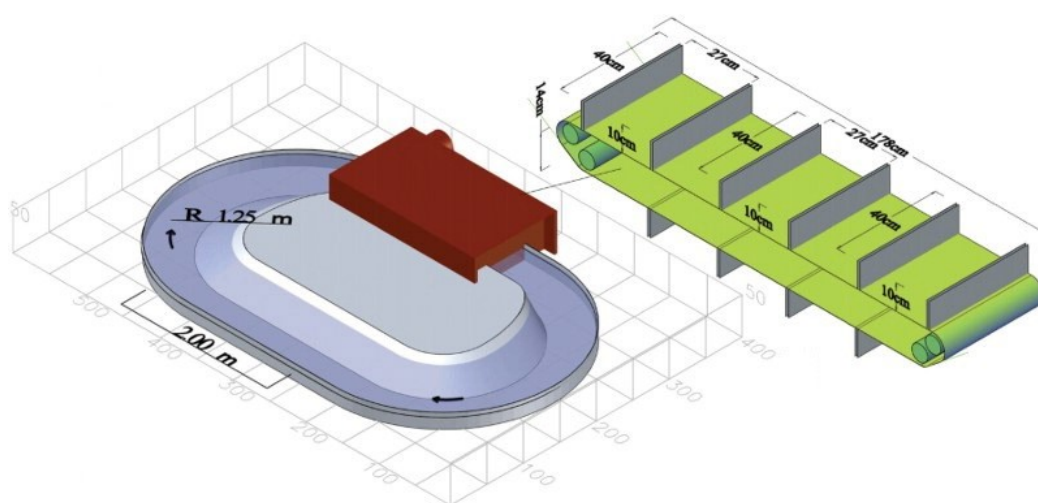
Figure 6. Example of a racetrack flume, including an enlarged 3D model of the belt-drive (green) used to generate flow (modified from Farhadi et al., 2017). Licensed under CC BY 4.0.

Similar to straight flumes, 'smooth' flow can be created by inserting perforated grids upstream and downstream of the study area/paddle belt (Conti-Jerpe et al., 2022; Robinson et al., 2007). To straighten flow and reduce across-stream motion (i.e., secondary flows) through the semicircular turns, a series of vanes are placed in the bend parallel to the flume walls (Robinson et al., 2007; Tamburri et al., 1996). Water is constantly recirculated in the system

by a device that does not require an external tank or harm microinvertebrates, as demonstrated by Clarke et al. (2009) in a 50 cm racetrack flume with a 5 cm thick grid of 1 cm^2 squares to straighten flows downstream of the paddle. A similar racetrack design was used to test the clearance rate of rotifers by corals (Conti-Jerpe et al., 2022). Neither Clarke et al. (2009) or Conti-Jerpe et al. (2022) investigated bedload (i.e., movement of particles along the substrate) or suspended load (i.e., movement of particles suspended in water) transport. Thus, the authors did not attempt to recreate natural hydraulic conditions or allow microinvertebrates to settle on the substrate. To effectively examine critical entrainment thresholds of microinvertebrates, animals should be added (either free-swimming or via box core) to the test area of the racetrack flume and be allowed to settle under no-flow conditions. Water velocity should be gradually increased and the abundance of drifting microinvertebrates sampled via a pump or drift net downstream of the test area.

The size of racetrack flumes range from 45 cm (Conti-Jerpe et al., 2022) to > 17 m (Dijkstra et al., 2006). Longer flumes are assumed to be more capable of developing boundary layers representative of natural riverine environments. A review of the hydrodynamic characteristics of twelve flumes of four designs, including straight and racetrack, concluded straight and racetrack designs are appropriate for investigating the bedload transport of organisms (Jonsson et al., 2006). The large racetrack flume (17.55 m long, 0.60 m wide) at the Netherlands Institute of Ecology was particularly performant, with a current generated by a belt drive that could reach 40 cm s^{-1} (Dijkstra & Uittenbogaard, 2010). The flume possessed collimators (i.e., baffle elements) that acted as a low-band filter to cut out large-scale eddies and semicircle vanes at each bend, and the test area located downstream of the working channel, allowing an adequate boundary layer to develop. However, even small racetrack and straight flumes (e.g., approximately 170–300 cm) were sufficient for boundary layers to develop, largely as a result of the collimators and propulsion generators (e.g., paddles and propellers; Jonsson et al., 2006). Given appropriate baffle elements are included, flumes as small as 170 cm may be sufficient for studying the transport of small organisms. In addition to easier construction, smaller flumes reduce the volume of water and the number of microinvertebrates needed, further simplifying the investigation.

The compact and straightforward design of recirculating racetrack flumes allows for cheap construction and operation, and the hydrodynamics can be easily modified through vanes and perforated grids. Like straight flumes, they can be modified to receive box cores for an accurate investigation into the transport of microinvertebrates.

3.3.3. Annular flumes

Annular flumes (sea carousels) are circular channels that generate flow via the rotation of a lid (e.g., Figure 7). This design lacks an entrance to the 'test area', producing a theoretically infinite test area and eliminating entry and exit conditions. Though less commonly used than straight and racetrack flumes, annular flumes have been used to investigate sediment erosion and deposition (Glasbergen et al., 2015; Stone et al., 2008), the impact of bivalves on sediment resuspension (Widdows et al., 1998), habitat selection of juvenile crabs (Hedvall et al., 1998) and copepod consumption rates by filter feeders (Bartsch et al., 2013). It has been argued that the constant channel geometry and infinite flow length should result in a fully developed boundary layer – a prerequisite when investigating bed erosion (Amos et al., 1992). However, the curvature of tanks and the rotation of lids produces centrifugal forces resulting in the generation of secondary flows, which are considered a major disadvantage of annular flumes. Secondary flows are theorised to be responsible for the undeveloped boundary layers observed in the two annular flumes analysed by Jonsson et al. (2006). To reduce secondary flows, tanks (i.e., the bottom and side walls) can be rotated in the opposite direction of lids, creating a 'rotating annular flume'. Although secondary flows are not eliminated entirely, rotating annular flumes have well-defined boundary layers (Hunt, 2004), making them ideal for erosion studies without the need for collimators. However, consideration must be given to correctly optimise the rotation ratios of the lid and tank (Yang et al., 2000; Yang et al., 2015). Microinvertebrates could be added, allowed to settle, and exposed to increasing flow velocities. Critical entrainment velocities could be estimated by sampling a small volume of the water column and quantifying the number of drifting animals. However, creating a rotating annular flume poses a serious engineering challenge relative to other flume designs, which may outweigh the benefits for studies with limited resources.
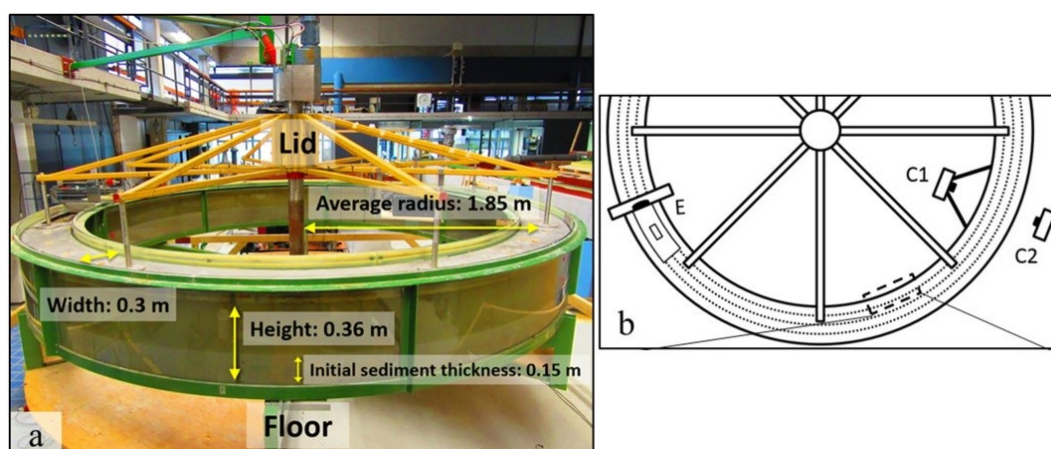
Figure 7. (a) Example of a rotating annular flume. The floor and sidewalls are attached and rotate; the lid rotates independently in the opposite direction. (b) top-view schematic of the flume channel showing cameras (C1 and C2) to capture the morphological development of the channel (modified from Baar et al., 2017). Licensed under CC BY-NC-ND 4.0.

Several studies have taken inspiration from annular flumes and created a simplified design involving a circular tank with a smaller, cylindrical insert placed in the centre to build a circular channel. Sluss et al. (2008) were able to generate circular flow at 6.4 cm s^{-1} and 32 cm s^{-1} using a 1,600 L tank, a 208 L barrel insert, and a series of pumps. Microinvertebrates were sampled via a manual bilge pump and manually enumerated. Kynard et al. (2014) used a more complicated design to test the dispersal of larval and juvenile fish. Circular tanks (1.6 m diameter) with a porous centre insert were used to generate flow (up to 40 cm s^{-1}). The porous insert was offset from the centre, and various velocity shelters (e.g., rocks) were used to create habitat variation in the channel. Fish dispersal was measured using a camera that tracked the number of upstream and downstream passes, whereas habitat use was measured by visual inspection (Kynard et al., 2014). Vertical velocity profiles were not measured in either experiment, though Kynard et al. (2014) state years of experiments have suggested the shape and size of the flume did not impact downstream movement patterns of target fish species. However, secondary flows produced by circular channels have been observed to inhibit the development of a boundary layer (Jonsson et al., 2006), which could seriously impact the bedload transport of sediments and microinvertebrates.

Secondary flows and the absence of a developed boundary layer in standard annular flumes limit their use in research on microinvertebrate bedload transport. Rotating annular flumes have reduced the issue of secondary flows and may represent an ideal design. Relative to the belt drive of racetrack flumes, the rotating lid of annular flumes generates consistent hydraulic conditions throughout the length of the channel, removing the need for a single 'test area'. Unfortunately, given the complexity of rotating annular flumes, their construction and operation may pose serious engineering challenges.

3.3.4.   Flow chambers and video tracking

A flow chamber is a loosely defined flow apparatus that shares many similarities with flumes. Flow chambers are generally small, transparent channels or pipes that allow the monitoring of individual animals. For example, the swimming ability of microcrustaceans in flowing water was estimated by placing them in a gravity-fed, cylindrical flow chamber (20 cm long, 3 cm wide) and monitoring their swimming ability under gradually increasing flows of up to 10 cm s^{-1} (Richardson, 1992). Richardson (1992) did not characterise flow in the chamber, however, the design was based on Dussart (1987), who investigated the critical entrainment velocities of freshwater snails, recording a Reynolds number of R = 16,538 at 86 cm s^{-1}, likely making the flow fully turbulent. Like all flow experiments, some concessions were made. The short length of the horizontal flow chamber likely prevented the formation of a fully developed boundary layer and rotifers were excluded because they were too small to monitor by eye.

Video tracking is often paired with flow chamber designs, which allows simultaneous tracking of multiple microcrustaceans movement patterns in flowing water with high spatio-temporal resolution. The movement of 100 *Eurytemora affinis* (Copepoda) were tracked under turbulence using three-dimensional particle tracking velocimetry (PTV) (Michalec et al., 2015). Four 60 mm synchronised EoSens cameras (Mikrotron) calibrated using a small reference object of known coordinates, recorded a 10 cm^3 volume of water at different angles, allowing the three-dimensional position of microcrustaceans to be derived. Turbulence was generated in the chamber using a forcing device (Hoyer et al., 2005), and flow was characterised by the light scattered off neutrally buoyant polyamide particles in a 6 cm^3 volume of water. PTV techniques have been applied at larger scales; for instance, Sidler et al. (2018a) used a 2 m flume to track the counter-current swimming of the copepod *Eucyclops serrulatus* in 15 cm^3 of water using four synchronised EoSens cameras (Mikrotron) mounted above the flume. The streambed was composed of transparent beads, allowing copepod movement in the sediment to be tracked.

Applying video tracking to rotifers is difficult, owing to their small size. The two-dimensional movements of rotifers have been tracked using microscopy and specialised cameras (e.g., Kiørboe et al., 2014; Obertegger et al., 2018). Rotifer movements (swimming directions and speed) were monitored in a microtiter plate using a standard DSLR camera and open-source software (Colangeli et al., 2018). However, these experiments were not performed in flowing water. It is possible to design a rotifer flowing experiment using microscopy by adapting the design of flow chambers. For example, an integrated flow system featuring a 0.3 x 20 mm^2 flow chamber fitted with a standard microscope slide allows for microscopic investigation into flow responses (Kriesi et al., 2019). In theory, a similar design could track the two-dimensional movements of rotifers in relation to a thin layer of substrate, following a workflow similar to Obertegger et al. (2018), who used a suite of open-source software to film, process, and analyse the swimming trajectories of rotifers. However, at this scale and water velocity, the flow would most likely be viscous and unrepresentative of a natural river channel. Furthermore, the high spatio-temporal resolution offered by video tracking and PTV would not be necessary to identify entrainment thresholds, making the specialised equipment and training required difficult to justify.

3.4. Sourcing and culturing microinvertebrates

3.4.1. Sourcing microinvertebrates

If entrainment of microinvertebrates is tested in the laboratory, a microinvertebrate seed population will be needed. Microinvertebrates can be sourced in situ, from commercial vendors or existing scientific, or aquacultural cultures. If the entrainment of a single species is investigated in isolation, individuals must be separated from field samples or acquired from monocultures (if one exists). Once a seed population is acquired, the laborious task of culturing can begin by providing the population with suitable conditions for proliferation, so enough can be harvested for experimentation.

The sourcing of microinvertebrates can be time-consuming. The most readily available source of microinvertebrates are those available commercially. Species of the rotifer genus *Brachinous* (e.g., *Brachionus calyciflorus* & *Brachionus plicatilis*) are available for purchase online in Australia as eggs or live individuals. Cladocerans (i.e., *Daphnia*) and copepods (e.g., calanoid, cyclopoid & harpacticoid copepods) are also available for purchase (e.g., aquaticlivefood.com.au). In general, the genera *Daphnia* and *Brachionus* are greatly overrepresented in the commercial market, making it challenging to find vendors offering additional taxa. Alternatively, microinvertebrates can be sourced from water column or sediment field samples. For instance, *Daphnia magna* has been identified and separated by eye from 100 mL samples of pond water containing rotifers, cladocerans and copepods and cultured to a density of over 200 Ind.L^{-1} using a combination of yeast and green water (microalgae-rich water) (Khan et al., 2020). While resting eggs of cladocerans (i.e., *D. magna* & *Bosmina longirostris*) were sampled from sediments of freshwater bodies and allowed to hatch, whereupon they were transferred to beakers or jars for reproduction or experimentation (Sakamoto et al., 2007; Sison-Mangus et al., 2015).

Microinvertebrates in bottom sediment or water column samples can be isolated by sieving samples through gradually finer mesh nets to separate them by size. Isolating rotifers in this manner is difficult, given their size and morphological similarity. After sieving samples, rotifer taxa can be isolated using microscopy and fine pipettes (Madhu et al., 2016; Ricci, 1984; Suthers et al., 2009). Stemberger (1981) successfully cultured the rotifers *Asplanchna priodonta*, *Asplanchna herricki*, *Synchaeta pectinata*, *Synchaeta oblonga* and *Polyarthra major.* The author used a 20 µm mesh net to isolate mixed species of rotifers and separated them with a disposable Pasteur pipette and a dissecting microscope. Five to ten rotifers of one species were transferred to a depression spot plate and washed with a sterile medium before being transferred to Stender dishes. They were fed cultured microflagellates and diatoms, and

the medium was replaced every three days. Rotifer cultures with the fastest growth were transferred to Griffin beakers (250–1,000 mL) to reproduce.

Only a small subset of microinvertebrates have been successfully cultured, and while general guidelines exist for certain taxa, culturing populations large enough for experimentation will likely require some trial and error for most species.

Microinvertebrates can be sourced in the field via sediment cores (i.e., 'box cores'; Coull et al., 1989; Palmer, 1988; Palmer, 1992; Papanicolaou, 2007). To obtain a box core sample of sediment and overlying water, an Eckman grab sampler (approximately 20 cm diameter, 15 cm deep) can be inserted into the sediment or mudflat and a bottom plate is secured to prevent the sediment from falling. The box core samples can be taken to a lab and allowed to equilibrate before insertion into a flume (ideally within 24 hours of sampling). This approach does not allow experimentation on a single species in isolation but avoids the challenging task of isolating and culturing microinvertebrates. Additionally, the inclusion of stratigraphically undisturbed sediment allows experiments to be performed in the lab with substrates representative of natural environments.

3.4.2.   Culturing microinvertebrates: Culture methods

There are three basic culturing methods for microinvertebrates: (1) batch, (2) semi-continuous and (3) continuous. Batch cultures inoculate a low density of microinvertebrates into an algae-dense culture medium ('green water') to proliferate. Once the algae are consumed, microinvertebrates are harvested and a sample can be retained to seed new cultures (Lubzens, 1987). Rotifer densities in batch cultures are lower than in other methods, rarely exceeding 500–1,000 Ind.mL^{-1} (Suantika et al., 2000; Yoshimatsu & Hossain, 2014). These densities may be considered low for aquacultural purposes but should suffice for experiments using observed densities representative of the lower River Murray. Although batch cultures are easy to start, they are prone to population crashes at high densities due to the accumulation of organic matter and deterioration of water quality. Semi-continuous cultures inoculate microinvertebrates into algae-dense mediums to proliferate, and a certain volume of culture medium (typically ~10%) is harvested and replenished daily to minimize the impact of organic matter build-up and maintain water quality. Removal and replenishment of culture medium allows the persistence of cultures for months or years. For example, a semi-continuous culture in a 38 L tank fed fresh culture medium via a pipe connected to a 38 L algae tank has sustained populations of *Daphnia* sp. and *Moina* sp. for months (Rottmann et al., 1992). The small tank volume is not sufficient for large-scale commercial purposes but is ideal for small-scale production of microinvertebrates that can be maintained for long periods. Continuous cultures (i.e., chemostat cultures) constantly feed fresh medium into the culture

while removing old culture medium so the culture volume remains constant. Alternatively, old culture medium can be filtered and recirculated back into the culture. This culturing method allows for the greatest biomass production. By exchanging 300% of culture medium daily, *B. plicatilis* densities of 2,500 Ind.mL^{-1} have been obtained (Suantika et al., 2000).

3.4.3.   Culturing microinvertebrates: Culture conditions

Most research involving microinvertebrate culturing relates to the genera *Daphnia* (pelagic cladocerans; Bhosle, 2020) and *Brachionus* (predominantly pelagic rotifers; Ogata, 2017) for aquaculture feed. Consequently, knowledge on culturing other species of microinvertebrates is lacking, with some species being much more amenable to rearing than others. Fundamentally, culturing microinvertebrates requires a suitable food source (e.g., algae) and a medium in which the food source and microinvertebrates can grow and reproduce. Three commonly used mediums are COMBO (Kilham et al., 1998), ADaM (Klüttgen et al., 1994) and WC (Guillard & Lorenzen, 1972) combined with tap water or filtered (~45 μm) natural water. They can be made in-house or purchased from online vendors (e.g., aquaticlivefood.com.au, utex.org). Microinvertebrate dietary preferences vary owing to differences in morphology and behaviour. For example, eleven out of 22 freshwater rotifer species from the genera *Brachionus, Keratella, Notholca*, *Ascomorpha*, *Synchaeta*, *Polyarthra*, *Pompholyx*, and *Filinia* were successfully cultured on diets of *Rhodomonas minuta* or *Stichococcus bacillary* (May 1987). *Bosmina longispina was successfully cultured* in three of five algal cultures, with the fastest growth in a mix of the diatom *Stephanodiscus hantzschii* and the flagella *R. minuta*, while *Daphnia longispina* was cultured in all five and exhibited the fastest growth when fed *R. minuta* (Lundstedt & Brett, 1991). Algae is an excellent food source for most microinvertebrates but culturing it can be laborious and may lead to population bottlenecks if insufficient amounts are provided. Adding inexpensive commercially available baker's yeast (*Saccharomyces cerevisiae*) in a 1:1 ratio with algae can supplement algal growth without significantly impacting growth rates of microcrustaceans or rotifers (Lubzens, 1987; Peña-Aguado et al., 2005).

Microinvertebrates are generally cultured between 20–30 °C under approximately 3,000 lux with a 16:8 light:dark photoperiod (e.g. Eckert et al., 2021; Klüttgen et al., 1994; Rahman et al., 2023). Microinvertebrate pH tolerances vary, though a roughly neutral pH has been found ideal for population growth (i.e., ~6–8; Bērziņš & Pejler, 1987; Davis & Ozburn, 1969; Hooper et al., 2008; Yin & Niu, 2008). Salinity concentrations of 1.5–3.0 g L^{-1} NaCl (0.15–0.3%) have been found to adversely affect populations of freshwater microinvertebrates to varying degrees, with freshwater rotifers and cladocerans unable to survive and reproduce in salinities higher than 5 g L^{-1} NaCl (Sarma et al., 2006).

In summary, sourcing, isolating and culturing many of the microinvertebrates of the lower River Murray is possible, but complexity increases exponentially as the number of species increases, particularly if they require unique food sources, and may be prohibitive.

3.5. Experimental designs

The numerous methods reviewed in this report each have distinct advantages and limitations in their ability to derive microinvertebrate entrainment thresholds and drift distance. Field-based methods such as direct water column monitoring derive entrainment thresholds under representative hydraulic and habitat conditions at a scale most relevant to managers but are limited in obtaining the fine-scale mechanistic insights possible from a laboratory flume. Therefore, the subsequent sections propose three complementary experiments suitable for deriving entrainment thresholds and drift distance for microinvertebrates in the lower River Murray. These include a field-based experimental creek, a laboratory-based flume experiment, and a desk-based meta-analysis leveraging microinvertebrate data collected across the study site over recent years.

3.5.1. Field study: Experimental channel/creek

As discussed in section 3.3, in situ studies have the advantage of capturing natural riverine conditions and microinvertebrate communities (Table 3). An *in situ* study that measures the magnitude of drifting microinvertebrates, and their change over distance and water velocity, could provide invaluable results at a scale relevant to ecological processes and river management.

Table 3. Advantages and disadvantages of performing a microinvertebrate entrainment investigation in an experimental field channel.

Advantages	Disadvantages
Representative of a natural environment.	Not performed under controlled conditions.
Results that are at a scale relevant to ecological processes and management.	Upstream impacts difficult to account for.
Long distances ideal for measuring drift distances and drop-out rates of entrained microinvertebrates.	Less suited to measure precise microinvertebrate entrainment velocities than flume studies.
Microinvertebrate sourcing and culturing is not needed.	No control of microinvertebrate community composition.

Channel conditions

To conduct an *in situ* study, an appropriate channel must be chosen. The length of the channel should extend at least 1 km, as a previous study has shown microinvertebrate biomass decreased by approximately 50% and 90% at distances of roughly 100 m and 1,000 m from lake outlets, respectively, in streams with mean current velocities of 51–63 cm s^{-1} (Eriksson, 2001). Ideally, a channel longer than 1 km would be used, as some streams may still contain significant microinvertebrate biomass after 9 km (Eriksson, 2001). The channel must possess the flexibility to adjust water velocities within the required range. Considering the critical entrainment velocities in Table 2, testing cross-sectional water velocities ranging from 5 to 40 cm s^{-1} (e.g., 5, 10, 15, 20, 30, 40 cm s^{-1}) is recommended. A velocity of 5 cm s^{-1} is below microinvertebrate critical entrainment thresholds (Palmer 1992; Czerniawski, 2012), whereas 40 cm s^{-1} is greater than biofilm scouring velocities (Majdi et al., 2012), and may not be feasible in many streams. At a minimum, a maximum water velocity of 20 cm s^{-1} should be included. It is essential to minimise the influx of microinvertebrates from other sources into the channel. Accordingly, channels with a single inlet and minimal slackwaters are preferred. If a single inlet channel is unattainable, the contribution of alternative sources to downstream microinvertebrate populations needs to be quantified by measuring microinvertebrate density and discharge following the same protocol employed for experimental sites. Evaluating how velocity manipulations affect water levels upstream and downstream of research sites is important, given fluctuations in the inundation of littoral zones and slackwaters may provide additional sources of microinvertebrates and affect investigations of longitudinal dispersion. The smallest possible change in water levels and inundation is advisable while maintaining a channel length of at least 1000 m.

Sampling design

Microinvertebrate sampling should be conducted once in late November or early December, during warmer conditions and higher productivity. Sampling should be undertaken at increasing distances from the main channel inlet. For a channel spanning 1 km, it is suggested to position the sampling sites at distances of 50, 100, 200, 500, and 1,000 m downstream of the inlet. For a longer channel, an additional site may be placed 2 km downstream of the inlet. Sampling intensity is heightened within the first 500 metres, as many microinvertebrates are anticipated to be eliminated from the drift at lower velocities, particularly larger-bodied microcrustaceans (Eriksson, 2001). A site upstream of the inlet is crucial to provide baseline data for the microinvertebrate source population that enters the channel prior to velocity manipulation. Sampling of the upstream site will occur at the same frequency as downstream sites (that is, once per stepwise increase in water velocity) to account for changes in the

microinvertebrate source community over time. The upstream site should be approximately 50–100 m from hydrological structures to avoid the influence of backflow or other disturbances. Prior to a formal experiment, trials are recommended (field reconnaissance) to determine channel conditions and how flow manipulations influence them, as the specifics of sampling may require adjustments based on channel depth and current velocity. Therefore, the following protocol (Figure 8) provides a generalised approach that can be adjusted as needed.

All microinvertebrate sampling should aim to be conducted within a single day to minimise confounding variables. If sampling must be performed over multiple days, a similar pattern of gradual water velocity increase is recommended, as rapid changes in velocity may result in different microinvertebrate responses. At each stepwise increase in velocity, microinvertebrate sampling will be performed at each site (including the upstream site) using a 4 litre Haney trap deployed at pre-determined heights above the sediment surface (e.g., 0 m, 1 m, 2 m). At each water height, one replicate consisting of two 4 L Haney trap samples will be collected and filtered through a 37 μm mesh plankton net into a 200 mL PET bottle and preserved with approximately 75% ethanol. A total of three 8 L replicates will be collected per depth at each site for each water velocity. After thoroughly mixing, a 1 mL subsample of each replicate will be taken to identify and count the microinvertebrates using a microscope. At the time of sampling, water physicochemical parameters (e.g., water temperature, dissolved oxygen, turbidity) should be measured at each depth.

An Acoustic Doppler Current Profiler (ADCP) can be used to measure channel vertical and horizontal velocity profiles at each site to calculate cross-sectional discharge (Furst et al., 2019a). Additionally, velocity profiles may be taken at major channel bends, as velocity conditions may vary considerably with channel morphology, influencing microinvertebrate transport, though this task may be highly laborious. Alternatively, hydraulic modelling may be used to estimate velocity conditions along the length of the channel at far greater spatial resolutions.

Following the identification and enumeration of microinvertebrate samples, data can be analysed with hydraulic variables to reveal how microinvertebrate density and community composition change over distance at a given water velocity. To account for variations in environmental condition over the experiment, water physicochemical parameters will be measured at sites using a multiparameter probe (e.g., Xylem YSI Sonde; Furst et al., 2020).

The final number of samples, water velocities tested, and the level of taxonomic resolution may vary depending on the experimental channel's specific conditions and available budget. As an example, a 2 km channel with seven sites, six water velocities, and a depth of 3 m will

yield 504 replicates. The budget required to carry out this field work, in addition to microinvertebrate identification and enumeration, analysis and writing, is expected to cost approximately \$181,983–203,583 (see Supplementary S1 for cost breakdown).
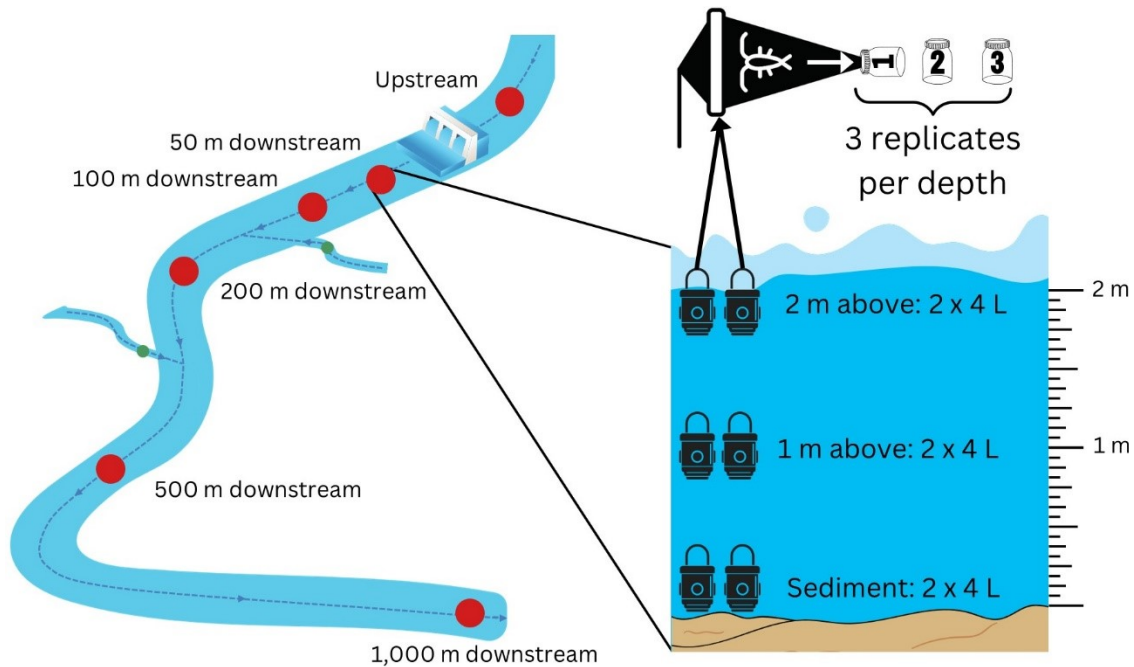
Figure 8. Conceptualised sampling protocol for an experimental channel. At each site (red circle) three (2 x 4 L) water samples are collected at three depths (sediment, 1 m, 2 m) and concentrated into a 200 mL PET bottle. Sampling is then repeated at each site for eery stepwise increase in water velocity. Additional sampling sites (green circles) represent secondary channel inlets and inundated areas that may need to be sampled.

3.5.2. Laboratory study: Experimental flume

The strengths and limitations of a laboratory flume experiment make it suited for small-scale experiments (Table 4). Notably, a flume experiment allows for repeated measures and fine-scale investigations into the mechanism of microinvertebrate entrainment, though its size constraints limit the assessment of drift distances.

Table 4. Advantages and disadvantages of performing a microinvertebrate entrainment investigation in a laboratory setting.

Advantages	Disadvantages
Performed in a controlled environment.	Less representative of natural environments.
Capable of estimating critical entrainment velocities of microinvertebrates	Short distance not suitable for estimating advective losses of microinvertebrate drift.
Informed fine-scale mechanism of entrainment.	Extrapolating results to larger systems will be challenging.
Higher reproducibility and easier replication.	Requires sourcing or culturing of microinvertebrates.

<u>Flume conditions</u>

To test microinvertebrate entrainment thresholds in the laboratory, a flume must be constructed or hired from an Australian institution, however, not all flumes will be suitable. The flumes at The University of Adelaide operate on a shared reservoir of chlorinated water, making them infeasible. An approximately 300 cm long flume with baffle elements at the inlet should be sufficient to develop a boundary layer. A range of water velocities similar to that in the experimental channel (0–40 cm s^{-1}; see section 3.5.1) must be achievable. If a flume must be constructed, it can be built of plexiglass or plywood, and its construction should follow the recommendations of Muschenheim et al. (1989), which provide a solid foundation for flume theory, construction and practice. A 300 cm flume with a width of 20 cm and a flow depth of 10 cm, flow rates of 240, 360, and 480 L min^{-1} are needed to achieve water velocities of 20, 30 and 40 cm s^{-1}, respectively (Figure 9). Tilting the flume (typically 0.5–3%) and modifying the exit conditions can increase the water velocity over the test section (Muschenheim et al., 1989). A sterile sediment substrate should be placed throughout the channel to increase the flume's representativeness of a natural stream. However, adding a substrate will lower the water velocity considerably, requiring increased flow rates and modification of exit conditions to reach desired water velocities. Additionally, sediment transport may occur at higher velocities, interfering with microinvertebrate entrainment. According to both Shield's formula and Hjulström's curve, grain sizes larger than approximately 2.7 and 3.7 mm may resist erosion when experimenting with water velocities of 30 and 40 cm s^{-1}, respectively. However,

these approximations will vary depending on experimental conditions and should therefore be confirmed during flume validation.

Experimental design

Microinvertebrates will be collected from the River Murray, preferably between late November and early December, and transferred into two 50 L drums using a peristaltic pump. To ensure adequate capture of microinvertebrates, water collection should take place from vegetation-rich slackwaters. The drums will be transported to the laboratory, where the microinvertebrates may be kept alive for several days in aerated water. Prior to the experiment, the drums will be mixed, and a 5 L sample will be taken and concentrated into a 200 mL PET bottle using a 37 µm mesh plankton net. The flume will be filled to the desired depth and the working section closed off using two thin barriers across the width of the flume. Microinvertebrates will be added to the working section and left for 5 minutes to settle throughout the water column of the test section. The barriers will be removed, and an initial water velocity of 1 cm s^{-1} will be generated. A 37 µm mesh plankton net fitted with a 100 mL PET bottle will be placed at the exit of the flume to capture microinvertebrates that exhibit passive drift at 1 cm s^{-1}. After 5 minutes, the net will be removed and replaced, and the water velocity increased to 5 cm s^{-1} for 5 minutes. The removed net will be rinsed with ethanol to ensure captured microinvertebrates are concentrated into the 100 mL PET bottle.

The process will be repeated for every 5 cm s^{-1} increment until a velocity of 40 cm s^{-1} is achieved. A total of 10 flume operations for each velocity are recommended at each velocity for a large enough sample size to determine differences in drifting microinvertebrates between flow velocities, yielding 90 samples. The responses of microinvertebrate taxa to increases in flow velocity will be estimated by identifying and enumerating drifting microinvertebrates from three 1 mL subsamples taken from each sample. The density of drifting microinvertebrates may be estimated by carefully monitoring the discharge of the flume (particularly during net changes). To conduct such a flume experiment, including microinvertebrate identification and enumeration, flume construction materials, and microinvertebrate sourcing, a budget of approximately \$65,192–67,192 is recommended (see supplementary S2 for detailed breakdown).
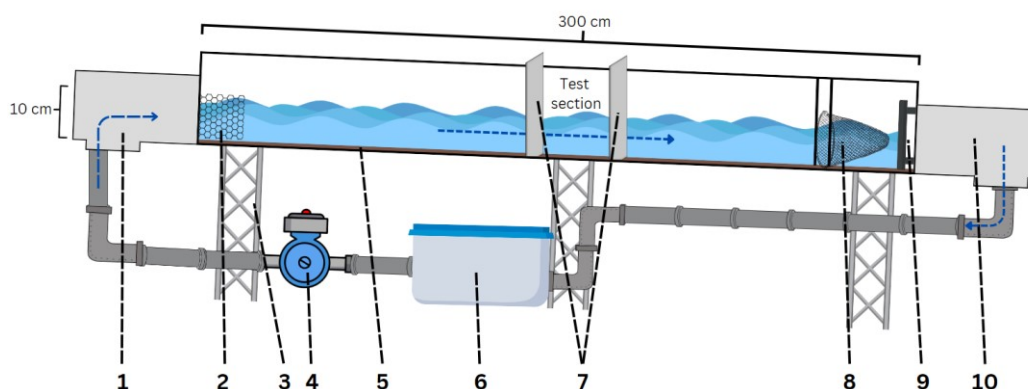
Figure 9. Example of a flume design (300L x 20W x 10D cm) to test microinvertebrate entrainment. (1) Flow inlet, (2) Flow straightener/honeycomb structure, (3) Height-adjustable support structure, (4) Pump and flow meter, (5) sediment substrate, (6) reservoir, (7) Removable walls to isolate test section, (8) 37 µm mesh plankton net, (9) Height-adjustable outlet gate, (10) outlet. Note: the plankton net may hinder flow rate. Therefore, net placement and reservoir size need to be considered to ensure filtration does not reduce flow rate.

3.5.3. Meta-analysis of past sampling data and monitoring projects with hydraulic modelling

Numerous studies and monitoring projects have explored microinvertebrate community dynamics within the lower River Murray (Table 5). The combined efforts of investigations have identified over 400 microinvertebrate species (including protists) within the system. Despite extensive monitoring and research, most data have yet to be collated, presenting an opportunity for a comprehensive meta-analysis. A meta-analysis could provide a broader understanding of the overall trends in microinvertebrate communities and their responses to varying hydraulic conditions. While existing studies have incorporated hydraulic measurements such as water velocity and flow rate, hydraulic measurements are often limited to specific sampling sites, thereby neglecting the effects of upstream hydraulic conditions (Table 6). Additionally, hydraulic measurements may vary between studies (e.g., discharge volume versus water velocity), making direct comparison between studies difficult. A holistic approach complementary to lab and field experiments could include using past microinvertebrate assemblage data coupled with retroactive hydraulic modelling data following a methodology similar to Gibbs et al. (2020). Applying this approach to the studies in Table 5 may allow for the development of a rich repository of microinvertebrate data spanning dozens of sites, multiple years, and hundreds of taxa. Carrying out such a project will require a budget of approximately $87,500, inclusive of project management, hydraulic modelling, statistics, and report writing.

Another approach that may be complementary to the primary field and laboratory experiments is collaborating with existing monitoring projects (e.g., the Flow-MER Project and the Murray Channel Project) that take place in the River Murray (Table 5). This collaboration could be a

cost-effective approach to sampling microinvertebrates in the Lower River Murray. Using a similar protocol proposed in section 3.5.1, microinvertebrate sampling targeting different parts of the hydrograph and in different sections (velocity gradient) of the weir pool may be performed during weir pool operations, providing a snapshot of how microinvertebrates may respond to altered hydraulic conditions.

Table 5. Recent microinvertebrate studies that have been performed in the lower River Murray.

Sites	Site visits	Taxa monitored	Month-Year(s)	Reference
3 sites, downstream of Lock 1, 4, and 6.	7	Rotifers, copepods, ostracods, and cladocerans (and littoral or pelagic associations).	Oct - Jan 2019-20 to current.	Ye et al., 2023
26 sites, upstream of Lock 1 to Howlong, NSW.	3-5	Rotifers, copepods, cladocerans, and ostracods.	Nov 2016; Feb, May, and Nov 2017; Feb 2018.	Furst et al., 2019a
4 sites, downstream of Lock 7 to downstream of Lock 10.	2	Rotifers, copepods, and cladocerans.	Oct 2015 - Nov 2015	Furst et al., 2018
6 sites, Lock 4 to Tocumwal.	7	Rotifers, copepods, cladocerans, and ostracods (and littoral or pelagic associations).	Sep 2019 - Dec 2019	Furst et al., 2020
2 sites, downstream of Lock 1 and 6.	29	Rotifers, copepods, cladocerans, and ostracods (and littoral or pelagic associations).	Sep - Jan from 2014 - 2018	Ye, et al., 2020
31 sites, Lock 1–6, 9 sites have littoral samples.	12-13	Rotifers, copepods, cladocerans, and ostracods.	Sep 2020 - Dec 2020.	Dornan et al., 2021
9 sites between the Chowilla anabranch and Lock 5.	5	Rotifer, copepods, cladocerans, and ostracods.	Nov 2017 – Nov 2018.	Gibbs et al., 2020.

Table 6. Advantages and disadvantages of desk-based analysis of microinvertebrate entrainment using past sampling data and collaborating with ongoing monitoring projects for sample collection.

Past data analyses advantages	Past data analyses disadvantages
Large microinvertebrate datasets.	Different sampling methodologies may influence results.
Does not require specialised equipment or field sampling.	Confounding effects of unmeasured variables between studies (geomorphology, temperature, etc.).
Spans a wide diversity of hydrological variables.	Inconsistent/availability of hydraulic data (e.g. velocity, turbulence). May require retroactive hydrological/hydraulic modelling.
Collaborative monitoring advantages	**Collaborative monitoring disadvantages**
Minimal sampling logistics.	Challenging to control upstream effects (slackwaters, water velocity, etc.)
Potential for long-term sampling.	Limited sampling intensity.
Representative of a natural environment.	Not performed under controlled conditions.
Cost-effective method for obtaining microinvertebrate samples.	Unable to alter only water velocity while keeping sampling location and time approximately static.

3.6.   Conclusion

Determining the dynamics of microinvertebrate drift is a multi-faceted challenge, combining physical and biological processes. Previous attempts to derive critical entrainment thresholds have varied in their execution, and thresholds have varied accordingly. However, a water velocity of approximately 10 cm s^{-1} is a common threshold beyond which the magnitude of drifting microinvertebrates tends to increase. However, differences in taxa size (e.g., between rotifers and microcrustaceans), hydraulics, and habitat will strongly influence this threshold. Three experimental designs are recommended to investigate the entrainment of microinvertebrates within the lower River Murray.

The first is a field-based experiment using a 1–2 km long channel/creek where microinvertebrate drift can be intensively monitored. This design is representative of natural environments and is well-suited for investigating how drift magnitude, drift distance, and drift losses respond to artificial changes in channel hydraulics. A major challenge of this design is accounting for secondary sources of microinvertebrates entering the drift.

The second is a laboratory-based experiment using a 3 m flume to monitor the number of entrained microinvertebrates at different water velocities. This design will allow for fine-scale investigations into what water velocities different microinvertebrate taxa become entrained, though size constraints limit investigations into drift distance and re-entry. The major challenge of this design is ensuring the hydraulic conditions within the flume are representative of natural environments.

The third is a desk-based approach that will identify, collate, and analyse the pre-existing lower River Murray microinvertebrate data to establish a statistical relationship with microinvertebrate drift and hydraulic conditions at the time of sampling. While the results generated from analysing such a vast dataset will be representative of natural environments, there are several challenges with such an undertaking. For instance, inconsistent hydraulic data will require retroactive hydrological modelling and biases are likely to be present between different sampling approaches. Alternatively, collaborating with existing long-term monitoring projects may be a cost-effective alternative to obtaining microinvertebrate data, co-opting a similar microinvertebrate sampling protocol used in the experimental creek.

The above approaches, or a combination of them, are recommended for implementation during the following stages of this project. The three approaches are designed to independently contribute to understanding entrainment mechanisms and can be undertaken in any order. The approaches are also complementary and the delivery of all three experiments will likely be required to build a comprehensive understanding of entrainment

processes in the lower River Murray. The results generated from these approaches will help in understanding microinvertebrate drift dynamics, informing environmental water delivery and river operations to achieve optimal ecological outcomes in the lower River Murray.

4. REFERENCES

Aberle, J., Nikora, V., McLean, S., Doscher, C., McEwan, I., Green, M., Goring, D. and Walsh, J., 2003. Straight benthic flow-through flume for in situ measurement of cohesive sediment dynamics. Journal of Hydraulic Engineering, 129 (1), 63–67.

Allan, J. D. and Feifarek, B. P., 1989. Distances traveled by drifting mayfly nymphs: Factors influencing return to the substrate. Journal of the North American Benthological Society, 8 (4), 322–330.

Almén, A-K., Brutemark, A., Jutfelt, F., Riebesell, U. and Engström-Öst, J., 2017. Ocean acidification causes no detectable effect on swimming activity and body size in a common Copepod. Hydrobiologia, 802 (1), 235–243.

Amos, C. L., Grant, J., Daborn, G. R. and Black, K., 1992. Sea Carousel—A benthic, annular flume. Estuarine, Coastal and Shelf Science, 34 (6), 557–577.

Appel, D. S., Gerrish, G. A., Fisher, E. J. and Fritts, M. W., 2020. Zooplankton sampling in large riverine systems: A gear comparison. River Research and Applications, 36 (1), 102–114.

Armonies, W., 1988. Physical factors influencing active emergence of meiofauna from boreal intertidal sediment. Marine Ecology Progress Series, 49 (3), 277–286.

Arnott, S. E., Celis-Salgado, M. P., Valleau, R. E., DeSellas, A. M., Paterson, A. M., Yan, N. D., Smol, J. P., and Rusak, J. A., 2020. Road Salt Impacts Freshwater Zooplankton at Concentrations below Current Water Quality Guidelines. Environmental Science & Technology, 54 (15), 9398–9407.

Australian Bureau of Statistics, 2021. Water use on Australian farms: Statistics on agricultural water use (including pastures and crops irrigated) and irrigation water sources, ABS, Australian Government, accessed 06 June 2022, <https://www.abs.gov.au/statistics/industry/agriculture/water-use-australian-farms/latest-release>

Bandara, K., Varpe, Ø., Wijewardene, L., Tverberg, V. and Eiane, K., 2021. Two hundred years of zooplankton vertical migration research. Biological Reviews, 96 (4), 1547–1589.

Baranyi, C., Hein, T., Holarek, C., Keckeis, S. and Schiemer, F., 2002. Zooplankton biomass and community structure in a Danube River floodplain system: effects of hydrology. Freshwater Biology, 47 (3), 473–482.

Bartsch, A., Robinson, S. M. C., Liutkus, M., Ang, K. P., Webb, J. and Pearce, C. M., 2013. Filtration of sea louse, *Lepeophtheirus salmonis*, copepodids by the blue mussel, *Mytilus edulis*, and the Atlantic sea scallop, *Placopecten magellanicus*, under different flow, light and copepodid-density regimes. Journal of Fish Diseases, 36 (3), 361–370.

Basu, B. K., Kalff, J. and Pinel-Alloul, B., 2000. The influence of macrophyte beds on plankton communities and their export from fluvial lakes in the St Lawrence River. Freshwater Biology, 45 (4), 373–382.

Battauz, Y. S., José de Paggi, S. B. and Paggi, J. C., Macrophytes as dispersal vectors of zooplankton resting stages in a subtropical riverine floodplain. Aquatic Ecology, 51 (2), 191–201.

Beaulieu, S. E., Sengco, M. R. and Anderson, D. M., 2005. Using clay to control harmful algal blooms: deposition and resuspension of clay/algal flocs. Harmful Algae, 4 (1), 123–138.

Bērziņš, B. and Pejler, B., 1987. Rotifer occurrence in relation to pH. Hydrobiologia 147, 107–116.

Bhosle, R. V., 2020. Production of Daphnia for Freshwater Nursery Rearing of Cultivable Fishes. Biotica Research Today, 2 (11), 1218–1221.

Bice, C. M., Zampatti, B. P. and James, C., 2016. The influence of weir pool raising on main channel hydraulics in the lower River Murray, South Australia, in 2015. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. SARDI Publication No. F2015/000381- 2. SARDI Research Report Series No. 904. 40pp.

Bice, C. M., Gibbs, M. S., Kilsby, N. N., Mallen-Cooper, M. and Zampatti, B. P., 2017. Putting the "river" back into the Lower River Murray: quantifying the hydraulic impact of river regulation to guide ecological restoration. Transactions of the Royal Society of South Australia, 141 (2), 108–131.

Bice, C. M., Giatas, G. C., Brewer, E. A., Catalano, S., Furst, D., Oliver, R., Revill, A. T., Shiel, R., Ye, Q. and Zampatti, B., 2023. Commonwealth Environmental Water Office Monitoring, Evaluation and Research Project: Lower Murray 2019–2022 Research Report: Diet and basal carbon sources of early life stage Murray cod in the Lower Murray River. A report prepared for the Commonwealth Environmental Water Office by the South Australian Research and Development Institute, Aquatic Sciences.

Blanckaert, K., Garcia, X-F., Ricardo, A-M., Chen, Q. and Pusch, M. T., 2013. The role of turbulence in the hydraulic environment of benthic invertebrates. Ecohydrology, 6 (4), 700–712.

Bolduc, P., Bertolo, A. and Pinel-Alloul, B., 2016. Does submerged aquatic vegetation shape zooplankton community structure and functional diversity? A test with a shallow fluvial lake system. Hydrobiologia, 778 (1), 151–165.

Bouma, T. J., van Duren, L. A., Temmerman, S., Claverie, T., Blanco-Garcia, A., Ysebaert, T. and Herman, P. M. J., 2007. Spatial flow and sedimentation patterns within patches of epibenthic structures: Combining field, flume and modelling experiments. Continental Shelf Research, 27 (8), 1020–1045.

Brittain, J. E. and Eikeland, T. J., 1988. Invertebrate drift — A review. Hydrobiologia, 166 (1), 77–93.

Brown, B. L., Wahl, C. and Swan, C. M., 2018. Experimentally disentangling the influence of dispersal and habitat filtering on benthic invertebrate community structure. Freshwater Biology, 63 (1), 48–61.

Bruno, M. C., Siviglia, A., Carolli, M. and Maiolini, B., 2012. Multiple drift responses of benthic invertebrates to interacting hydropeaking and thermopeaking waves. Ecohydrology, 6 (4), 511–522.

Bunn, S. E. and Arthington, A. H., 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management, 30 (4), 492–507.

Burks, R. L., Lodge, D. M., Jeppesen, E. and Lauridsen, T. L., 2002. Diel horizontal migration of zooplankton: costs and benefits of inhabiting the littoral. Freshwater Biology, 47 (3), 343–365.

Burdis, R. M. and Hirsch, J. K., 2016. Crustacean zooplankton dynamics in a natural riverine lake, Upper Mississippi River. Journal of Freshwater Ecology, 32 (1), 247–265.

Campbell, R. N. B., 1985. Comparison of the drift of live and dead Baetis nymphs in a weakening water current. Hydrobiologia, 126, 229–236.

Casper, A. F. and Thorp, J. H., 2007. Diel and lateral patterns of zooplankton distribution in the St. Lawrence River. River Research and Applications, 23 (1), 73–85.

Childers, D. L. and Day, J. W., 1988. A flow-through flume technique for quantifying nutrient materials fluxes in microtidal estuaries. Estuarine, Coastal and Shelf Science, 27 (5), 183–494.

Chimney, M. J., Winner, R. W. and Seilkop, S. K., 1981. Prey utilization by Chaoborus punctipennis Say in a small, eutrophic reservoir. Hydrobiologia, 85, 193–199.

Ciborowski, J. J. H., 1983. Downstream and lateral transport of nymphs of two mayfly species (Ephemeroptera). Canadian Journal of Fisheries and Aquatic Sciences, 40 (11), 2025–2029.

Cisewski, B., Strass, V. H., Rhein, M., Krägefsky, S., 2010. Seasonal variation of diel vertical migration of zooplankton from ADCP backscatter time series data in the Lazarev Sea, Antarctica. Deep Sea Research Part I: Oceanographic Research Papers, 57 (1), 78–94.

Clarke, R. D., Finelli, C.M. and Buskey, E.J., 2009. Water flow controls distribution and feeding behavior of two co-occurring coral reef fishes: II. Laboratory experiments. Coral Reefs, 28 (2), 475–488.

Colangeli, P., Schlägel, U. E., Obertegger, U., Petermann, J. S., Tiedemann, R. and Weithoff, G., 2018. Negative phototactic response to UVR in three cosmopolitan rotifers: a video analysis approach. Hydrobiologia, 844 (1), 43–54.

Conti-Jerpe, I. E., Pawlik, J. R. and Finelli, C. M., 2022. Evidence for trophic niche partitioning among three temperate gorgonian octocorals. Coral Reefs, 41 (4), 907–920.

Cooling, M. P. and Boulton, A. J., 1993. Aspects of the hyporheic zone below the terminus of a South Australian arid-zone stream. Australian Journal of Marine and Freshwater Research, 44 (3), 411–426.

Cottier, F. R., Tarling, G. A., Wold, A. and Falk-Petersen, S., 2006. Unsynchronised and synchronised vertical migration of zooplankton in a high Arctic fjord. Limnology and Oceanography, 51 (6), 2586–2599.

Coull, B. C., Palmer, M. A. and Myers, P. E., 1989. Controls on the vertical distribution of meiobenthos in mud: field and flume studies with juvenile fish. Marine Ecology Progress Series, 55 (2/3), 133–139.

Czerniawski, R., 2012. Spatial pattern of potamozooplankton community of the slowly flowing fishless stream in relation to abiotic and biotic factors. Polish Journal of Ecology, 60 (2), 323–338.

Czerniawski, R. and Sługocki, Ł., 2017. Analysis of zooplankton assemblages from man-made ditches in relation to current velocity. International Journal of Oceanography and Hydrobiology, 46 (2), 199–211.

Davis, P. and Ozburn, G. W., 1969. The pH tolerance of *Daphnia pulex* (Leydig, emend., Richard). Canadian Journal of Zoology, 47 (6), 1173–1175.

Davies, J. A., 1986. Boundary layers, flow microinvertebrates and stream benthos. In De Deckker, P. and Williams, W. D. (eds) Limnology in Australia. Monographiae Biologicae, vol 61. Springer, Dordrecht.

Davies, J. A. and Barmuta, L. A., 1989. An ecologically useful classification of mean and near-bed flows in streams and rivers. Freshwater Biology, 21 (2), 271–282.

Davies, P. E., Harris, J. H., Hillman, T. J. and Walker, K. F., 2010. The sustainable rivers audit: Assessing river ecosystem health in the Murray-Darling Basin, Australia. Marine and Freshwater Research, 61 (7), 764–777.

Debastiani-Júnior, J. R., Elmoor-Loureiro, L. M. A. and Nogueira, M. G., 2016. Habitat architecture influencing microcrustaceans composition: a case study on freshwater Cladocera (Crustacea Branchiopoda), Brazilian Journal of Biology, 76 (1), 93–100.

Denny, M. W., 1993. Air and water: the biology and physics of life's media. Princeton University Press, Princeton, NJ, pp. 341.

DEW, 2020. South Australian River Murray Basin Plan Environmental Outcome Evaluation: SA Channel and Floodplain Priority Environmental Assets, DEW Technical report 2020/19, Government of South Australia, Department for Environment and Water, Adelaide.

DEW, 2021. 2021-22 Water for the Environment Annual Plan: For the South Australian River Murray. Government of South Australia, Department for Environment and Water, Adelaide.

DEW, 2022. Water Data SA. Government of South Australia, Department for Environment and Water, Adelaide. Accessed 23 August 2022, https://water.data.sa.gov.au/

Dijkstra, J., Uittenbogaard, R. and Stive, M., 2006. 'Modelling hydrodynamics in Eelgrass (*Zostera marina*) beds'. In Smith, J. M. (ed), Coastal Engineering 2006, World Scientific Publishing Company, California.

Dijkstra, J. and Uittenbogaard, R., 2010. Modeling the interaction between flow and highly flexible aquatic vegetation. Water Resources Research, 46 (12), W12547.

Dodson, S. I., Hanazato, T. and Gorski, P. R., 1995. Behavioral responses of *Daphnia Pulex* exposed to carbaryl and chaoborus kairomone. Environmental Toxicology and Chemistry, 14 (1), 43–50.

Dole-Olivier, M. J., Marmonier, P. and Beffy, J. L., 1997. Response of invertebrates of lotic disturbance: is the hyporheic zone a patch refugium? Freshwater Biology, 37 (2), 257–276.

Dornan, T. N., Mills, J. G., Shiel, R. J., Keneally, C., Dorji, T., Deane, D., Ye, Q. and Brookes, J. D., 2021. Monitoring microinvertebrate response to environmental water events in the

SA River Murray in 2020: A report prepared for the Department for Environment and Water, South Australia, Australia.

Doubek, J. P., Campbell, K. L., Doubek, K. M., Hamre, K. D., Lofton, M. E., McClure, R. P., Ward, N. K. and Carey, C. C., 2018. The effects of hypolimnetic anoxia on the diel vertical migration of freshwater crustacean zooplankton. Ecosphere, 9 (7), e02332.

Dussart, G. B. J., 1987. Effects of water flow on the detachment of some aquatic pulmonate gastropods. American Malacological Bulletin, 5 (1), 65–72.

Eckert, E. M., Anicic, N., and Fontaneto, D., 2021. Freshwater zooplankton microbiome composition is highly flexible and strongly influenced by the environment. Molecular Ecology, 30 (6), 1545–1558.

Ekau, W., Auel, H., Pörtner, H-O. and Gilbert, D., 2010. Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish). Biogeosciences, 7, 1669–1699.

Elliott, D. T., Harris, C. K. and Tang, K. W., 2010. Dead in the water: The fate of Copepod carcasses in the York River estuary, Virginia. Limnology and Oceanography, 55 (5), 1821–1834.

Eriksson, Å. I., 2001. Longitudinal changes in the abundance of filter feeders and zooplankton in lake-outlet streams in northern Sweden. Annales De Limnologie-International Journal of Limnology, 37 (3), 199–209.

Farhadi, A., Mayrhofer, A., Tritthart, M., Glas, M. and Habersack, H., 2018. Accuracy and comparison of standard k-ϵ with two variants of k-ω turbulence models in fluvial applications. Engineering Applications of Computational Fluid Mechanics, 12 (1), 216–235.

Field-dodgson, M. S., 1985. A simple and efficient drift sampler. New Zealand Journal of Marine and Freshwater Research, 19 (2), 167–172.

Finelli, C. and Sumerel, A., 2014. Particle size, flow speed, and body size interactions determine feeding rates of a solitary ascidian *Styela plicata*: A flume experiment. Marine Ecology Progress Series, 495, 193–204.

Flierl, G., Grünbaum, D., Levins, S. and Olson, D., 1999. From individuals to aggregations: the interplay between behaviour and physics. Journal of Theoretical Biology, 196 (4), 397–454.

Folt, C. L. and Burns, C. W., 1999. Biological drivers of zooplankton patchiness. Trends in Ecology & Evolution, 14 (8), 300–305.

Furst, D., Aldridge, K., Shiel, R., Ganf, G., Mills, S. and Brookes, J., 2014. Floodplain connectivity facilitates significant export of zooplankton to the main River Murray channel during a flood event. Inland Waters, 4 (4), 413–424.

Furst, D., Aldridge, K., Bice, C., Zampatti, B. and Ye, Q., 2018. Ecological response to the Lake Victoria bypass trial 2015–2017. Report to the Commonwealth Environmental Water Office, Canberra.

Furst, D., Aldridge, K., Bice, C., Zampatti, B. and Ye, Q., 2019a. The influence of longitudinal hydrological connectivity on resource availability and lower order food web structure in

the Murray River. A Report to the Commonwealth Environmental Water Office and Murray-Darling Basin Authority, Canberra.

Furst, D., Aldridge, K., Bice, C., Zampatti, B. and Ye, Q., 2019b. The influence of flow translucency and connectivity on resource availability and lower order food web structure in the Murray River. A report to the Commonwealth Environmental Water Office, Canberra.

Furst, D., Bucater, L. and Ye Q., 2019c. Zooplankton community structure in relation to water quality and salt-wedge conditions in the Murray Estuary in spring/summer 2018-19. A report to the Commonwealth Environmental Water Office, Canberra.

Furst, D., Ye, Q., Bice, C., McInerny, P., Biswas, T., Rees, G. and Watts, R., 2020. Zooplankton response to a multi-site environmental watering event during spring 2019 in the Murray River. A report to the Commonwealth Environmental Office, Canberra. Project number CEWO – 2000007157.

García-Comas, C., Lee, Y-C., Chang, C-Y., Gong, G-C. and Hsieh, C-h., 2016. Comparison of Copepod species-based and individual-size-based community structuring. Journal of Plankton Research. 38 (4), 1006–1020.

Garza-Mouriño, G., Silva-Briano, M., Nandini, S., Sarma, S. and Castellanos-Paez, M. E., 2005. Morphological and morphometrical variations of selected Rotifer species in response to predation: a seasonal study of selected brachionid species from Lake Xochimilco (Mexico). Hydrobiologia, 546 (1), 169–179.

Genin, A., Jaffe, J. S, Reef, R., Richter, C. and Franks, P. J. S., 2005. Swimming against the flow: A mechanism of zooplankton aggregation. Science, 308 (5723) 860–862.

Gibbins, C., Vericat, D. and Batalla, R. J., 2007. When is stream invertebrate drift catastrophic? The role of hydraulics and sediment transport in initiating drift during flood events. Freshwater Biology, 52 (12), 2369–2384.

Gibbins, C., Batalla, R. J. and Vericat, D., 2010. Invertebrate drift and benthic exhaustion during disturbance: Response of mayflies (Ephemeroptera) to increasing shear stress and river-bed instability. River Research and Applications, 26 (4), 499–511.

Gibbins, C. N., Vericat, D., Batalla, R. J. and Buendia, C., 2016. Which variables should be used to link invertebrate drift to river hydraulic conditions? Fundamental and Applied Limnology, 187 (3), 191–205.

Gibbs, M. S., Bice, C., Brookes, J., Furst, D., Gao, L., Joehnk, K., Marklund, M., Zampatti, B. and Wallace, T., 2020. Ecological connectivity of the River Murray: Managing ecological outcomes and water quality risks through integrated river management. Goyder Institute for Water Research Technical Report Series No. 20/03.

Gilbert, J. J. and Stemberger, R. S., 1984. Asplanchna-induced polymorphism in the Rotifer *Keratella slacki*. Limnology and Oceanography, 29 (6), 1309–1316.

Glas, M., Tritthart, M., Zens, B., Keckeis, H., Lechner, A., Kaminskas, T. and Habersack, H., 2017. Modelling the dispersal of riverine fish larvae: from a raster-based analysis of movement patterns within a racetrack flume to a rheoreaction-based correlated random walk (RCRW) model approach, 1 (1), 1474–1489.

Glasbergen K, Stone M, Krishnappan B, Dixon J, Silins U. 2015. The effect of coarse gravel on cohesive sediment entrapment in an annular flume. Proceedings of the International Association of Hydrological Sciences, 367, 157–162.

Gomez, B., 1978. 'Flumes'. In Fairbridge, R. R. and Bourgeois, J. (eds), Sedimentology: Encyclopedia of Earth Science. Springer, Berlin, Heidelberg.

González-Ortiz, V., Egea, L. G., Jiménez-Ramos, R., Moreno-Marín, F., Pérez-Lloréns, J. L., Bouma, T. J. and Brun, F. G., 2014. Interactions between Seagrass Complexity, Hydrodynamic Flow and Biomixing Alter Food Availability for Associated Filter-Feeding Organisms. PLOS ONE, 9 (8). e104949.

Gordon, N. D., McMahon, T. A., Finlayson, B. L., Gippel, C. J. and Nathan, R. J., 1992. Stream Hydrology: an introduction for ecologists. John Wiley, Chichester, UK.

Górski, K., Collier, K. J., Duggan, I. C., Taylor, C. M. and Hamilton, D. P., 2013. Connectivity and complexity of floodplain habitats govern zooplankton dynamics in a large temperate river system. Freshwater Biology, 58 (7), 1458–1470.

Green, J. D. and Shiel, R. J., 1995. Calanoid Copepods as Rotifer taxonomists. Quekett Journal of Microscopy, 37 (1), 491–492.

Greenwood, T. L., Green, J. D., Hicks, B. J. and Chapman, M. A., 1999. Seasonal abundance of small cladocerans in Lake Mangakaware, Waikato, New Zealand. New Zealand Journal of Marine and Freshwater Research, 33 (3), 399–415.

Guillard, R. R. L. and Lorenzen, C. J., 1972. Yellow-green algae with chlorophyllide C. Journal of Phycology, 8 (1), 10–14.

Hall, C. J., and Burns, C. W., 2003. Responses of crustacean zooplankton to seasonal and tidal salinity changes in the coastal Lake Waihola, New Zealand. New Zealand Journal of Marine and Freshwater Research, 37 (1), 31–43.

Hart, D. D. and Finelli, C. M., 1999. Physical-biological coupling in streams: the pervasive effects of flow on benthic organisms. Annual Review of Ecology and Systematics, 30 (1), 363–395.

Haskell, C. A. and Stanford, J. A., 2006. Ecology of an estuarine mysid shrimp in the Columbia river (USA). River Research and Applications, 22 (7), 739–753.

Havel, J. E. and Shurin, J. B., 2004. Mechanisms, effects, and scales of dispersal in freshwater zooplankton. Limnology and Oceanography, 49 (4), 1229–1238.

Havens, K. E. and Heath, R. T., 1989. Acid and aluminum effects on freshwater zooplankton: An in situ mesocosm study. Environmental Pollution, 62 (2–3), 195–211.

Hayes, J. W., Goodwin, E. O., Shearer, K. A. and Hicks, D. M., 2018. Relationship between background invertebrate drift concentration and flow over natural flow recession and prediction with a drift transport model. Canadian Journal of Fisheries and Aquatic Sciences, 76 (6), 871–885.

Hedvall, O., Moksnes, P-O. and Pihl, L., 1998. Active habitat selection by megalopae and juvenile shore crabs *Carcinus maenas*: a laboratory study in an annular flume. Hydrobiologia, 375, 89–100.

Hooper, H. L., Connon, R., Callaghan, A., Fryer, G., Yarwood-Buchanan, S., Biggs, J., Maund, S. J., Hutchinson, T. H. and Sibly, R. M., 2008. The ecological niche of *Daphnia magna* characterized using population growth rate. Ecology, 89 (4), 1015–1022.

Hoover, T., 1994. Hydrodynamic controls on the movement of invertebrate larvae and organic matter in small streams. PhD thesis, University of British Columbia, Vancouver.

Horppila, J., Härkönen, L., Hellén, N., Estlander, S., Pekcan-Hekim, Z. and Ojala, A., 2018. Rotifer communities under variable predation-turbulence combinations. Hydrobiologia, 828 (1), 339–351.

Hoyer, K., Holzner, M., Lüthi, B., Guala, M., Liberzon, A. and Kinzelbach, W., 2005. 3D scanning particle tracking velocimetry. Experiments in Fluids, 39 (5), 923–934.

Hunt, H. L., 2004. Effects of epibenthic predators in flow: transport and mortality of juveniles of the soft shell clam Mya arenaria. Marine Ecology Progress Series, 279, 151–160.

Ikeda, T., 1985. Metabolic rates of epipelagic marine zooplankton as a function of body mass and temperature. Marine Biology, 85 (1), 1–11.

Jaeger, A., Posselt, M., Schaper, J. L., Betterle, A., Rutere, C., Coll, C., Mechelke, J., Raza, M., Meinikmann, K., Portmann, A., Blaen, P. J., Horn, M. A., Krause, S. and Lewandowski, J., 2021. Transformation of organic micropollutants along hyporheic flow in bedforms of river-simulating flumes. Scientific Reports, 11 (1), 13034.

Jonsson, P. R., van Duren, L. A., Amielh, M., Asmus, R., Aspden, R. J., Daunys, D., Friedrichs, M., Friend, P. L., Olivier, F., Pope, N., Precht, E., Sauriau, P-G. and Schaaf, E., 2006. Making water flow: a comparison of the hydrodynamic characteristics of 12 different benthic biological flumes. Aquatic Ecology, 40 (4), 409–438.

Karabin, A. and Ejsmont-Karabin, J., 2005. An Evidence for Vertical Migrations of Small Rotifers – a Case of Rotifer Community in a Dystrophic Lake. Hydrobiologia, 546 (1), 381–386.

Karpowicz, M., Ejsmont-Karabin, J., Kozłowska, J., Feniova, I. and Dzialowski, A. R., 2020. Zooplankton Community Responses to Oxygen Stress. Water, 12 (3), 706.

Kennedy, T. A., Yackulic, C. B., Cross, W. F., Grams, P. E., Yard, M. D. and Copp, A. J., 2013. The relation between invertebrate drift and two primary controls, discharge and benthic densities, in a large regulated river. Freshwater Biology, 59 (3), 557–572.

Khan, M., Hasan, M., Sumon, K. and Rashid, P. H., 2020. Culture of freshwater zooplankton *Daphnia magna* fed with different feed combination. Bangladesh Journal of Fisheries. 32 (1), 55–59.

Kilham, S. S., Kreeger, D .A., Lynn, S. G., Goulden, C. E. and Herrera, L., 1998. COMBO: a defined freshwater culture medium for algae and zooplankton. Hydrobiologia, 377 (1), 147–159.

Kiørboe, T., Jiang, H., Gonçalves, R. J., Nielsen, L. T. and Wadhwa, N., 2014. Flow disturbances generated by feeding and swimming zooplankton. Proceedings of the National Academy of Sciences, 111 (32), 11738–11743.

Kirillin, G., Grossart, H-P. and Tang, K. W., 2012. Modeling sinking rate of zooplankton carcasses: Effects of stratification and mixing. Limnology and Oceanography, 57 (3), 881–894.

Klüttgen, B., Dülmer, U., Engels., M. and Ratte, H. T., 1994. ADaM, an artificial freshwater for the culture of zooplankton. Water Research, 28 (3), 743–746.

Kobayashi, T., Gibbs, P., Dixon, P. I. and Shiel, R. J., 1996. Grazing by a river zooplankton community: Importance of microzooplankton. Marine and Freshwater Research, 47 (8), 1025–1036.

Kriesi, C., Steinert, M., Marmaras, A., Danzer, C., Meskenaite, V. and Kurtcuoglu, V., 2019. Integrated Flow Chamber System for Live Cell Microscopy. Frontiers in Bioengineering and Biotechnology, 7, 91.

Kynard, B., Parker, E., Kynard, B. E. and Horgan, M., 2014. Effect of velocity regime on ontogenetic dispersal and habitat use of Kootenai River White Sturgeon (*Acipenser transmontanus*, Richardson, 1836) early life stages: An artificial stream study. Journal of Applied Ichthyology, 30 (6), 1160–1167.

Lagergren, R., Lord, H. and Stenson, J. A. E., 2001. Influence of temperature on hydrodynamic costs of morphological defences in zooplankton: experiments on models of Eubosmina (Cladocera). Functional Ecology, 14 (3), 380–387.

Lair, N., 2005. Abiotic vs. biotic factors: lessons drawn from Rotifers in the Middle Loire, a meandering river monitored from 1995 to 2002, during low flow periods. Hydrobiologia, 546, 457–472.

Lair, N., 2006. A review of regulation mechanisms of metazoan plankton in riverine ecosystems: aquatic habitat versus biota. River Research and Applications, 22 (5), 567–593.

Lampert, W., 1993. Ultimate causes of diel vertical migration of zooplankton: New evidence for the predator-avoidance hypothesis. Archiv für Hydrobiologie Special Issues Advances in Limnology 39: 79–88.

Lancaster, J., Buffin-Bélanger, T., Reid, I. and Rice, S. P., 2006. Flow- and substratum-mediated movement by a stream insect. Freshwater Biology, 51 (6), 1053–1069.

Larsson, P. and Kleiven, O. T., 1996. 'Food search and swimming speed in Daphnia'. In Lenz, P. H., Hartline, D. K., Purcell, J. E. and Macmillan, D. L. (eds), Zooplankton: Sensory Ecology and Physiology, 375–387, Gordon and Breach, Amsterdam.

Locke, A., 1991. Zooplankton responses to acidification: A review of laboratory bioassays. Water, Air, and Soil Pollution, 60 (1), 135–148.

Loiterton, B., Sundbom, M., and Vrede, T., 2004. Separating physical and physiological effects of temperature on zooplankton feeding rate. Aquatic Sciences, 66 (1), 123–129.

Lorke, A., McGinnis, D. F., Spaak, P. and Wüest, A., 2004. Acoustic observations of zooplankton in lakes using a Doppler current profiler. Freshwater Biology, 49 (10), 1280–1292.

Lubzens, E., 1987. 'Raising rotifers for use in aquaculture'. In: May, L., Wallace, R. and Herzig, A. (eds) Rotifer Symposium IV. Developments in Hydrobiology, 42. Springer, Dordrecht.

Lundstedt, L. and Brett, M. T., 1991. Differential growth rates of three cladoceran species in response to mono- and mixed-algal cultures. Limnology and Oceanography, 36 (1), 159–165.

Madhu, K., Madhu, R., Mohandas, M. P. and Vijayan, M. T., 2016. Isolation, identification and culture of the marine rotifer *Colurella adriatica* Ehrenberg, 1831 (Family: Lepadellidae) from Andaman & Nicobar Islands: A promising live feed for larval rearing of high value shellfishes and finfishes. Journal of the Marine Biological Association of India, 58 (1), 5–12.

Majdi, N., Mialet, B., Boyer, S., Tackx, M., Leflaive, J., Boulêtreau, S., Ten-Hage, L., Julien, F., Fernandez, R. and Buffan-Dubau, E., 2012. The relationship between epilithic biofilm stability and its associated meiofauna under two patterns of flood disturbance. Journal of the North American Benthological Society, 31 (1), 38–50.

Mallen-Cooper, M. and Zampatti, B. P., 2018. History, hydrology and hydraulics: Rethinking the ecological management of large rivers. Ecohydraulics, 11 (5), e1965.

May, L., 1987. Culturing freshwater, planktonic rotifers on *Rhodomonas minuta* var. *nannoplanctica Skuja* and *Stichococcus bacillaris Nageli.* Journal of Plankton Research, 9 (6), 1217–1223.

May, L., Bailey-Watts, A. E. and Kirka, A., 2001. The relationship between *Trichocerca pusilla* (Jennings), *Aulacoseira spp*. and water temperature in Loch Leven, Scotland, U.K. Hydrobiologia, 446 (1), 29–34.

Medeiros, E. S. F. and Arthington, A. H., 2008. The importance of zooplankton in the diets of three native fish species in floodplain waterholes of a dryland river, the Macintyre River, Australia. Plankton Studies, 614 (1), 19–31.

Michalec, F-G., Holzner, M., Hwang, J-S., Souissi, S., 2012. Three dimensional observation of salinity-induced changes in the swimming behavior of the estuarine calanoid Copepod *Pseudodiaptomus annandalei*. Journal of Experimental Marine Biology and Ecology, 438, 24-31.

Michalec F-G., Souissi, S. and Holzner, M., 2015. Turbulence triggers vigorous swimming but hinders motion strategy in planktonic copepods. Journal of the Royal Society: Interface Interface, 12 (106), 20150158.

Michels, E., Cottenie, K., Neys, L., De Gelas, K., Coppin, P. and De Meester, L., 2001. Geographical and genetic distances among zooplankton populations in a set of interconnected ponds: a plea for using GIS modelling of the effective geographical distance. Molecular Ecology, 10 (8), 1929–1938.

Modenutti, B., 1998. Planktonic Rotifers of Samborombón River Basin (Argentina). Hydrobiologia, 387, 259–265.

Moore, S. K. and Suthers, I. M., 2006. Evaluation and correction of subresolved particles by the optical plankton counter in three Australian estuaries with pristine to highly modified catchments, Journal of Geophysical Research, Oceans, 111 (C5).

Mueller, C. E., Larsson, A. I., Veuger, B., Middelburg, J. J. and van Oevelen, D., 2014. Opportunistic feeding on various organic food sources by the cold-water coral *Lophelia pertusa*. Biogeosciences, 11 (1), 123–133.

Murray–Darling Basin Authority, 2012. Hydrologic modelling to inform the proposed Basin Plan - methods and results, MDBA, Australian Government, Canberra, No. 17/12.

Murray–Darling Basin Authority, 2020. The Basin Plan Evaluation 2020, MDBA, Australian Government, Canberra, accessed 06 June 2022.

Murray–Darling Basin Authority, 2021a. The Murray-Darling Basin and why it's important, MDBA, Australian Government, Canberra, accessed 06 June 2022, https://www.mdba.gov.au/importance-murray-darling-basin

Murray–Darling Basin Authority, 2021b. Lower Murray: Snapshot, MDBA, Australian Government, Canberra, accessed 22 August 2022, https://www.mdba.gov.au/water-management/catchments/lower-murray

Muschenheim, D. K., Grant, J. and Mills, E. L., 1986. Flumes for benthic ecologists: theory, construction and practice. Marine Ecology Progress Series, 28, 1185–196.

Naman, S. M., Rosonfeld, J. S. and Richardson, J. S., 2016. Causes and consequences of invertebrate drift in running waters: from individuals to populations and trophic fluxes. Canadian Journal of Fisheries and Aquatic Sciences, 73 (8), 1292–1305.

Nielsen, D. L., Brock, M. A., Petrie, R. and Crossle, K., 2007. The impact of salinity pulses on the emergence of plant and zooplankton from wetland seed and egg banks. Freshwater Biology, 52 (5), 784-795.

Nielsen, D. L., Gigney, G. and Watson, G., 2010. Riverine habitat heterogeneity: the role of slackwaters in providing hydrologic buffers for benthic microfauna. Hydrobiologia, 638 (1), 181–191.

Nilsson, C., Reidy, C. A., Dynesius, M. and Revenga, C., 2005. Fragmentation and flow regulation of the world's large river systems. Science, 308 (5720), 405–408.

Noss, C., Dabrunz, A., Rosenfeldt, R. R., Lorke, A. and Schulz, R., 2013. Three-dimensional analysis of the swimming behavior of *Daphnia magna* exposed to nanosized titanium dioxide. PLoS ONE, 8 (11), e80960.

Nowell, A. and Jumars, P., 1987. Flumes: theoretical and experimental consideration for simulation of benthic environments. Oceanography and Marine Biology Annual Review, 25, 91–112.

Núñez-Ortiz, A. R., Nandini, S. and Sarma, S. S. S., 2022. Prey preference of *Stenostomum cf. virginianum Nuttycombe*, 1931 (Platyhelminthes); a case study in the littoral zone of a tropical reservoir. Ecohydrology & Hydrobiology, 22 (1), 168–177.

Obertegger, U., Flaim, G., Braioni, M., Sommaruga, R., Corradini, F. and Borsato, A., 2007. Water residence time as a driving force of zooplankton structure and succession. Aquatic Sciences, 69 (4), 575–583.

Obertegger, U., Cieplinski, A., Raatz, M. and Colangeli, P., 2018. Switching between swimming states in rotifers – case study *Keratella cochlearis*. Marine and Freshwater Behaviour and Physiology, 51 (3), 159–173.

Ogata, Y., 2017. 'Use of Freshwater Brachionus for Aquaculture'. In: Hagiwara, A. and Yoshinaga, T. (eds) Rotifers. Fisheries Science Series. Springer, Singapore.

O'Keefe, T. C., Brewer, M. C. and Dodson, S. I., 1998. Swimming behavior of Daphnia: its role in determining predation risk. Journal of Plankton Research, 20 (5), 973–984.

Olivier, F., Desroy, N. and Retière, C., 1996. Habitat selection and adult-recruit interactions in *Pectinaria koreni* (Malmgren) (Annelida: Polychaeta) post-larval populations: Results of flume experiments. Journal of Sea Research, 36 (3), 217–226.

Palmer, M. A., 1988. Epibenthic Predators and Marine Meiofauna: Separating Predation, Disturbance, and Hydrodynamic Effects. Ecology, 69 (4), 1251–1259.

Palmer, M. A., 1990. Understanding the movement dynamics of a stream-dwelling meiofauna community using marine analogs. Stygologia, 5 (2), 67–74.

Palmer, M. A., 1992. Incorporating lotic meiofauna into our understanding of faunal transport processes. Limnology and Oceanography, 37 (2), 329-341.

Palmer, M. A., Bely, A. E. and Berg, K. F., 1992. Response of invertebrates to lotic disturbance: a test of the hyporheic refuge hypothesis. Oecologia, 89 (2), 182–194.

Palmer, M. A., Arensburger, P., Martin, A. P. and Denman, D. W., 1996. Disturbance and patch-specific responses: the interactive effects of woody debris and floods on lotic invertebrates. Oecologia, 105 (2), 247–257.

Papanicolaou, T., Elhakeem, M. and Hilldale, R., 2007. Secondary current effects on cohesive river bank erosion. Water Resources Research, 43 (12), W12418.

Pasour, V. B. and Ellner, S. P., 2010. Computational and analytic perspectives on the drift paradox. SIAM Journal on Applied Dynamical Systems, 9 (2), 333–356.

Peña-Aguado, F., Nandini, S. and Sarma, S. S. S., 2005. Differences in population growth of rotifers and cladocerans raised on algal diets supplemented with yeast. Limnologica, 35 (4), 298-303.

Perić, M. S., Dražina, T., Špoljar, M., Radanović, I., Primc, B. and Habdija, I., 2014. Meiofauna constitute a considerable portion of invertebrate drift among moss-rich patches within a karst hydrosystem. Biologia, 69 (3), 363–380.

Pourriot, R., Rougier, C. and Miquelis, A., 1997. Origin and development of river zooplankton: example of the Marne. Hydrobiologia, 345, 143–148.

Rahman, H., Azani, N., Suhaimi, H., Yatim, S. R., Yuslan, A. and Rasdi, N. W., 2023. A review on different zooplankton culturing techniques and common problems associated with declining density. IOP Conference Series: Earth and Environmental Science, 1147 (1), 012012.

Record, N. R. and de Young, B., 2006. Patterns of diel vertical migration of zooplankton in acoustic Doppler velocity and backscatter data on the Newfoundland Shelf. Canadian Journal of Fisheries and Aquatic Sciences, 63 (12), 2708–2721.

Rees, G. N., Biswas, T. K., Gilling, D., Watts, R. J., Liu, X., Oliver, R., Pengelly, J., Zygmunt, L. Ye, Q., McInerney, P., Thompson, R., Malthus, T. and Joehnk, K., 2021. River Murray Channel Productivity Monitoring of the Southern Spring Flow 2020. A technical report to the Murray-Darling Basin Authority, CSIRO Land & Water, Canberra, ACT 2601.

Reichard, M. and Janáč, M., 2016. 'Use of Drift Nets to Infer Fish Transport and Migration Strategies in Inland Aquatic Ecosystems'. In Morais, P. and Daverat, F. (eds), An Introduction to Fish Migration. CRC Press, Boca Raton.

Reynolds, C. S., 2000. Hydroecology of river plankton: the role of variability in channel flow. Hydrological Processes, 14 (16–17), 3119–3132.

Ricci, C., 1984. Culturing of some bdelloid rotifers. Hydrobiologia, 112 (1), 45–51.

Richardson, W. B., 1992. Microcrustacea in flowing water: experimental analysis of washout times and a field test. Freshwater Biology, 28 (2), 217–230.

Ringelberg, J., 1999. The photobehaviour of *Daphnia spp*. as a model to explain diel vertical migration in zooplankton. Biological Reviews, 74 (4), 397–423.

Rinke, K. and Petzoldt, T., 2008. Individual-based simulation of diel vertical migration of Daphnia: A synthesis of proximate and ultimate factors. Limnologica, 38 (3–4), 269–285.

Rinke, K., Huber, A. M. R., Kempke, S., Eder, M., Wolf, T., Probst, W. N. and Rothhaupta, K-O., 2009. Lake-wide distributions of temperature, phytoplankton, zooplankton, and fish in the pelagic zone of a large lake. Limnology and Oceanography, 54 (4), 1306–1322.

Rizo, E. Z., Xu, S., Tang, Q., Papa, R.D.S., Dumont, H.J., Qian, S.S. and Han, B-P., 2019. A global analysis of cladoceran body size and its variation linking to habitat, distribution and taxonomy. Zoological Journal of the Linnean Society, 187 (4), 1119–130.

Robertson, A. L., Lancaster, J., Belyea, L. R. and Hildrew, A. G., 1997. Hydraulic habitat and the assemblage structure of stream benthic microcrustacea. Journal of the North American Benthological Society, 16 (3), 562–575.

Robinson, H. E., Finelli, C. M. and Buskey, E. J., 2007. The turbulent life of copepods: effects of water flow over a coral reef on their ability to detect and evade predators. Marine Ecology Progress Series, 349, 171–181.

Roman, M. R., Gauzens, A. L., Rhinehart, W. K. and White, J. R., 1993. Effects of low oxygen waters on Chesapeake Bay zooplankton. Limnology and Oceanography, 38 (8), 1603–1614.

Rottmann, R. W., Graves, J. S., Watson, C. and Yanong, P. E., 1992. 'Culture techniques of Moina: the ideal Daphnia for feeding freshwater fish fry'. In UF/IFAS Tropical Aquaculture Laboratory 813; The Institute of Food and Agricultural Sciences IFAS Publishing: Ocala, FL, USA, 1992; pp. 671–5230.

Rzoska J. 1978. On the nature of rivers: with case stories of Nile, Zaire, and Amazon. Essay by Julian Rzoska. The Hague (Netherlands): Dr. W. Junk.

Sakamoto, M., Chang, K-H. and Hanazato, T., 2007. Plastic phenotypes of antennule shape in *Bosmina longirostris* controlled by physical stimuli from predators. Limnology and oceanography, 52 (5), 2072–2078.

Sampson, S. J., Chick, J. H. and Pegg, M. A., 2009. Diet overlap among two Asian carp and three native fishes in backwater lakes on the Illinois and Mississippi rivers. Biological Invasions, 11 (3), 483–496.

Sandlund, O. T., 1982. The drift of zooplankton and microzoobenthos in the river Strandaelva, western Norway. Hydrobiologia, 94, 33–48.

Sarma, S. S. S., Nandini, S., Morales-Ventura, J., Delgado-Martínez, I. and González-Valverde, L., 2006. Effects of NaCl salinity on the population dynamics of freshwater zooplankton (Rotifers and cladocerans). Aquatic Ecology, 40 (3), 349–360.

Schanz, A., Polte, P. and Asmus, H., 2002. Cascading effects of hydrodynamics on an epiphyte-grazer system in intertidal seagrass beds of the Wadden Sea. Marine Biology, 141, 287–297.

Scheingross, J. S. and Lamb, M. P., 2016. Sediment transport through self-adjusting, bedrock walled waterfall plunge pools. Journal of Geophysical Research, 121 (5), 939–963.

Scofield, A. E., Watkins, J. M. and Rudstam, L. G., 2020. Heterogeneity in zooplankton distributions and vertical migrations: Application of a laser optical plankton counter in offshore Lake Michigan. Journal of Great Lakes Research, 46 (4), 780–797.

Seuront, L., 2006. Effect of salinity on the swimming behaviour of the estuarine calanoid Copepod *Eurytemora affinis*. Journal of Plankton Research, 28 (9), 805–813.

Shang, X., Wang, G. and Li, S., 2008. Resisting flow – laboratory study of rheotaxis of the estuarine Copepod *Pseudodiaptomus annandalei*. Marine and Freshwater Behaviour and Physiology, 41 (2), 109–124.

Shiel, R. J., Walker, K. F. and Williams, W. D., 1982. Plankton of the Lower River Murray, South Australia. Marine and Freshwater Research, 33 (2), 301–324.

Shiel, R, J., 1984. Plankton of the Murray-Darling system, with particular reference to the zooplankton. PhD thesis, The University of Adelaide, Adelaide.

Shiel, R. J. and Walker, K. F., 1984. 'Zooplankton of regulated and unregulated rivers: The Murray-Darling river system, Australia'. In Lillehammer, A. and Saltveit, S. J. (eds), Regulated Rivers, 263–270. Universitetsforlaget AS, Oslo.

Shiel, R. J., 1985. Zooplankton of the Darling River system, Australia. Internationale Vereinigung für Theoretische und Angewandte Limnologie: Verhandlungen, 22, 2136–2140. In SIL Proceedings, 1922-2010.

Sidler, D., Michalec, F-G., Detert, M. and Holzner, M., 2017. Three-dimensional tracking of the motion of benthic copepods in the free water and inside the transparent sediment bed of a laboratory flume. Limnology and Oceanography: Methods, 15 (2), 125–139.

Sidler, D., Michalec, F-G. and Holzner, M., 2018a. Counter-current swimming of lotic Copepods as a possible mechanism for drift avoidance. Ecohydrology, 11 (7), e1992.

Sidler, D., Michalec, F-G. and Holzner, M., 2018b. Behavioral response of the freshwater cyclopoid Copepod *Eucyclops serrulatus* to hydropeaking and thermopeaking in a laboratory flume. Journal of Freshwater Biology, 33 (1), 115–127.

Silvester, N. R. and Sleigh, M. A., 1985. The forces on microorganisms at surfaces in flowing water. Freshwater Biology, 15 (4), 433–448.

Simoncelli, S., Thackeray, S. J., and Wain, D. J., 2019. Effect of temperature on zooplankton vertical migration velocity. Hydrobiologia, 829 (1), 143–166.

Sindlinger, L. R., Biggs, D. C. and DiMarco, S. F., 2005. Temporal and spatial variability of ADCP backscatter on a continental slope. Continental Shelf Research. 25 (2), 259–275.

Sison-Mangus, M. P., Mushegian, A. A. and Ebert, D., 2015. Water fleas require microbiota for survival, growth and reproduction. The ISME Journal, 9 (1), 59–67.

Sluss, T. D., Cobbs, G. A. and Thorp, J. H., 2008. Impact of turbulence on riverine zooplankton: a mesocosm experiment. Freshwater Biology. 53 (10), 1999–2010.

Smeti, H., Pagano, M., Menkes, C., Boissieu, F., Lebourges-Dhaussy, A., Hunt, B. P. V., Allain, V., Rodier, M., Kestenare, E., and Sammari, C., 2015. patial and temporal variability of zooplankton off New Caledonia (Southwestern Pacific) from acoustics and net measurements. Journal of Geophysical Research, 120 (4), 2676–2700.

Smith, I. R., 1975. Turbulence in lakes and rivers, scientific publication No. 29, Freshwater Biological Association, UK (as cited in Gordon et al., 1992).

Smith, F. and Brown, A. V., 2006. Effects of flow on meiofauna colonization in artificial streams and reference sites within the Illinois River, Arkansas. Hydrobiologia, 571 (1), 169–180.

Stemberger, R. S., 1981. A General Approach to the Culture of Planktonic Rotifers. Canadian Journal of Fisheries and Aquatic Sciences, 38 (6), 721–724.

Stemberger, R. S. and Gilbert, J. J., 1987. Rotifer Threshold Food Concentrations and the Size-Efficiency Hypothesis. Ecology, 68 (1), 181–187.

Stone, M., Krishnappan, B. G. and Emelko, M. B., 2008. The effect of bed age and shear stress on the particle morphology of eroded cohesive river sediment in an annular flume. Water Research, 42 (15), 4179–4187.

Stubbington, R., 2012. The hyporheic zone as an invertebrate refuge: A review of variability in space, time, taxa and behaviour. Marine and Freshwater Research, 63 (4), 293–311.

Suantika, G., Dhert, P., Nurhudah, M. and Sorgeloos, P., 2000. High-density production of the rotifer *Brachionus plicatilis* in a recirculation system: consideration of water quality, zootechnical and nutritional aspects. Aquacultural Engineering, 21 (3), 201–213.

Sun, X. and Arnott, S. E., 2022. Interactive effects of increased salinity and heatwaves on freshwater zooplankton communities in simultaneous and sequential treatments. Freshwater Biology, 67 (9), 1604–1617.

Suthers, I. M., Bowling, L., Kobayashi, T. and Rissik, D., 2009. 'Sampling methods for plankton'. In Suthers, I. M., Rissik, D. and Richardson, A. J. (eds), Plankton: A guide to their ecology for water quality. CRC Press, Boca Raton.

Svetlichny, L. S. and Hubareva, E. S., 2002. Effect of oxygen concentration on metabolism and locomotory activity of *Moina micrura* (Cladocera) cultured under hypo- and normoxia. Marine Biology, 141 (1), 145–151.

Svetlichny, L. S., Larsen, P. S. and Kiørboe, T., 2020. Kinematic and dynamic scaling of copepod swimming. Fluids, 5 (2), 68.

Szeligowska, M., Trudnowska, E., Boehnke, R., Dąbrowska, A-M., Wiktor, J. M., Sagan, S. and Błachowiak-Samołyk, K., 2020. Spatial patterns of particles and plankton in the

warming Arctic Fjord (Isfjorden, West Spitsbergen) in seven consecutive mid-summers (2013-2019). Frontiers in Marine Science, 7, 584.

Tamburri, M. N., Finelli, C. M., Wethey, D. S. and Zimmer-Faust, R. K., 1996. Chemical induction of larval settlement behavior in flow. Biological Bulletin, 191 (3), 367–373.

Visser, A. W. and Stips, A., 2002. Turbulence and zooplankton production: insights from PROVESS. Journal of Sea Research, 47 (3–4), 317–329.

Walker, K. F. and Thoms, M. C., 1993. Environmental effects of flow regulation on the lower River Murray, Australia. Regulated Rivers: Research & Management, 8 (1–2), 103–119.

Walker, K. F., 2006. 'Serial weirs, cumulative effects: The Lower River Murray, Australia'. In Kingsford, R. T. (Ed.), Ecology of desert rivers, 248–279. Cambridge: Cambridge University Press.

Wallace, R. L. and Smith, H. A., 2009. 'Rotifera'. In Likens, G. E. (Ed.), Encyclopedia of Inland Waters, 689–703. Oxford: Academic Press.

Walks, D. J., 2007. Persistence of plankton in flowing water. Canadian Journal of Fisheries and Aquatic Sciences, 64 (12), 1693–1702.

Whitman, R. L. and Clark, W. J., 1984. Ecological studies of the sand-dwelling community of an East Texas stream. Freshwater Invertebrate Biology, 3 (2), 59–79.

Widdows, J., Brinsley, M. D., Salkeld, P. N. and Elliott, M., 1998. Use of annular flumes to determine the influence of current velocity and bivalves on material flux at the sediment-water interface. Estuaries, 21 (4), 552–559.

Wiebe, P. H. and Benfield, M. C., 2003. From the Hensen net toward four-dimensional biological oceanography. Progress in Oceanography, 56 (1), 7–136.

Williamson, C. E., 1983. Invertebrate predation on planktonic Rotifers. Hydrobiologia, 104, 385–396.

Williamson, C. E., 1987. Predator-prey interactions between omnivorous diaptomid Copepods and Rotifers: The role of prey morphology and behavior. Limnology and Oceanography, 32 (1), 167–177.

Yang, Z., Baptista, A. and Darland, J., 2000. Numerical modeling of flow characteristics in a rotating annular flume. Dynamics of Atmospheres and Oceans, 31 (1), 271–294.

Yang, S-H., Im, I-T., Hwang, K-N., Cho, Y-S. and Ryu, H-R., 2015. A numerical study on optimal rotation ratio and bottom shear stress in the counter-rotation mode of an annular flume. Journal of Hydro-environment Research, 9 (4), 473–481.

Ye, Q., Giatas, G., Aldridge, K., Busch, B., Gibbs, M., Hipsey, M., Lorenz, Z., Oliver, R., Shiel, R. and Zampatti, B., 2016. Long-term intervention monitoring for the ecological responses of Commonwealth environmental water delivered to the Lower Murray River Selected Area in 2014/15.

Ye, Q., Giatas, G., Brookes, J., Furst, D., Gibbs, M., Oliver, R., Shiel, R., Zampatti, B., Aldridge, K., Bucater, L., Busch, B., Hipsey, M. R., Lorenz, Z., Maas, R., and Woodhead, J., 2020. Commonwealth Environmental Water Office Long-Term Intervention Monitoring Project 2014–2019: Lower Murray River Technical Report. A report prepared

for the Commonwealth Environmental Water Office by the South Australian Research and Development Institute, Aquatic Sciences.

Ye, Q., Giatas, G., Bice, C., Brookes, J., Furst, D., Gibbs, M., Nicol, J., Oliver, R., Shiel, R., Zampatti, B., Bucater, L., Deane, D., Hipsey, M., Huang, P., Lorenz, Z. and Zhai, S., 2021. Commonwealth Environmental Water Office Monitoring, Evaluation and Research Project: Lower Murray 2019-20 Technical Report. A report prepared for the Commonwealth Environmental Water Office by the South Australian Research and Development Institute, Aquatic Sciences.

Ye, Q., Giatas, G., Bice, C., Brookes, J., Furst, D., Gibbs, M., Nicol, J., Oliver, R., Zampatti, B., Bucater, L., Deane, D., Frahn, K., Hipsey, M., Kok, C., Huang, P., Lorenz, Z., Mills, J., Shiel, R. and Zhai, S., 2023. Commonwealth Environmental Water Office Monitoring, Evaluation and Research Project: Lower Murray 2021-22 Technical Report. A report prepared for the Commonwealth Environmental Water Office by the South Australian Research and Development Institute, Aquatic Sciences.

Yin, X. W. and Niu, C. J., 2008. Effect of pH on survival, reproduction, egg viability and growth rate of five closely related rotifer species. Aquatic Ecology, 42 (4), 607–616.

Yoshimatsu, T. and Hossain, M. A., 2014. Recent advances in the high-density rotifer culture in Japan. Aquaculture International, 22 (5), 1587–1603.

Zens, B., Glas, M., Tritthart, M., Habersack, H. and Keckeis, H., 2018. Movement patterns and rheoreaction of larvae of a fluvial specialist (nase, *Chondrostoma nasus*): the role of active versus passive components of behaviour in dispersal. Canadian Journal of Fisheries and Aquatic Sciences, 75 (2), 193–200.

Zhou, J., Han, X., Qin, B., Casenave, C. and Yang, G., 2016. Response of zooplankton community to turbulence in large, shallow Lake Taihu: a mesocosm experiment. Fundamental and Applied Limnology. 187 (4), 315–324.

5. APPENDIX

Appendix 1. List of rotifers, cladocerans and copepods within the lower River Murray in 2014-15, 2015-16, 2016-17 and 2017-2018 and their classification based on their preferred habitat. Data acquired from the Long-term Intervention Monitoring Project 2014-2019 (Ye et al., 2020), licensed under CC-BY 3.0.

Species identified	Group	Classification
Habrotrocha sp.	Rotifer	Littoral
Philodina alata NR for Aust	Rotifer	Littoral
Philodina sp.	Rotifer	Littoral
Rotaria neptunia	Rotifer	Littoral
Rotaria sp.	Rotifer	Littoral
indet. bdelloid [sm]	Rotifer	Littoral
indet. bdelloid [lg]	Rotifer	Littoral
Asplanchna cf. brightwellii	Rotifer	Pelagic
Asplanchna priodonta	Rotifer	Pelagic
Asplanchna sp.	Rotifer	Pelagic
Asplanchnopus sp.	Rotifer	Pelagic
Anuraeopsis coelata	Rotifer	Pelagic
Anuraeopsis fissa	Rotifer	Pelagic
Brachionus angularis	Rotifer	Pelagic
Brachionus bennini	Rotifer	Littoral (facultatively pelagic)
Brachionus bidens	Rotifer	Pelagic
Brachionus bidentatus	Rotifer	Littoral (facultatively pelagic)
Brachionus budapestinensis	Rotifer	Pelagic
Brachionus calyciflorus amphiceros	Rotifer	Pelagic
Brachionus calyciflorus s.l.	Rotifer	Pelagic
Brachionus caudatus personatus	Rotifer	Pelagic
Brachionus dichotomus reductus	Rotifer	Pelagic
Brachionus diversicornis	Rotifer	Pelagic
Brachionus durgae	Rotifer	Pelagic
Brachionus falcatus	Rotifer	Pelagic
Brachionus keikoa	Rotifer	Pelagic

Brachionus lyratus	Rotifer	Pelagic
Brachionus nilsoni	Rotifer	Pelagic
Brachionus novaezegiandiae	Rotifer	Pelagic
Brachionus quadridentatus cluniorbicularis	Rotifer	Littoral (facultatively pelagic)
Brachionus quadridentatus s str.	Rotifer	Pelagic
Brachionus rubens	Rotifer	Pelagic
Brachionus urceolaris	Rotifer	Pelagic
Brachionus n. sp. [angularis-lyratus group]	Rotifer	Pelagic
Brachionus sp.	Rotifer	Pelagic
Keratella amelicana	Rotifer	Pelagic
Keratella australis	Rotifer	Pelagic
Keratella cochlearis	Rotifer	Pelagic
Keratella javana	Rotifer	Pelagic
Keratella lenzi	Rotifer	Pelagic
Keratella procurva	Rotifer	Pelagic
Keratella quadrata	Rotifer	Pelagic
Keratella shieli	Rotifer	Pelagic
Keratella slack	Rotifer	Pelagic
Keratella lecto	Rotifer	Pelagic
Keratella tropica	Rotifer	Pelagic
Plationus patuus	Rotifer	Pelagic
Platyias quadricornis	Rotifer	Pelagic
Collotheca pelagica	Rotifer	Pelagic
Collotheca cf. tenuilobata	Rotifer	Pelagic
Collotheca sp.	Rotifer	Littoral
Conochilus dossuarus	Rotifer	Pelagic
Conochilus natans	Rotifer	Pelagic
cf. Dicranophoroides sp.	Rotifer	Littoral
cf. Dicranophorus sp.	Rotifer	Littoral
cf. Encentrumspo	Rotifer	Littoral

Kostea wockei	Rotifer	Littoral
Cyrtania tuba	Rotifer	Littoral
cf. Epiphanes sp.	Rotifer	Pelagic
cf. Microcodices sp.	Rotifer	Pelagic
Proalides tentoculatus	Rotifer	Pelagic
Proalides sp.	Rotifer	Pelagic
Beauchampiela eudactylota	Rotifer	Littoral
Euchianis sp.	Rotifer	Littoral
Ptygura sp.	Rotifer	Pelagic
ficsculariid sp. [cf. Sinanatherinc]	Rotifer	Littoral
Ascomorpha cf. ovalis	Rotifer	Pelagic
Ascomorpha saitans	Rotifer	Pelagic
Gastropus minor	Rotifer	Pelagic
Hexarthra braziliensis	Rotifer	Pelagic
Hexarthra intermedia	Rotifer	Pelagic
Hexarthra sp.	Rotifer	Pelagic
Lecane bulla	Rotifer	Littoral
lecane b n. sp.	Rotifer	Littoral
Lecane closterocerca	Rotifer	Littoral
Lecane crepida	Rotifer	Littoral
Lecane curvicornis	Rotifer	Littoral
Lecane flexilis	Rotifer	Littoral
Lecane halsei	Rotifer	Littoral
Lecane hamata	Rotifer	Littoral
Lecane nr hamata ?n. sp.	Rotifer	Littoral
Lecane ludwigü	Rotifer	Littoral
Lecane luna	Rotifer	Littoral
Lecane lunaris	Rotifer	Littoral
Lecane obtusa	Rotifer	Littoral
Lecane signifera	Rotifer	Littoral

Lecane stenroosi	Rotifer	Littoral
Lecane ungulata	Rotifer	Littoral
Lecane is. str.) sp.	Rotifer	Littoral
Lecane (M.) sp. a	Rotifer	Littoral
Lecane (M.) sp. b	Rotifer	Littoral
Colurella obtusa	Rotifer	Littoral
Colurella uncinata bicuspidata	Rotifer	Littoral
Colurella sp.	Rotifer	Littoral
lepadella acuminata	Rotifer	Littoral
Lepadella patella	Rotifer	Littoral
Lepadella rhomboides	Rotifer	Littoral
Lepadella sp.	Rotifer	Littoral
Squatinella sp.	Rotifer	Littoral
Lindia sp.	Rotifer	Littoral
Lophocharis salpina	Rotifer	Littoral
cf. Proales sp.	Rotifer	Littoral
Cephalodeila catellina	Rotifer	Littoral
Cephalodella forficula	Rotifer	Littoral
Cephalodella gibba	Rotifer	Littoral
Cephalodella sp. a [v. sm]	Rotifer	Littoral
Cephalodella sp. b [med]	Rotifer	Littoral
Cephalodella sp. c [lg. elongare toes]	Rotifer	Littoral
Eosphera anthadis	Rotifer	Littoral
Eosphara sp.	Rotifer	Littoral
Monommata sp.	Rotifer	Littoral
Notommata cf. prodota	Rotifer	Littoral
Notommata spp.	Rotifer	Littoral
cf. Resticula sp. [?n.sp.]	Rotifer	Littoral
cf. Taphrocampa sp.	Rotifer	Littoral
indet. elong. notommatid	Rotifer	Littoral

Scaridium cf. longicaudum	Rotifer	Littoral
Polyarthra dolichoptera	Rotifer	Pelagic
Polyarthra vulgaris	Rotifer	Pelagic
Synchaeta oblonga	Rotifer	Pelagic
Synchaeta pectinata [med-lg, >100 µm]	Rotifer	Pelagic
Synchaeta n. 5.[tiny]	Rotifer	Pelagic
Pompholyx complanata	Rotifer	Pelagic
Testudinella patina	Rotifer	Pelagic
Trichocerca agnatha	Rotifer	Littoral
Trichocerca bicristata	Rotifer	Littoral
Trichocerca bidens	Rotifer	Littoral
Trichocerca cf. insignis	Rotifer	Littoral
Trichocerca pusilla	Rotifer	Littoral (facultatively pelagic)
Trichocerca rattus carinata [was sp.a]	Rotifer	Littoral
Trichocerca similis	Rotifer	Littoral (facultatively pelagic)
Trichocerca similis grandis	Rotifer	Littoral (facultatively pelagic)
Trichocerca cf. tigris	Rotifer	Littoral
Trichocerca cf. weberi	Rotifer	Littoral
Trichocerca sp. b [tiny]	Rotifer	Littoral
Trichocerca sp. c [long toe, med]	Rotifer	Littoral
Trichocerca sp. d [gracile, med toe(s)]	Rotifer	Littoral
Trichocerca sp. e [sm bulb body, long toe]	Rotifer	Littoral
Trichocerca sp. f [oblate body, short toe]	Rotifer	Littoral
Trichocerca sp. g [small curved gracile, short toe]	Rotifer	Littoral
Trichocerca sp. h [robust, long toe]	Rotifer	Littoral
Macrochaetus sp.	Rotifer	Littoral
Trichotria tetractis similis	Rotifer	Littoral
Filinia australiensis	Rotifer	Pelagic
Filinia brachiata	Rotifer	Pelagic
Filinia grandis	Rotifer	Pelagic

Filinia longiseta	Rotifer	Pelagic
Filinia opoliensis	Rotifer	Pelagic
Filinia passa	Rotifer	Pelagic
Filinia pejleri	Rotifer	Pelagic
Filinia terminalis	Rotifer	Pelagic
indet. 2-toed rotifer [sm]	Rotifer	Littoral
indet. glob. rotifer	Rotifer	Littoral
indet. plicate rotifer	Rotifer	Littoral
Bosmina meridionalis	Cladoceran	Pelagic
Armatalona macrocopa	Cladoceran	Littoral
Chydorus cf. eurynotus	Cladoceran	Littoral
Leberis diaphanus	Cladoceran	Littoral
Picripleuroxus quasidenticulatus	Cladoceran	Littoral
Pseudochydorus globosus	Cladoceran	Littoral
Pseudomonospilus diporus	Cladoceran	Littoral
indet. chydorid	Cladoceran	Littoral
Ceriodaphnia cornuta	Cladoceran	Pelagic
Ceriodaphnia sp. [non-cornuta]	Cladoceran	Pelagic
Daphnia carinata s.l.	Cladoceran	Pelagic
Daphnia galeata	Cladoceran	Pelagic
Daphnia lumholtzi	Cladoceran	Pelagic
Daphnia sp. [non-lumh. late embryos]	Cladoceran	Pelagic
Simocephalus sp.	Cladoceran	Littoral
Ilyocryptus sp. [juv]	Cladoceran	Littoral
Macrothrix sp.	Cladoceran	Littoral
Moina cf. australiensis	Cladoceran	Pelagic
Moina micrura	Cladoceran	Pelagic
Moina cf. tenuicornis	Cladoceran	Pelagic
Neothrix sp.	Cladoceran	Littoral
Diaphanosoma excisum	Cladoceran	Pelagic

Boeckella triarticulata	Copepod	Pelagic
Calamoecia ampulla	Copepod	Pelagic
Calamoecia sp.	Copepod	Pelagic
Gladioferens sp. [female]	Copepod	Pelagic
calanoid copepodite	Copepod	Pelagic
calanoid nauplii	Copepod	Pelagic
Acanthocyclops cf. vernalis	Copepod	Littoral
Australocyclops australis	Copepod	Littoral
Mesocyclops notius	Copepod	Littoral
Microcyclops varicans	Copepod	Littoral
Thermocyclops	Copepod	Littoral
indet subadult cyclopoid	Copepod	Littoral
cyclopoid copepodite	Copepod	Littoral
cyclopoid nauplii	Copepod	Littoral
indet. cyclopoid nauplius	Copepod	Littoral
indet. harpac.	Copepod	Littoral
harpac. copepodite	Copepod	Littoral
indet. copepod nauplius	Copepod	Littoral
Limnocythere sp.	Ostracod	Littoral
indet. ostracod [juv.]	Ostracod	Littoral