Northern Australia Environmental Resources Hub

National Environmental Science Programme

Environmental flows synthesis to support uptake of environmental flows research in northern Australia

Final report

MJ Kennard, LS Beesley, S. Bunn, M Burford, RM Burrows, CA Canham, D Crook, MM Douglas, E Garcia, A King, SA Setterfield, K O'Mara, J Marshall, BJ Pusey, B Stewart-Koster, M Venarsky

Griffith University · The University of Western Australia · Charles Darwin University Australia

This report should be cited as:

Kennard MJ,[1] Beesley LS,[2] Bunn S,[1] Burford M,[1] Burrows RM,[1] Canham CA,[2] Crook D,[3] Douglas MM,[2] Garcia E,[3] King A,[3] Macgregor G,[4] Marshall J,[4] O'Mara K,[1] Pusey BJ,[2] Setterfield SA,[2] Stewart-Koster B[1] and Venarsky M[1] (2022) Environmental flows synthesis to enhance uptake of environmental flows research in northern Australia. Griffith University, Brisbane.

1. Australian Rivers Institute, Griffith University, Brisbane
2. School of Biological Sciences, The University of Western Australia, Perth
3. Research Institute for the Environment and Livelihoods, Charles Darwin University, Darwin
4. Queensland Department of Environment and Science, Brisbane

Cover photograph

Front cover: The Daly River at Oolloo Crossing, Wagaman Country (photo Michael Douglas).

This report is available for download from the Northern Australia Environmental Resources (NAER) Hub website at nespnorthern.edu.au.

The Hub is supported through funding from the Australian Government's National Environmental Science Program (NESP). The NESP NAER Hub is hosted by Charles Darwin University.

Contents

List of figures

List of tables

List of boxes

1. Introduction

River flows support healthy ecosystems that provide a wealth of economic, social and cultural goods and services such as fisheries, recreation and tourism attractions, bush tucker, clean water, fertile floodplains and more. Understanding the links between river flows and healthy ecosystems is therefore critical to determining how much water is needed to maintain these goods and services. In places where these links are unknown, water planners need to infer relationships from similar places until enough local field data is collected and analysed.

Environmental flows research conducted through the Northern Australia Environmental Resources Hub of the Australian Government's National Environmental Science Program (NESP) has focused on 1) quantifying critical flow needs to sustain freshwater and coastal ecosystems, biodiversity and productivity in tropical northern Australia and 2) predicting ecological responses to flow alteration from water-resource developments. Much of this work has been conducted in the Fitzroy River (Western Australia), Daly River (Northern Territory) and rivers in Queensland's southern Gulf of Carpentaria, and builds on previous work in these catchments. To maximise the usefulness of this research, it is important to evaluate how transferable research findings are to other locations and scales, and identify the key considerations when applying this knowledge. Understanding the inferential strength of flow–ecology links and their transferability to other locations is important for robust water planning assessment of flow-related impacts of development proposals and climate change in catchments with limited field data.

Chapter 2 of this report identifies potential constraints, opportunities and key considerations for transfer of flow-ecology knowledge. In particular, we evaluate the inferential strength of different types of ecological response relationships and issues of scope and scale. We also consider transfer and scaling of ecological responses through space and time.

Chapter 3 describes key flow-ecology principles to inform water planning and management (drawn from Douglas et al. 2019[1]) and provides a synthesis of supporting evidence from NESP Northern Australia Hub environmental flow research in each focal catchment and from other studies in northern Australia.

Chapter 4 uses a case-study approach to review the quantity and quality of evidence supporting key principles relating to tropical freshwater food webs, evaluates potential transferability of aquatic food web research in northern Australia, and identifies spatial and conceptual gaps in our understanding of their ecology and management.

In Chapter 5, we synthesise ecohydrological risks associated with hydrologic alteration, river impoundment, fragmentation and other threats to ecological integrity.

Chapter 6 concludes by identifying management options to mitigate risks and enhance societal benefits of water resource development in northern Australia with a focus on strategic water resource planning and management, environmental flow management and water infrastructure management.

---

[1] Douglas MM, Jackson S, Canham CA, Laborde S, Beesley L, Kennard MJ, Pusey BJ, Loomes R and Setterfield SA (2019) Conceptualising hydro-socio-ecological relationships to enable more integrated and inclusive water allocation planning. *One Earth* 1:361–373.

2. Constraints, opportunities and key considerations for transfer of flow-ecology knowledge

2.1 Context

Environmental flows research conducted through the Northern Australia Environmental Resources Hub of the Australian Government's National Environmental Science Program (NESP) focused on 1) quantifying critical flow needs to sustain freshwater and coastal ecosystems, biodiversity and productivity in northern Australia and 2) predicting ecological responses to flow alteration from water-resource developments. Outputs from the research include flow-ecology response relationships in the form of conceptual, qualitative and quantitative models with supporting narrative and/or guiding principles. These flow-ecology response relationships have been derived from correlative/observational data from field studies, laboratory experiments, expert opinion and desktop reviews of relevant studies conducted elsewhere. Each approach is valid (Norris et al. 2011) but each has strengths and weaknesses in terms of the inferential strength of the ecological-response relationship to inform environmental flow decision-making.

2.2 Inferential strength of ecological response relationships and issues of scope and scale

The inferential strength of an ecological-response relationship reflects the quantity and quality of evidence available that supports that relationship. In other words, how true is the relationship (i.e. is there demonstrated cause and effect) and where else and when could the relationship be validly applied (how general is the relationship)? The type of scientific evidence used to generate ecological response relationships varies widely, is usually based on a blend of inductive and deductive reasoning (Susser 1986), and may include correlative/observational data, manipulative experimental data (laboratory or field), expert opinion derived through elicitation, and multiple lines and levels of evidence, combining some or all the above (see Norris et al. 2011).

Key considerations concerning the inferential strength of information to draw conclusions or make predictions in new contexts also relate to issues of scope and scale (Mac Nally 2002; Corwin et al. 2006). Scope and scale typically concern the spatial extent of environmental or ecological systems and the duration of processes associated with them (Figure 2-1). Large systems tend to have long histories and long-period dynamics, whereas small systems may respond over shorter time frames, within the constraints imposed at larger/longer scales. Cross-scale interactions also mean that small-scale processes may have non-linear effects on large-scale processes and vice versa (Corwin et al. 2006).

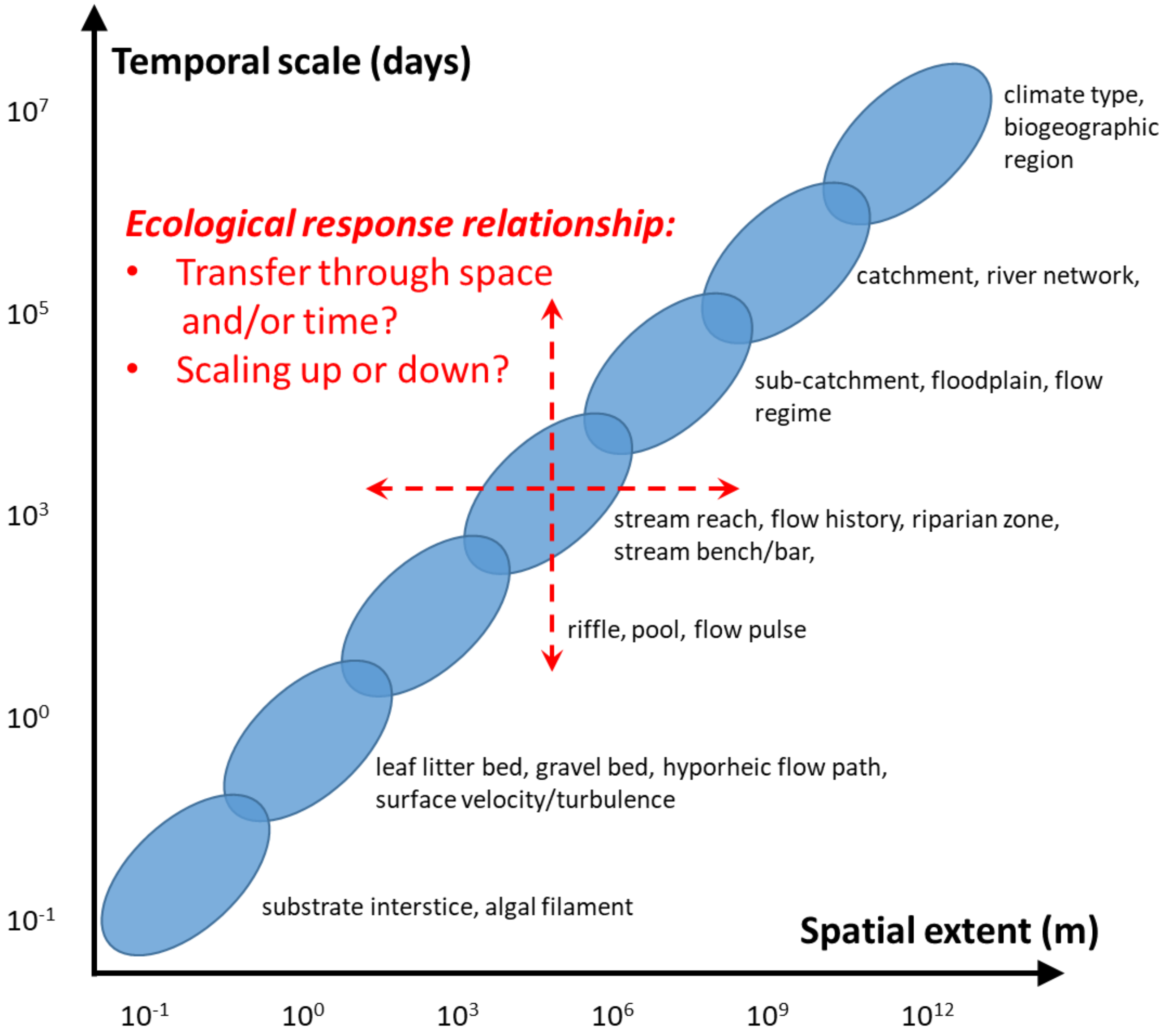

Figure 2-1. Conceptualisation of general spatial and temporal domains associated with freshwater ecosystems. The inferential strength of ecological response relationships generated at a particular scale will decline with increasing departure from the spatio-temporal domain(s) from which data were collected and the ecological response generated (source: modified from Boulton and Brock 1999, Mac Nally 2002, Andersen et al. 2016).

Issues of scope and scale highlight questions of whether ecological research is conducted at inappropriate scales for many ecological objects, especially in temporal terms (studies too short in duration), whether the choice of scale matches the needs of natural resource and conservation managers, and whether inferences drawn from restricted scales can be transferred to other situations and scales (upscaling, for example). It is relatively straightforward to identify the overall spatial extent and duration of a particular study system (e.g. a field study conducted in a particular river basin over a 3-year period), the size of sampling units in which data is collected (e.g. habitat patches within stream reaches) and the sampling frequency used (e.g. surveys conducted bimonthly). While specification of sampling details provides precise information on the implied relevance of the study, it does not necessarily help to identify the extent to which this information can be transferred or scaled up (or down).

2.3 Transfer and scaling of ecological responses through space and time

Ecologists have long sought to distinguish relationships that are general from those that are idiosyncratic to a narrow range of conditions (Peters 1991; Wenger and Olden 2012). Although relationships that are limited in scope and scale may be interesting and informative, they are not necessarily broadly applicable or likely to constitute a general rule, and hence be useful for environmental management. Instead, models are sought that are variously (and interchangeably) said to have generality, generalisability and/or transferability to datasets or situations other than the one for which they were developed (Wenger and Olden 2012). Most ecologists view the generality of a model as being proportional to the number of biological systems or environmental conditions that a model can capture or to which its conclusions can be applied (Evans et al. 2013).

The issue of transferability has been the subject of ecological interest for a number of years but has greatly increased with the rise of the field of species distribution modelling in the 2000s (Elith and Leathwick 2009). Researchers have investigated whether a species distribution model developed in one region can successfully predict distributions in a different region (e.g. Kennard et al. 2007) and whether models developed in one time period can predict distributions in a different time period with different weather or climatic conditions (e.g. Kennard et al. 2006). In addition, studies have investigated whether relationships between hydrological conditions and species abundances or biomass are transferable across both space and time (Kennard et al. 2007; Chen and Olden 2017).

In some places, climates will shift to entirely novel ones that lack current analogues (Williams, et al. 2007), potentially further limiting transferability of a predictive ecological models calibrated under an entirely different set of environmental conditions. Such questions of generality are equally applicable to models of physical phenomena (e.g. models of temperature), of ecological processes (e.g. denitrification rates) or of population parameters (e.g. growth rates) (Wenger and Olden 2012). The key challenge is that there can be considerable spatial or temporal heterogeneity in environment-ecology response relationships, and this heterogeneity can limit model generality (Wenger and Olden 2012).

Key to the issue of transferability is that ecological response relationships can most reliably be transferred to situations with environmental conditions (through space and time) within the scale and scope (Figure 2-1) of the conditions in which the relationship was developed. Transfer beyond this range should be made with caution. Environmental or biological regionalisations or classifications (e.g. of hydrology, groundwater-dependent ecosystem type, climate, bioregion; see Olden et al. 2012) can assist with deciding on appropriate situations for model/knowledge transfer, provided that the environmental attributes used to inform the assessment are functionally/mechanistically related to the response variables of interest (Poff et al. 2010).

Importantly, different ecological response variables likely vary in their transferability, and for different reasons. For example, measures of ecological processes (e.g. organic matter decomposition) may vary due to changes in resource supply and local physical properties of the environment, which are in turn linked to seasonal climate conditions and the nature of land–water connections, functional attributes of biotic communities (e.g. based on species' traits describing morphology, resource use, life history, etc) may be constrained by phylogenetic history (Sternberg and Kennard 2013), and species distributions may be constrained by biogeographic factors such as regional species pools and spatial connectivity (Poff 1997; Sternberg et al. 2014).

These issues highlight the need to understand the factors responsible for shaping ecological responses generated in a particular setting and potential confounding influences before the response relationship can be reliably applied elsewhere (e.g. to predict ecological responses to groundwater drawdown). Conceptual models that articulate ecological response relationships and include key drivers and potential confounding factors can aid in this process (Commonwealth of Australia 2015). The improved understanding of ecological responses to changes in surface water and groundwater hydrology generated through the NESP e-flows projects enabled the development of conceptual models that can facilitate the transferability of the findings of the research program to other situations for use by scientists and water managers.

2.4 References

Andersen M., Barron O., Bond N., Burrows R., Eberhard S., Emelyanova I., Fensham R., Froend R., Kennard M., Marsh N., Pettit N., Rossini R., Rutlidge R., Valdez D. & Ward D. (2016) Research to inform the assessment of ecohydrological responses to coal seam gas extraction and coal mining, Department of the Environment and Energy, Commonwealth of Australia.

Boulton A.J. & Brock M.A. (1999). Australian Freshwater Ecology: Processes and Management. Gleneagles Publishing. Glen Osmond.

Chen W. & Olden J.D. (2018). Evaluating transferability of flow–ecology relationships across space, time and taxonomy. *Freshwater Biology* 63: 817–830.

Commonwealth of Australia (2015). Modelling water-related ecological responses to coal seam gas extraction and coal mining, prepared by Auricht Projects and the Commonwealth Scientific and Industrial Research Organisation (CSIRO) for the Department of the Environment, Commonwealth of Australia’.

Corwin D.L., Hopmans J. & de Rooij G.H. (2006). From field-to landscape-scale vadose zone processes: scale issues, modelling, and monitoring. *Vadose Zone Journal* 5: 129-139.

Elith J. & Leathwick J.R. (2009). Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics* 40: 677–697.

Evans M.R., Grimm V., Johst K., Knuuttila T., de Langhe R., Lessells C.M., Merz M., O’Malley M.A., Orzack S.H., Weisberg M., Wilkinson D.J., Wolkenhauer O. & Benton T.G. (2013). Do simple models lead to generality in ecology? *Trends in Ecology & Evolution* 28: 578 – 583.

Kennard M.J., Pusey B.J., Arthington A.H., Harch B.D. & Mackay S.J. (2006). Development and application of a predictive model of freshwater fish assemblage composition to evaluate river health in eastern Australia. *Hydrobiologia* 572: 33–57

Kennard M.J., Olden J.D., Arthington A.H., Pusey B.J. & Poff N.L. (2007). Multiscale effects of flow regime, habitat, and their interaction on fish assemblage structure in eastern Australia. *Canadian Journal of Fisheries and Aquatic Sciences* 64: 1346–1359

Mac Nally R. (2002). Improving inference in ecological research: issues of scope, scale, and model validation. *Comments on Theoretical Biology* 7: 237–256.

Norris R.H., Webb J.A., Nichols S.J., Stewardson M.J. & Harrison E.T. (2011). Analyzing cause and effect in environmental assessments: using weighted evidence from the literature. *Freshwater Science* 31: 5-21.

Olden J.D., Kennard M.J. & Pusey B.J. (2012). A framework for hydrologic classification with a review of methodologies and applications in ecohydrology. *Ecohydrology*. 5: 503–518

Peters R.H. (1991). A Critique of Ecology. Cambridge University Press, Cambridge, UK.

Poff N.L., Richter B., Arthington A.H., Bunn S.E., Naiman R.J., Kendy E., Acreman M., Apse C., Bledsoe B.P., Freeman M., Henriksen J., Jacobson R.B., Kennen J., Merritt D.M., O'Keefe J., Olden J., Rogers K., Tharme R.E. & Warner A. (2010). The Ecological Limits of Hydrologic Alteration (ELOHA): a new framework for developing regional environmental flow standards. *Freshwater Biology* 55: 147-170.

Sternberg D., Kennard M.J. & Balcombe S.R. (2014). Biogeographic determinants of Australian freshwater fish life-history indices assessed within a spatio-phylogenetic framework. *Global Ecology and Biogeography* 23: 1387–1397.

Susser M. (1986). The logic of Sir Karl Popper and the practice of epidemiology. *American Journal of Epidemiology* 124: 711–718.

Wenger S.J. & Olden J.D. (2012). Assessing transferability of ecological models: an underappreciated aspect of statistical validation. *Methods in Ecology and Evolution* 3: 260–267.

Williams J.W., Jackson S.T. & Kutzbacht J.E. (2007). Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences of the United States of America* 104: 5738–5742.

3. Key flow-ecology principles and synthesis of supporting evidence from NESP Northern Australia Hub environmental flow research in each focal catchment and from other studies in northern Australia

Douglas et al. (2019) identified a set of key flow-ecology principles to inform water planning and management in the Fitzroy River, north-western Australia. These principles were generated from a review of relevant flow-ecology research conducted in the Fitzroy River, elsewhere in northern Australia and from other wet-dry tropical regions around the world. The principles centred around the importance of surface and groundwater in maintaining the distribution and quality of riverine environments, including the lateral, longitudinal and vertical connectivity between environments during 4 different flow phases (Figure 3-1). In addition, the importance of short-term and long-term antecedent hydrological conditions, lag effects and long-term climatic changes and cycles was recognised (Douglas et al. 2019). We have synthesised evidenced in support of these principles from the NESP Northern Hub environmental flow research projects in each focal catchment and from other studies in northern Australia (Table 3-1).

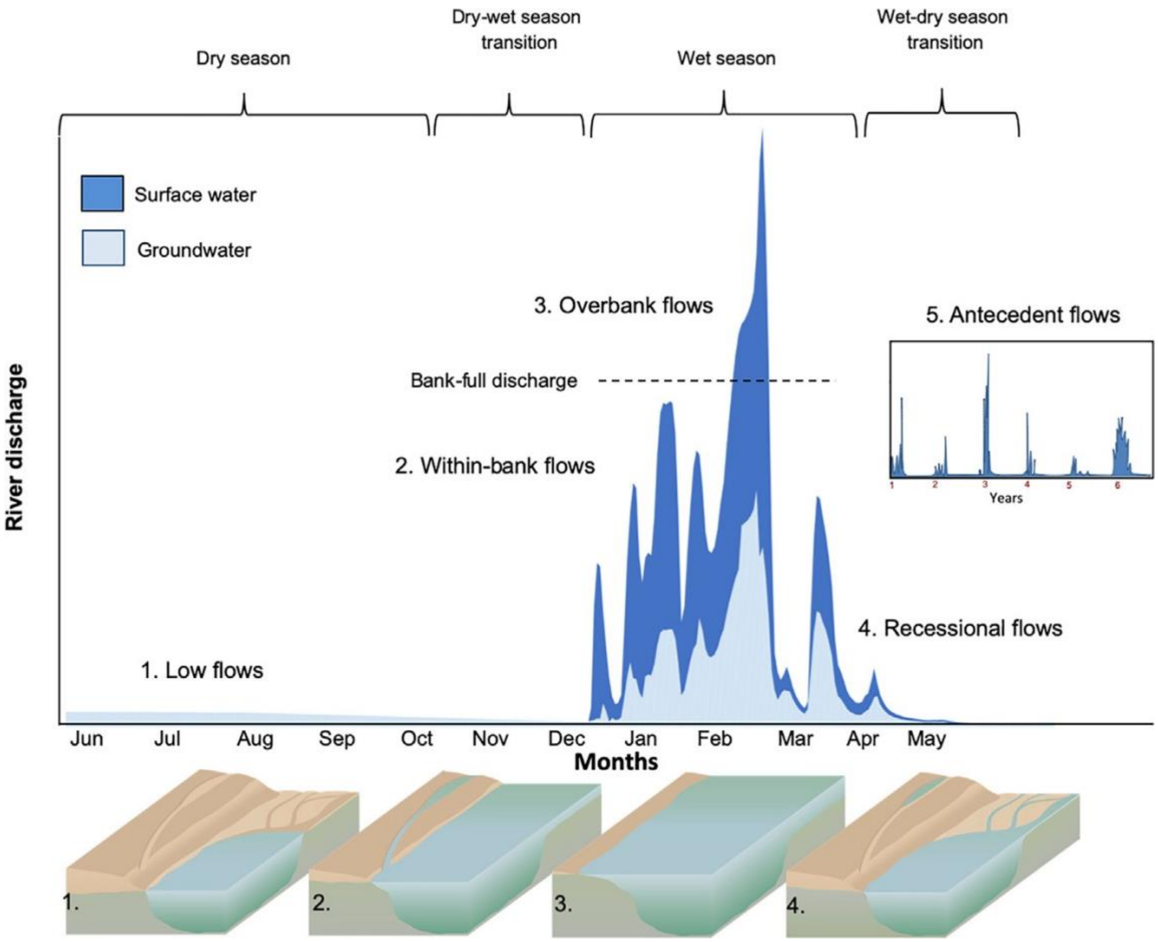

Figure 3-1. A stylised depiction of an annual hydrograph of the Fitzroy River showing the 4 seasonal flow phases and associated aquatic habitats present in the river's lower reaches. A fifth flow phase describing inter-annual variation in flow (i.e. antecedent flows) is shown in the inset. The general contribution of surface and groundwater to river flow is illustrative only. Source: Douglas et al. (2019).

Table 3-1. Key flow-ecology principles (adapted from Douglas et al. 2019) and synthesis of supporting evidence from NESP Northern Australia Hub environmental flows research in each focal catchment and from other studies in northern Australia.

Principle	Sub-principle	Evidence from NESP projects: Mitchell freshwater – NESP project 1.3.1	Daly freshwater – NESP project 1.3.2	Fitzroy freshwater – NESP project 1.3.3	Estuaries (Mitchell, Gilbert, Flinders) – NESP project 1.4	Evidence from other studies in northern Australia
Within-bank flows promote longitudinal connectivity and are important for the ecology of the river and its estuary.	Within-bank flows restore longitudinal connectivity in cease-to-flow reaches and facilitate the passage of animals along the length of the river, including movement to and from the estuary. These connections facilitate longitudinal food-web subsidies that support growth and reproduction.	• Connectivity influences fish movement, with more migration to highly connected river reaches. • Many fish species use connectivity to feed elsewhere in the catchment in the wet season, facilitating longitudinal food-web subsidies (O'Mara et al. 2021).	• Fish in channel habitats use wet-season connectivity to feed elsewhere in the catchment. • Connectivity is intact and facilitates longitudinal food-web subsidies. • While most pig-nosed turtles are resident, the females that move do so when with the first wet-season flows occur and at the end of the wet season. • Connections to the estuary are important for movement of fish, particularly barramundi. • Migration to freshwater results in a growth advantage in barramundi (Roberts et al. 2019). • Faster growth as juveniles results in higher fecundity in adult barramundi (Roberts et al. 2021).	• Flow in the main channel is important in predicting the abundance and condition of some species (cherabin and catfish, respectively). • Juvenile cherabin are abundant in main-channel pools in the lower reaches of the river, providing indirect evidence that adults use an estuarine nursery. • No evidence found for transport of remote carbon from the floodplain or estuary into the lower main-channel of the river by large-bodied fish. However, limitations hampered research.	• Connectivity between the estuary and river ensures barramundi can access the coast to complete obligate spawning migrations which contribute to the fishery. • Barramundi that spend time in freshwater grow larger and faster.	• Connectivity is important for movement of aquatic organisms to forage, disperse and reproduce (e.g. Bishop, Pidgeon & Walden, 1995; Staunton-Smith et al. 2004; Novak et al. 2015; Pusey et al. 2018). • Flow-driven movements provide food-web connectivity along the length of the river channel and to the estuary and floodplain (Jardine et al. 2012b; Novak et al. 2017). • Movement has shown to be advantageous for growth or condition in other studies from the Fitzroy River. For example, wet-season floods cue the downstream movement of dwarf sawfish from the lower estuarine reaches of the Fitzroy River into King Sound. This movement is reversed in the dry season (Morgan et al. 2021). Body condition of sawfish in the Fitzroy River is influenced by flow (Lear et al. 2021). Increased barramundi growth has also been linked to periods of high flow (Robins et al. 2006). • Few studies on movement, connectivity and growth relationships exist (prior to NESP) for tropical northern Australian rivers other than the Fitzroy River.
	The frequency and magnitude of within-bank flows is important for maintaining	• Connectivity strongly influences characteristics of fish habitat.	• Wet-season flows maintain habitat diversity in the Daly. • Flow velocity and depth influence the	• Flows that shape riverine habitat are important for the persistence of habitat specific species. For	• Scouring flows transport sediments to the nearshore coastal zone. These fine sediments remain in	• Habitat preferences identified for algae (Townsend & Gell, 2005), macroinvertebrates (Leigh & Sheldon, 2009; Leigh, 2013), fish (Arthington et al. 2015), and sharks (Lyon et al. 2017) in rivers and estuaries in northern Australia.

Principle	Sub-principle	Evidence from NESP projects: Mitchell freshwater – NESP project 1.3.1	Daly freshwater – NESP project 1.3.2	Fitzroy freshwater – NESP project 1.3.3	Estuaries (Mitchell, Gilbert, Flinders) – NESP project 1.4	Evidence from other studies in northern Australia
	habitat quality. This includes flows that scour the river, maintain within channel geomorphic complexity (pools, bars and riffles), and prevent siltation of hyporheic sediments.	• Fish species composition and abundance is related to habitat complexity, with some species showing preference for particular substrates.	available surface area for productive algal species in channel habitats. • A variety of habitat characteristics are present and the fish communities fall into four habitat guilds. Water depth, velocity, instream structures, and bank shape are key habitat characteristics separating the four guilds (Keller et al. 2019).	example, scouring flows support fish species with high water requirements. • Riparian trees that occupy the riverbank (*Melaleuca argentea, M. leucadendra* and *Eucalyptus camaldulensis*) have traits that allow them to survive high-velocity flows.	the nearshore coastal zone and move up and down the coast. Tidal resuspension causes prolonged nutrient release.	• Within-bank flows contribute large woody debris (trees) into the river to provide habitat for fish (Pettit et al. 2013). • Within-bank flows may create poor water quality (low oxygen early during the wet season (Townsend, Boland & Wrigley, 1992; Townsend, 1994), and then improve water quality (Garcia et al. 2015). • The availability of habitat for algal species influences the primary carbon source for food webs (e.g. Bunn, Davies & Kellaway, 1997; Jardine et al. 2013), with different contributions of terrestrial carbon between perennial and intermittent reaches (Pettit et al. 2012). • Tropical rivers with reliable flow throughout the catchment year round maintain a high diversity of habitats and fish species (Pusey, Arthington & Read, 1995), because habitat-biota relationships are flow dependent (e.g. Stewart-Koster et al. 2011).
	Within-bank flows influence the size, persistence, and quality of flood-runner pools.			• The magnitude of wet season flows determines the water quality and fish species richness of flood-runner pools, with higher fish species richness in flood-runner pools observed in a year with protracted overbank flows. • Flood-runner pools provide nursery habitat for some fish species and juvenile bony bream that access these pools grow faster. • Higher zooplankton abundance in flood-runner pools compared to the river		• Within-bank flows may create poor water quality (low oxygen early during the wet season; Townsend et al. 1992; Townsend, 1994), and then improve water quality (Garcia et al. 2015).

Principle	Sub-principle	Evidence from NESP projects: Mitchell freshwater – NESP project 1.3.1	Daly freshwater – NESP project 1.3.2	Fitzroy freshwater – NESP project 1.3.3	Estuaries (Mitchell, Gilbert, Flinders) – NESP project 1.4	Evidence from other studies in northern Australia
				channel may support these juvenile fishes.		
	Within-bank flows influence the productivity of the estuary.	• Mitchell estuary included in NESP project 1.4	• Juvenile barramundi are more likely to remain in estuarine habitats during high-rainfall wet seasons; however, in low rainfall years, juvenile barramundi are more likely to migrate into freshwaters in search of more productive growth habitats. • Movement of juvenile barramundi between the estuary and freshwater areas of the Daly River in low-flow years suggests that productivity of the estuary is linked to flow, with higher flow wet seasons transporting more nutrients to the estuary (Roberts et al. 2019).		• Nutrients associated with flow are critical to estuarine productivity. • Estuaries in the Gulf are nutrient limited so productivity relies on export from the catchment (Burford & Faggotter, 2021). • Juvenile prawns exit the estuary and join the Gulf fishery with floods as the salinity drops. • Barramundi and prawn catches are related to river flow (Broadley et al. 2020). • Wetter years with larger flows support increased growth, abundance and biomass of coastal barramundi in estuaries receiving both perennial and intermittent flow (Leahy & Robins, 2021; Robins et al. 2021).	• Within-bank flows deliver nutrient inputs into the estuary (Brodie & Mitchell, 2005; Hamilton & Gehrke, 2005). • Relationship between river flow and estuarine productivity observed for other northern Australian rivers, including the Ord (Burford et al. 2011) and Norman (Burford et al. 2012; Duggan et al. 2014) rivers, but not for Darwin Harbour, which had highest nutrient input from incoming tides and only minor nutrient input from adjacent rivers (Burford et al. 2008). • Increased productivity promotes the growth and recruitment of marine and partially freshwater species, such as barramundi and cherabin (Russell & Garrett, 1985; Staunton-Smith et al. 2004; McCulloch et al. 2005; Robins et al. 2005, 2006; Tanimoto et al. 2012; Novak et al. 2015). • Within-bank flows drive spatial and temporal variation in estuarine fish diversity and distribution (Cyrus & Blaber, 1992; Pusey et al. 2015).
Overbank (flood) flows provide lateral connectivity, maintaining the health of the riparian zone, floodplain, and	Overbank flows provide connectivity between the river and its floodplain, including high-value floodplain	• Connectivity to the floodplain is critical because over 90% of primary productivity in the catchment comes from algae on the floodplain (Molinari et al. 2021b).	• Some fish species, such as barramundi, utilise lateral connections to productive floodplain wetlands to forage for food.	• Fish use overbank flows to access these productive habitats. • Algal biofilm is the primary carbon source in floodplain wetland food webs.	• Access to freshwater habitats to feed, particularly productive floodplain wetlands, increases the growth rates of barramundi. • Overbank flows are important to ensure	• Overbank flows in the Fitzroy mobilise inorganic nutrients (N, P) that may support instream primary production and the food web (Fellman et al. 2013). • Macrophytes on the Kakadu floodplain are an important surface for epiphytic algae which are the primary carbon source for floodplain food webs there (Pettit et al. 2011) and in other river systems (Pettit et al. 2016).

Principle	Sub-principle	Evidence from NESP projects				Evidence from other studies in northern Australia
		Mitchell freshwater – NESP project 1.3.1	Daly freshwater – NESP project 1.3.2	Fitzroy freshwater – NESP project 1.3.3	Estuaries (Mitchell, Gilbert, Flinders) – NESP project 1.4	
off-channel wetlands, and facilitating lateral food web subsidies.	sites (biodiversity, productivity, and cultural significance).	• Algae is consumed by macroinvertebrates which concentrate fatty acids to provide high quality food for fish. • Wetlands are important as they contain abundant macrophytes which provide a surface for epiphytic algal growth (Molinari et al. 2021a) and habitat for macroinvertebrates. • Fish use wet-season connections to migrate in and out of floodplain wetlands to forage in more productive habitats (O'Mara et al. 2021). Overbank flows are therefore important for lateral food web subsidies.		• Higher zooplankton density in floodplain pools compared to main-channel pools.	barramundi in wetlands can migrate to the estuary and contribute to the fishery, particularly in areas with naturally longer periods of floodplain inundation, such as the Mitchell River.	• Food-web connectivity occurs when fish feed on floodplain or marine resources during the wet season (Thorburn & Rowland, 2008; Jardine et al. 2012b; Crook et al. 2020), but there is conflicting opinion on how much terrestrial carbon sources contribute to this (Hunt et al. 2012; Fellman et al. 2013; Thorburn, Gill & Morgan, 2014). • Access to floodplain habitats supports rapid fish growth (Jardine et al. 2012a). In some species (e.g. bony bream) energy is allocated to reproduction (Jardine et al. 2012b). • Overbank flows stimulate migration in terrestrial and aquatic snakes (Madsen & Shine, 2000).
	Overbank flows influence the dispersal and recruitment of riparian vegetation and surface water inputs to riparian plants.			• There is a zonation of riparian vegetation with differences in species assemblages and vegetation structure (canopy cover, basal area) over a hydrological gradient. • Duration of inundation from flood flows is a strong predictor of the occurrence of woody riparian plant species.		• Water depth and persistence of floodwaters determine vegetation patterning on the Mary River floodplain (Whitehead, Wilson & Bowman, 1990). • Vegetation types in in relation to floodplain inundation have been described for several northern Australian floodplains (e.g. Finlayson & Von Oertzen, 1993; Ward et al. 2014). • Overbank flows facilitate the dispersal of seeds across the floodplain (Pettit & Froend, 2001b a). • Overbank flows influence the distribution of *Melaleuca* species (Franklin et al. 2007). • Overbank flows shape the species richness, abundance and regeneration of rheophytic species (James et al. 2016).

Principle	Sub-principle	Evidence from NESP projects: Mitchell freshwater – NESP project 1.3.1	Daly freshwater – NESP project 1.3.2	Fitzroy freshwater – NESP project 1.3.3	Estuaries (Mitchell, Gilbert, Flinders) – NESP project 1.4	Evidence from other studies in northern Australia
						• Overbank flows provide access to riparian food sources (fruit, insects) for fishes (Davis et al. 2010).
	Overbank flows influence the size, persistence, and water quality of off-channel wetlands and the floodplain inundation extent is largely dependent on upstream flows.	• Upstream river flow is the most important factor determining inundation extent on the floodplain, followed by local rainfall (Ndehedehe et al. 2021). • Some fish species reside in wetlands permanently, while others move there to feed and find permanent water in the wet season. Permanent water is important for ensuring these wetland-specific species survive.	• Upstream river flows are the most important factor for determining the inundation extent of the Daly floodplain.	• Flood flows are linked to inundation. Wetter years provide more habitat which can influence the abundance of aquatic species such as cherabin.		• Wet-season floods are influential for inundation extent for several rivers including the Adelaide, Mary, Finiss, Fitzroy, Mitchell, and Wildman rivers (Nielsen et al. 2020). This has also been modelled for the Flinders and Gilbert floodplains (Karim et al. 2015). • Overbank flows replenish waterholes, improving water quality and the cover of aquatic plants (Pettit et al. 2012). • A gradient of fish species composition has been observed between floodplain and channel habitats (e.g. Arthington et al. 2015; Pusey et al. 2020), and the size and quality of the wetland can influence the fish species found there (Waltham & Schaffer, 2021). • Overbank flows may lead to fish kills caused by poor water quality (low oxygen) associated with first-flush runoff (Townsend et al. 1992; Townsend, 1994). • Overbank flows provide habitat for frogs, turtles, and other semi-aquatic species (Finlayson et al. 2006). • Overbank flows create a feeding and breeding habitat for wetland birds, including migratory species such as magpie geese (Bayliss & Yeomans, 1990; Finlayson et al. 2006).
Recessional flows are important for maintaining key habitats, particularly in the dry season. Maintenance of these habitats supports important ecological processes and particular species.	Recessional flows influence the extent and duration of in-channel connectivity, particularly in intermittent reaches. Spatial variation in longitudinal connectivity influences biological assemblages and animal	• Connectivity in the catchment becomes highly variable as wet-season flows subside and fish spend the dry season either in disconnected pools or the perennial main channel of the Mitchell. • Fish species composition in low-connectivity areas is influenced by dispersal opportunity, with more unique fish	• Connectivity influences fish habitat and as a result perennial and intermittently flowing reaches are utilised differently by fish for spawning, with perennially flowing reaches supporting a more diverse larval assemblage (Tyler et al. 2021).	• Connectivity is important for quality of fish habitat and migration opportunity between the estuary and river. For example, it is thought that cherabin larvae use an estuarine nursery because juvenile cherabin are abundant in lower reaches of the Fitzroy.		• Connectivity is important for movement of aquatic organisms to forage, find refuge for the dry season, and to spawn (e.g. Bishop et al. 1995; Staunton-Smith et al. 2004; Novak et al. 2015; Morgan et al. 2021). • Perennial and intermittent reaches can have different fish assemblages (Pusey et al. 2020).

Principle	Sub-principle	Evidence from NESP projects: Mitchell freshwater – NESP project 1.3.1	Daly freshwater – NESP project 1.3.2	Fitzroy freshwater – NESP project 1.3.3	Estuaries (Mitchell, Gilbert, Flinders) – NESP project 1.4	Evidence from other studies in northern Australia
	movement and spawning.	assemblages between adjacent sites of low connectivity and similar fish assemblages in highly connected adjacent sites.				
	Recessional flows influence the condition and composition of riparian vegetation reliant on surface water from the channel.			• The water sources used by riparian trees reflects the local hydrology, with trees using regional groundwater sources where it is available. • There is a relationship between some physiological traits of riparian trees and their distribution along a hydrological gradient.		• Distribution and relative abundance of vegetation types within and between floodplains of the Mary River, NT, is influenced by an interaction between erratic rainfalls and inter-plain variation in topography and hydrology. Catchment differences in soils and hydrology add to inter-plain variation (Whitehead et al. 1990).

Principle	Sub-principle	Evidence from NESP projects Mitchell freshwater – NESP project 1.3.1	Daly freshwater – NESP project 1.3.2	Fitzroy freshwater – NESP project 1.3.3	Estuaries (Mitchell, Gilbert, Flinders) – NESP project 1.4	Evidence from other studies in northern Australia
	Recessional flows influence the availability and quality of shallow, fast-flowing habitats (i.e. runs and riffles), which support particular algae, macro-invertebrate, and fish species.	• Habitat availability not only influences food webs through fish habitat preference but also through availability of high-quality food such as macroinvertebrates. • Macroinvertebrate community composition is influenced by microhabitat coverage, which is highly flow dependent.	• The diversity of habitats utilised by fish highlight the importance of maintaining dry season flows that support habitat complexity in the Daly River system. • Water velocity is a key factor influencing dry season habitat use of fish, particularly *Neoarius* spp. and juveniles of *S. butleri* and *H. fuliginosus* (Crook et al. 2021). • Flow is likely to have a significant effect on the dry season food web through its effect on resource availability. • High contributions of benthic macroalgae and macrophytes to diets of macroinvertebrates indicate species are differentially favoured by the hydrology at a site.	• While shallow fast-flowing habitat is preferred by some species, decreased abundance of other species occurs when the water gets too shallow.		• Dependence of some fish species on shallow, fast-flowing habitat has been demonstrated for several fish species in the Daly River (Stewart-Koster et al. 2011; Chan et al. 2012; King et al. 2015; Pusey et al. 2018). • Shallow, flowing habitats have been associated with particular plant and macroinvertebrate species in other river systems (Noller, Woods & Ross, 1994; Davis et al. 2015; Davis, Pusey & Pearson, 2018). • Rifle and run maintaining recessional flows provide habitat for species or life stages that prefer fast-flowing or very shallow water, such as filter-feeding invertebrates (Leigh, 2013). • Rifle and run maintaining recessional flows support increased algal primary productivity (Webster et al. 2005) and secondary (invertebrate) productivity instream (Leigh & Sheldon, 2009).

Principle	Sub-principle	Evidence from NESP projects: Mitchell freshwater – NESP project 1.3.1	Daly freshwater – NESP project 1.3.2	Fitzroy freshwater – NESP project 1.3.3	Estuaries (Mitchell, Gilbert, Flinders) – NESP project 1.4	Evidence from other studies in northern Australia
	Recessional flows influence the size, number, and quality of refugial dry-season pools, particularly historically perennial pools. Quality of refugial pools is important for sustaining fish biomass through the dry season.	• The size and quality of refugial pools is important for sustaining fish biomass because reliance of fish on local food sources increases as the dry season progresses (Venarsky et al. 2020).	• The size and quality of refugial pools is important for habitat use, with water depth and contraction of habitat influencing dry-season habitat use of fish.	• The size and quality of refugial pools is important for sustaining fish biomass because reliance of fish on local food sources increases as the dry season progresses. • Water quality decreases as pools shrink with the progression of the dry season. • Fish in main-channel pools during the dry season depend increasingly on energy from leaf litter or phytoplankton.		• Refugial pool quality is important for survival over the dry season for macroinvertebrates (Leigh, 2013) and fish (Townsend et al. 1992; Townsend, 1994; Erskine et al. 2005; Crook et al. 2020). • Pool quality may influence pool choice, as there is evidence for fish and crocodile homing back to dry-season refuges (Webb, Manolis & Buckworth, 1983; Crook et al. 2020). • Habitat complexity in pools is important for fish, cherabin and mussels (Keller et al. submitted). • The size of pools is also likely to influence the composition of the community present through predator-prey interactions (Pusey et al. 2018). • Recessional flows maintain refugial pools that sustain spawning habitat for some fish (e.g. barred grunter, rainbowfish, golden flathead goby) (Pusey et al. 2001, 2018).
	Recessional flows influence the extent of hyporheic habitat.					• Intermittent streams are important locations for particulate organic carbon processing and the hyporheic zone sustains this fundamental process even without surface flow (Burrows et al. 2017). Annual wetting is therefore important for maintaining saturation in this zone.
	Rates of rise and fall of flow events influence nutrient levels, primary production rates, the timing of migrations, and habitat colonisation.	• Rate of flood receding influences the primary productivity on the flood plain.			• First wet-season flood peaks are important for flushing prawns out of the estuary to the fishery. • Flood fall rate is likely to influence rate and timing of productivity increase as salinity rises in the estuary.	• Nutrient levels during flooding of the Herbert River have been found to be dependent on flood rise and fall rates (Mitchell, Bramley & Johnson, 1997).
Groundwater aquifers are important in maintaining	Groundwater inputs influence the dry season size,		• Flow in the Daly and Katherine rivers and some tributaries is perennial and	• Dry-season and peak wet-season groundwater inputs are important for		• Groundwater input is an important contributor to permanent water in some floodplain wetlands and the Mitchell River main channel, which flows through the dry season due to groundwater discharge from the

Principle	Sub-principle	Evidence from NESP projects				Evidence from other studies in northern Australia
		Mitchell freshwater – NESP project 1.3.1	Daly freshwater – NESP project 1.3.2	Fitzroy freshwater – NESP project 1.3.3	Estuaries (Mitchell, Gilbert, Flinders) – NESP project 1.4	
subterranean habitats, off-channel wetlands, riparian zones, and springs and can provide dry-season low flows which support runs, riffles, and pools in the main channel.	persistence, quality, and productivity of off-channel wetlands and springs; runs, riffles, and pools in the main channel; aquifer habitat; and the hyporheic zone.		supported from significant groundwater inputs from 3 karstic groundwater aquifers, resulting in a lengthy period of continuous and stable dry-season base flows (May to November). • Maintaining groundwater-derived flows in these areas during the late dry season is important for productivity and growth. For example, larval growth (indicator species *Craterocephalus stramineus*) is fastest at, and downstream of, a groundwater discharge zone compared with upstream. • Groundwater inputs in the early to mid dry season are important as they provide lower water temperatures that male pig-nosed turtles prefer for movement activity.	maintaining flow and connectivity in the Fitzroy River. • Catfish energy stores were lower in small shallow pools than large deep pools and decreased as the dry season progressed. • Juvenile cherabin were most abundant in main-channel pools low in the river. • Hydrological connectivity in the main channel of the river during the dry season is greater in parts of the river with connections to deep groundwater. • Groundwater inputs influence the food web through algal productivity. Algal biomass is driven by flow velocity and is greater in locations where upwelling of groundwater occurs. • Groundwater may contribute ancient dissolved organic carbon to the food web. • Leaves from riparian trees are likely an important food source for fish in lowland main-channel pools during the dry season.		Tertiary sediments and Great Artesian Basin aquifers (CSIRO, 2009). Springs discharging from the Great Artesian Basin provide an important source of environmental water (CSIRO, 2009). • Metabolism in Daly River reaches with groundwater input increases as the dry season progresses and groundwater becomes the dominant discharge source (Townsend, Webster & Schult, 2011). • Productivity can be higher where groundwater upwelling occurs (Boulton & Hancock, 2006; Burrows et al. 2020). • Groundwater aquifers create critical habitat for stygofauna (Cho, Park & Humphreys, 2005; Cook et al. 2012).

Principle	Sub-principle	Evidence from NESP projects: Mitchell freshwater – NESP project 1.3.1	Daly freshwater – NESP project 1.3.2	Fitzroy freshwater – NESP project 1.3.3	Estuaries (Mitchell, Gilbert, Flinders) – NESP project 1.4	Evidence from other studies in northern Australia
				• Fish abundance declines as pool depth declines, particularly when it falls below certain levels. • Water temperature increases as pools shrink but there is little change occurs in oxygen.		
	Groundwater aquifer proximity and discharge influences the condition and composition of riparian vegetation reliant on groundwater.			• Water sources used by riparian trees reflect local hydrogeology and resource availability, with trees closer to rivers using more surface water and those further away using more groundwater (Canham et al. 2021). • In locations where it is available, regional (older) groundwater is used by riparian trees. • Groundwater supports tree species with higher water requirements.		• Tree use of groundwater in the Daly catchment is dependent on tree positioning according to elevation and proximity to the river (O'Grady et al. 2006b a), and is greater in the dry season (Lamontagne et al. 2005). • Groundwater-dependent vegetation has also been mapped in other catchments (Alaibakhsh et al. 2017). • Groundwater sustains woodland plants during the dry season (Cook et al. 1998).
	Groundwater inputs maintain stable low flow for spawning fish.		• Perennial sites maintain higher fish larval diversity than intermittent sites year-round; however, larvae are more abundant in intermittent sites for some taxa (Tyler et al. 2021).			• The dry season low-flow period was found to be important for freshwater fish spawning (indicated by presence of larvae) and recruitment (indicated by presence of juveniles) in the Daly River (Doidge, 2014). • Rainbowfish spawning in streams has also been studied in northern Australia (Pusey et al. 2001).

Principle	Sub-principle	Evidence from NESP projects: Mitchell freshwater – NESP project 1.3.1	Daly freshwater – NESP project 1.3.2	Fitzroy freshwater – NESP project 1.3.3	Estuaries (Mitchell, Gilbert, Flinders) – NESP project 1.4	Evidence from other studies in northern Australia
			• Low-flow dry-season periods identified as important for many fish taxa.			
Antecedent hydrological conditions (flow regime over a range of temporal scales) and interannual variability in flow have an important influence on ecology, biodiversity and ecosystem processes.		• Reductions in wet-season flows are likely to impact floodplain inundation, particularly in years with limited cyclone activity in the Gulf of Carpentaria.	• Dry-season flows are important for maintaining suitable habitat area for some fish species, particularly those associated with shallow, high-velocity environments. • Antecedent conditions influence the spawning of some species which have discrete spawning windows. • Larval fish productivity is dependent on flow conditions.	• Year-to-year dry-season habitat quality is determined by discharge. • Antecedent conditions are likely to influence productivity, indicated by greater catfish energy stores in years following moderate to high wet-season flows and smaller in a year following very low flows (Beesley et al. 2021).	• Maintaining flows in low-flow and medium-flow years is critical for sustaining estuarine productivity. These flows deliver essential nutrients that fuel primary productivity (Burford & Faggotter, 2021). • The number of low flows of each season is important when predicting impacts of water-resource development on prawn catch. • The sequential pattern of river flow over multiple years is an important driver of barramundi population dynamics. • Given the variability in flow from year to year, and from river to river within a year, all Gulf rivers are important for sustaining downstream fisheries as well as estuarine ecosystems in general, as the network of rivers flowing into the Gulf of Carpentaria buffer one	• A relationship between wet-season flow and sawfish recruitment across years has been observed in the Fitzroy (Lear et al. 2019). • Greater fish species richness and riparian productivity has been found for rivers with less inter-annual variability (Jardine et al. 2015). • Antecedent conditions exert complex effects on fish. Recent variable flows can adversely impact the abundance of some juvenile fish (e.g. *Hephaestus fuliginosus*), and recent high flows can reduce abundance of juvenile barramundi (Stewart-Koster et al. 2011). Higher wet-season flow can increase the abundance of adult western rainbowfish in some areas but decrease them in others (Stewart-Koster et al. 2011). • Influence macroinvertebrate assemblage structure (Leigh, 2013; Davis et al. 2015). • Prolonged flow cessation that extends the dry season may reduce resistance and resilience of macroinvertebrate assemblages (Leigh, 2013).

Principle	Sub-principle	Evidence from NESP projects: Mitchell freshwater – NESP project 1.3.1	Daly freshwater – NESP project 1.3.2	Fitzroy freshwater – NESP project 1.3.3	Estuaries (Mitchell, Gilbert, Flinders) – NESP project 1.4	Evidence from other studies in northern Australia
					another in low-flow years.	
Magnitude, frequency, duration, and timing of key hydrological events are important for connectivity and productivity, animal movement, and spawning.		• Magnitude of flow and inundation duration are key determinants of connectivity between productive wetlands and river channels in the Mitchell catchment. Fish use these connections to feed in wetlands.	• The preservation of all the flow phases, including timing and duration, is important for fish spawning. • Potential preferences for spawning in different hydrological classes were observed for at least 19 fish taxa in the Daly River.	• Flow magnitude, timing, and duration are important for maintaining habitat diversity. • In the Daly, the likelihood of tree species occurrence is related to flood inundation duration and fish species richness in flood-runner pools is determined by flow magnitude. • An early wet-season flow caused a blackwater event and oxygen crash at one main-channel site leading to the loss of several fish species.	• Floodplains are likely to play a more important role for barramundi in the Mitchell River/estuary than in the Gilbert or Flinders due to longer periods of inundation of the Mitchell River floodplains. • The abundance of benthic macroinvertebrates on estuary mudflats and sandflats is highly seasonal. Therefore, the timing and duration of flooding is important for food availability to coincide with the visiting times of migrating shorebirds that feed in the estuaries. • Timing of first wet-season floods determine when the banana prawns in the estuary will move to the offshore fishery.	• The floodplain of the Fitzroy is inundated longer when topographic relief is low and flood magnitude and duration is longer (Karim et al. 2016). • Greater fish and aquatic bird species richness and riparian productivity may occur in rivers with regular timing and magnitude of floods each year (Jardine et al. 2015). • Inundation duration associated with increased recruitment of fishes and their predators (Madsen & Shine, 2000).

3.1 References

Alaibakhsh M., Emelyanova I., Barron O., Khiadani M. & Warren G. (2017). Large-scale regional delineation of riparian vegetation in the arid and semi-arid Pilbara region, WA. *Hydrological Processes* 31, 4269–4281

Arthington A.H., Godfrey P.C., Pearson R.G., Karim F. & Wallace J. (2015). Biodiversity values of remnant freshwater floodplain lagoons in agricultural catchments: evidence for fish of the Wet Tropics bioregion, northern Australia. *Aquatic Conservation: Marine and Freshwater Ecosystems* 25, 336–352

Bayliss P. & Yeomans K.M. (1990). Seasonal Distribution and Abundance of Magpie Geese, Anseranas-Semipalmata Latham, in the Northern Territory, and Their Relationship to Habitat, 1983-86. *Wildlife Research* 17, 15–38

Beesley L.S., Pusey B.J., Douglas M.M., Keogh C.S., Kennard M.J., Canham C.A., et al. (2021). When and where are catfish fat fish? Hydro-ecological determinants of energy reserves in the fork-tailed catfish, Neoarius graeffei, in an intermittent tropical river. *Freshwater Biology* 66, 1211–1224

Bishop K.A., Pidgeon R.W.J. & Walden D.J. (1995). Studies on fish movement dynamics in a tropical floodplain river: prerequisites for a procedure to monitor the impacts of mining. *Australian Journal of Ecology* 20, 81–107

Boulton A.J. & Hancock P.J. (2006). Rivers as groundwater-dependent ecosystems: a review of degrees of dependency, riverine processes and management implications. *australian Journal of Botany* 54, 133–144

Broadley A., Stewart-Koster B., Kenyon R.A., Burford M.A. & Brown C.J. (2020). Impact of water development on river flows and the catch of a commercial marine fishery. *Ecosphere* 11, e03194

Brodie J.E. & Mitchell A.W. (2005). Nutrients in Australian tropical rivers: Changes with agricultural development and implications for receiving environments. *Marine and Freshwater Research* 56, 279–302. https://doi.org/10.1071/MF04081

Bunn S.E., Davies P.M. & Kellaway D.M. (1997). Contributions of sugar cane and invasive pasture grass to the aquatic food web of a tropical lowland stream. *Marine and freshwater research* 48, 173–179

Burford M.A., Alongi D.M., McKinnon A.D. & Trott L.A. (2008). Primary production and nutrients in a tropical macrotidal estuary, Darwin Harbour, Australia. *Estuarine, Coastal and Shelf Science* 79, 440–448

Burford M.A. & Faggotter S.J. (2021). Comparing the importance of freshwater flows driving primary production in three tropical estuaries. *Marine Pollution Bulletin* 169, 112565

Burford M.A., Revill A.T., Palmer D.W., Clementson L., Robson B.J. & Webster I.T. (2011). River regulation alters drivers of primary productivity along a tropical river-estuary system. *Marine and Freshwater Research* 62, 141–151

Burford M.A., Webster I.T., Revill A.T., Kenyon R.A., Whittle M. & Curwen G. (2012). Controls on phytoplankton productivity in a wet–dry tropical estuary. *Estuarine, Coastal and Shelf Science* 113, 141–151

Burrows R.M., Beesley L., Douglas M.M., Pusey B.J. & Kennard M.J. (2020). Water velocity and groundwater upwelling influence benthic algal biomass in a sandy tropical river: implications for water-resource development. *Hydrobiologia* 847, 1207–1219

Burrows R.M., Rutlidge H., Bond N.R., Eberhard S.M., Auhl A., Andersen M.S., et al. (2017). High rates of organic carbon processing in the hyporheic zone of intermittent streams. *Scientific reports* 7, 1–11

Canham C.A., Duvert C., Beesley L.S., Douglas M.M., Setterfield S.A., Freestone F.L., et al. (2021). The use of regional and alluvial groundwater by riparian trees in the wet-dry tropics of northern Australia. *Hydrological Processes* 35, e14180

Chan T.U., Hart B.T., Kennard M.J., Pusey B.J., Shenton W., Douglas M.M., et al. (2012). Bayesian network models for environmental flow decision making in the Daly River, Northern Territory, Australia. *River Research and Applications* 28, 283–301

Cho J., Park J. & Humphreys W.F. (2005). A new genus and six new species of the Parabathynellidae (Bathynellacea, Syncarida) from the Kimberley region, Western Australia. *Journal of Natural History* 39, 2225–2255

Cook B.D., Abrams K.M., Marshall J., Perna C.N., Choy S., Guzik M.T., et al. (2012). Species diversity and genetic differentiation of stygofauna (Syncarida: Bathynellacea) across an alluvial aquifer in north-eastern Australia. *Australian Journal of Zoology* 60, 152–158

Cook P.G., Hatton T.J., Pidsley D., Herczeg A.L., Held A., O'Grady A., et al. (1998). Water balance of a tropical woodland ecosystem, Northern Australia: a combination of micro-meteorological, soil physical and groundwater chemical approaches. *Journal of Hydrology* 210, 161–177

Crook D.A., Buckle D.J., Morrongiello J.R., Allsop Q.A., Baldwin W., Saunders T.M., et al. (2020). Tracking the resource pulse: movement responses of fish to dynamic floodplain habitat in a tropical river. *Journal of Animal Ecology* 89, 795–807

Crook D.A., Keller K., Adair B.J., Luiz O.J., Waugh P.S., Schult J., et al. (2021). Use of radiotelemetry to quantify diel habitat preferences and minimum environmental flow requirements of a tropical riverine fish (Sooty grunter Hephaestus fuliginosus). *Ecohydrology*, e2290

CSIRO (2009). *Water in the Mitchell region, pp 347-416 in CSIRO (2009) Water in the Gulf of Carpentaria Drainage Division. A report to the Australian Government from the CSIRO Northern Australia Sustainable Yields Project. CSIRO Water for a Healthy Country Flagship, Au*.

Cyrus D.P. & Blaber S.J.M. (1992). Turbidity and salinity in a tropical northern Australian estuary and their influence on fish distribution. *Estuarine Coastal and Shelf Science* 35, 545–563

Davis A.M., Pearson R.G., Kneipp I.J., Benson L.J. & Fernandes L. (2015). Spatiotemporal variability and environmental determinants of invertebrate assemblage structure in an Australian dry-tropical river. *Freshwater Science* 34, 634–647

Davis A.M., Pusey B.J. & Pearson R.G. (2018). Big floods, big knowledge gap: Food web dynamics in a variable river system. *Ecology of Freshwater Fish* 27, 898–909

Davis A.M., Pusey B.J., Thorburn D.C., Dowe J.L., Morgan D.L. & Burrows D. (2010). Riparian contributions to the diet of terapontid grunters (Pisces: Terapontidae) in wet–dry tropical rivers. *Journal of Fish Biology* 76, 862–879

Doidge C.-A. (2014). Fish spawning and recruitment in a large floodplain river in the wet-dry tropics of northern Australia: are low flows important? Honours Thesis, Charles Darwin University.

Douglas M.M., Jackson S., Canham C.A., Laborde S., Beesley L., Kennard M.J., Pusey B.J., Loomes, R. & Setterfield S.A. (2019). Conceptualising hydro-socio-ecological relationships to enable more integrated and inclusive water allocation planning. *One Earth* 1: 361–373.

Duggan M., Connolly R.M., Whittle M., Curwen G. & Burford M.A. (2014). Effects of freshwater flow extremes on intertidal biota of a wet-dry tropical estuary. *Marine Ecology Progress Series* 502, 11–23

Erskine W.D., Saynor M.J., Erskine L., Evans K.G. & Moliere D.R. (2005). A preliminary typology of Australian tropical rivers and implications for fish community ecology. *Marine and Freshwater Research* 56, 253–267

Fellman J.B., Pettit N.E., Kalic J. & Grierson P.F. (2013). Influence of stream–floodplain biogeochemical linkages on aquatic foodweb structure along a gradient of stream size in a tropical catchment. *Freshwater Science* 32, 217–229

Finlayson C.M., Lowry J., Bellio M.G., Nou S., Pidgeon R., Walden D., et al. (2006). Biodiversity of the wetlands of the Kakadu Region, northern Australia. *Aquatic Sciences* 68, 374–399

Finlayson C.M. & Von Oertzen I. (1993). Wetlands of Australia: northern (tropical) Australia. In: *Wetlands of the world: Inventory, ecology and management Volume I*. pp. 195–243. Springer.

Franklin D.C., Brocklehurst P.S., Lynch D. & Bowman D.M.J.S. (2007). Niche differentiation and regeneration in the seasonally flooded Melaleuca forests of northern Australia. *Journal of Tropical Ecology* 23, 457–467

Garcia E.A., Pettit N.E., Warfe D.M., Davies P.M., Kyne P.M., Novak P., et al. (2015). Temporal variation in benthic primary production in streams of the Australian wet–dry tropics. *Hydrobiologia* 760, 43–55

Hamilton S.K. & Gehrke P.C. (2005). Australia's tropical river systems: current scientific understanding and critical knowledge gaps for sustainable management. *Marine and Freshwater Research* 56, 243–252

Hunt R.J., Jardine T.D., Hamilton S.K., Bunn S.E. & HUB T.R. and C.K.R. (2012). Temporal and spatial variation in ecosystem metabolism and food web carbon transfer in a wet-dry tropical river. *Freshwater Biology* 57, 435–450

James C.S., Mackay S.J., Arthington A.H., Capon S.J., Barnes A. & Pearson B. (2016). Does stream flow structure woody riparian vegetation in subtropical catchments? *Ecology and evolution* 6, 5950–5963

Jardine T., Hunt R., Faggotter S., Valdez D., Burford M. & Bunn S. (2013). Carbon from periphyton supports fish biomass in waterholes of a wet-dry tropical river . *River Research and Applications U6 - ctx_ver=Z39.88-2004&ctx_enc=info%3Aofi%2Fenc%3AUTF-8&rfr_id=info%3Asid%2Fsummon.serialssolutions.com&rft_val_fmt=info%3Aofi%2Ffmt%3Akev%3Amtx%3Ajournal&rft.genre=article&rft.atitle=Carbon+from+periphyton+supports+fis*

Jardine T.D., Bond N.R., Burford M.A., Kennard M.J., Ward D.P., Bayliss P., et al. (2015). Does flood rhythm drive ecosystem responses in tropical riverscapes? *Ecology* 96, 684–692. https://doi.org/10.1890/14-0991.1

Jardine T.D., Pettit N.E., Warfe D.M., Pusey B.J., Ward D.P., Douglas M.M., et al. (2012a). Consumer–resource coupling in wet–dry tropical rivers. *Journal of Animal Ecology* 81, 310–322

Jardine T.D., Pusey B.J., Hamilton S.K., Pettit N.E., Davies P.M., Douglas M.M., et al. (2012b). Fish mediate high food web connectivity in the lower reaches of a tropical floodplain river. *Oecologia* 168, 829–838. https://doi.org/10.1007/s00442-011-2148-0

Karim F., Dutta D., Marvanek S., Petheram C., Ticehurst C., Lerat J., et al. (2015). Assessing the impacts of climate change and dams on floodplain inundation and wetland connectivity in the wet–dry tropics of northern Australia . *Journal of Hydrology* 522, 80–94

Karim F., Petheram C., Marvanek S., Ticehurst C., Wallace J. & Hasan M. (2016). Impact of climate change on floodplain inundation and hydrological connectivity between wetlands and rivers in a tropical river catchment. *Hydrological Processes* 30, 1574–1593

Keller K., Allsop Q., Box J.B., Buckle D., Crook D.A., Douglas M.M., et al. (2019). Dry season habitat use of fishes in an Australian tropical river. *Scientific reports* 9, 1–14

King A.J., Townsend S.A., Douglas M.M. & Kennard M.J. (2015). Implications of water extraction on the low-flow hydrology and ecology of tropical savannah rivers: an appraisal for northern Australia. *Freshwater Science* 34, 741–758

Lamontagne S., Cook P.G., O'Grady A. & Eamus D. (2005). Groundwater use by vegetation in a tropical savanna riparian zone (Daly River, Australia). *Journal of Hydrology* 310, 280–293

Leahy S.M. & Robins J.B. (2021). River flows affect the growth of a tropical finfish in the wet-dry rivers of northern Australia, with implications for water resource development. *Hydrobiologia* 848, 4311–4333

Lear K.O., Gleiss A.C., Whitty J.M., Fazeldean T., Albert J.R., Green N., et al. (2019). Recruitment of a critically endangered sawfish into a riverine nursery depends on natural flow regimes. *Scientific reports* 9, 1–11

Lear K.O., Morgan D.L., Whitty J.M., Beatty S.J. & Gleiss A.C. (2021). Wet season flood magnitude drives resilience to dry season drought of a euryhaline elasmobranch in a dry-land river. *Science of The Total Environment* 750, 142234. https://doi.org/https://doi.org/10.1016/j.scitotenv.2020.142234

Leigh C. (2013). Dry-season changes in macroinvertebrate assemblages of highly seasonal rivers: responses to low flow, no flow and antecedent hydrology. *Hydrobiologia* 703, 95–112

Leigh C. & Sheldon F. (2009). Hydrological connectivity drives patterns of macroinvertebrate biodiversity in floodplain rivers of the Australian wet/dry tropics. *Freshwater Biology* 54, 549–571

Lyon B.J., Dwyer R.G., Pillans R.D., Campbell H.A. & Franklin C.E. (2017). Distribution, seasonal movements and habitat utilisation of an endangered shark, Glyphis glyphis, from northern Australia. *Marine Ecology Progress Series* 573, 203–213

Madsen T. & Shine R. (2000). Rain, fish and snakes: climatically driven population dynamics of Arafura filesnakes in tropical Australia. *Oecologia* 124, 208–215

McCulloch M., Cappo M., Aumend J. & Müller W. (2005). Tracing the life history of individual barramundi using laser ablation MC-ICP-MS Sr-isotopic and Sr/Ba ratios in otoliths. *Marine and Freshwater Research* 56, 637–644

Mitchell A.W., Bramley R.G. V & Johnson A.K.L. (1997). Export of nutrients and suspended sediment during a cyclone-mediated flood event in the Herbert River catchment, Australia. *Marine and Freshwater Research* 48, 79–88. https://doi.org/10.1071/mf96021

Molinari B., Stewart-Koster B., Adame M.F., Campbell M.D., McGregor G., Schulz C., et al*.* (2021a). Relationships between algal primary productivity and environmental variables in tropical floodplain wetlands. *Inland Waters* 0, 0–11. https://doi.org/10.1080/20442041.2020.1843932

Molinari B., Stewart-Koster B., Malthus T.J. & Bunn S.E. (2021b). Assessing Spatial Variation in Algal Productivity in a Tropical River Floodplain Using Satellite Remote Sensing. *Remote Sensing* 13, 1710

Morgan D.L., Lear K.O., Dobinson E., Gleiss A.C., Fazeldean T., Pillans R.D., et al*.* (2021). Seasonal use of a macrotidal estuary by the endangered dwarf sawfish, Pristis clavata. *Aquatic Conservation: Marine and Freshwater Ecosystems*

Ndehedehe C.E., Onojeghuo A.O., Stewart-Koster B., Bunn S.E. & Ferreira V.G. (2021). Upstream flows drive the productivity of floodplain ecosystems in tropical Queensland . *Ecological indicators* 125, 107546

Nielsen D.L., Merrin L.E., Pollino C.A., Karim F., Stratford D. & O'Sullivan J. (2020). Climate change and dam development: Effects on wetland connectivity and ecological habitat in tropical wetlands. *Ecohydrology* 13, e2228

Noller B.N., Woods P.H. & Ross B.J. (1994). Case studies of wetland filtration of mine waste water in constructed and naturally occurring systems in Northern Australia. *Water Science and Technology* 29, 257–265

Novak P.A., Bayliss P., Crook D.A., Garcia E.A., Pusey B.J. & Douglas M.M. (2017). Do upstream migrating, juvenile amphidromous shrimps, provide a marine subsidy to river ecosystems? *Freshwater biology* 62, 880–893

Novak P.A., Douglas M.M., Garcia E.A., Bayliss P. & Pusey B.J. (2015). A life-history account of Macrobrachium spinipes (Schenkel, 1902)(Cherabin) in a large tropical Australian River. *Freshwater Science* 34, 620–633

O'Grady A.P., Cook P.G., Howe P. & Werren G. (2006a). Groundwater use by dominant tree species in tropical remnant vegetation communities. *Australian Journal of Botany* 54, 155–171

O'Grady A.P., Eamus D., Cook P.G. & Lamontagne S. (2006b). Groundwater use by riparian vegetation in the wet–dry tropics of northern Australia. *Australian Journal of Botany* 54, 145–154

O'Mara K., Venarsky M., Stewart-Koster B., McGregor G.B., Schulz C., Kainz M., et al*.* (2021). Connectivity of Fish Communities in a Tropical Floodplain River System and Predicted Impacts of Potential New Dams. *Science of The Total Environment* 788, 147785

Pettit N.E., Bayliss P., Davies P.M., Hamilton S.K., Warfe D.M., Bunn S.E., et al*.* (2011). Seasonal contrasts in carbon resources and ecological processes on a tropical floodplain. *Freshwater biology* 56, 1047–1064

Pettit N.E. & Froend R.H. (2001a). Availability of seed for recruitment of riparian vegetation: a comparison of a tropical and a temperate river ecosystem in Australia. *Australian Journal of Botany* 49, 515–528

Pettit N.E. & Froend R.H. (2001b). Variability in flood disturbance and the impact on riparian tree recruitment in two contrasting river systems. *Wetlands Ecology and Management* 9, 13–25

Pettit N.E., Jardine T.D., Hamilton S.K., Sinnamon V., Valdez D., Davies P.M., et al*.* (2012). Seasonal changes in water quality and macrophytes and the impact of cattle on tropical floodplain waterholes. *Marine and Freshwater Research* 63, 788–800

Pettit N.E., Warfe D.M., Close P.G., Pusey B.J., Dobbs R., Davies C., et al. (2016). Carbon sources for aquatic food webs of riverine and lacustrine tropical waterholes with variable groundwater influence. *Marine and Freshwater Research* 68, 442–451

Pettit N.E., Warfe D.M., Kennard M.J., Pusey B.J., Davies P.M. & Douglas M.M. (2013). Dynamics of in-stream wood and its importance as fish habitat in a large tropical floodplain river. *River Research and Applications* 29, 864–875

Pusey B.J., Arthington A.H., Bird J.R. & Close P.G. (2001). Reproduction in three species of rainbowfish (Melanotaeniidae) from rainforest streams in northern Queensland, Australia. *Ecology of Freshwater Fish* 10, 75–87

Pusey B.J., Arthington A.H. & Read M.G. (1995). Species richness and spatial variation in fish assemblage structure in two rivers of the Wet Tropics of northern Queensland, Australia. *Environmental Biology of Fishes* 42, 181–199

Pusey B.J., Douglas M., Olden J.D., Jackson S., Allsop Q. & Kennard M.J. (2020). Connectivity, habitat, and flow regime influence fish assemblage structure: Implications for environmental water management in a perennial river of the wet–dry tropics of northern Australia. *Aquatic Conservation: Marine and Freshwater Ecosystems* 30, 1397–1411

Pusey B.J., Kennard M.J., Douglas M. & Allsop Q. (2018). Fish assemblage dynamics in an intermittent river of the northern Australian wet–dry tropics. *Ecology of Freshwater Fish* 27, 78–88

Pusey B.J., Kennard M.J., Larson H.K., Alsop Q., Hammer M. & Buckle D.J. (2015). Estuarine fishes of the south Alligator River, Kakadu national park, northern Australia. *Marine and Freshwater Research* 67, 1797–1812

Roberts B.H., Morrongiello J.R., King A.J., Morgan D.L., Saunders T.M., Woodhead J., et al. (2019). Migration to freshwater increases growth rates in a facultatively catadromous tropical fish. *Oecologia* 191, 253–260

Roberts B.H., Morrongiello J.R., Morgan D.L., King A.J., Saunders T.M. & Crook D.A. (2021). Faster juvenile growth promotes earlier sex change in a protandrous hermaphrodite (barramundi Lates calcarifer). *Scientific reports* 11, 1–10

Robins J., Mayer D., Staunton-Smith J., Halliday I., Sawynok B. & Sellin M. (2006). Variable growth rates of the tropical estuarine fish barramundi Lates calcarifer (Bloch) under different freshwater flow conditions. *Journal of Fish Biology* 69, 379–391. https://doi.org/10.1111/j.1095-8649.2006.01100.x

Robins J.B., Halliday I.A., Staunton-Smith J., Mayer D.G. & Sellin M.J. (2005). Freshwater-flow requirements of estuarine fisheries in tropical Australia: a review of the state of knowledge and application of a suggested approach. *Marine and Freshwater Research* 56, 343–360

Robins J.B., Leahy S., Sellin M., Woodhead J. & Mass R. (2021). *Analysis of finfish catch and growth*.

Russell D.J. & Garrett R.N. (1985). Early life history of barramundi, Lates calcarifer (Bloch), in north-eastern Queensland. *Marine and Freshwater Research* 36, 191–201

Staunton-Smith J., Robins J.B., Mayer D.G., Sellin M.J. & Halliday I.A. (2004). Does the quantity and timing of fresh water flowing into a dry tropical estuary affect year-class strength of barramundi (Lates calcarifer)? . *Marine & Freshwater Research* 55, 787–797

Stewart-Koster B., Olden J.D., Kennard M.J., Pusey B.J., Boone E.L., Douglas M., et al. (2011). Fish response to the temporal hierarchy of the natural flow regime in the Daly River, northern Australia. *Journal of Fish Biology* 79, 1525–1544

Tanimoto M., Robins J.B., O'Neill M.F., Halliday I.A. & Campbell A.B. (2012). Quantifying the effects of climate change and water abstraction on a population of barramundi (Lates calcarifer), a diadromous estuarine finfish. *Marine and Freshwater Research* 63, 715–726

Thorburn D.C., Gill H. & Morgan D.L. (2014). Predator and prey interactions of fishes of a tropical Western Australia river revealed by dietary and stable isotope analyses. *Journal of the Royal Society of Western Australia* 97, 363–387

Thorburn D.C. & Rowland A.J. (2008). Juvenile bull sharks' Carcharhinus leucas'(Valenciennes, 1839) in northern Australian rivers. *Beagle: Records of the Museums and Art Galleries of the Northern Territory, The* 24, 79–86

Townsend S.A. (1994). The occurrence of natural fish kills, and their causes, in the Darwin-Katherine-Jabiru region of northern Australia. *Internationale Vereinigung für Theoretische und Angewandte Limnologie: Mitteilungen* 24, 197–205

Townsend S.A., Boland K.T. & Wrigley T.J. (1992). Factors contributing to a fish kill in the Australian wet/dry tropics. *Water Research* 26, 1039–1044

Townsend S.A. & Gell P.A. (2005). The role of substrate type on benthic diatom assemblages in the Daly and Roper Rivers of the Australian wet/dry tropics. *Hydrobiologia* 548, 101–115

Townsend S.A., Webster I.T. & Schult J.H. (2011). Metabolism in a groundwater-fed river system in the Australian wet/dry tropics: tight coupling of photosynthesis and respiration. *Journal of the North American Benthological Society* 30, 603–620

Tyler K.J., Wedd D., Crook D.A., Kennard M.J. & King A.J. (2021). Hydrology drives variation in spawning phenologies and diversity of larval assemblages of Australian wet–dry tropical fish. *Freshwater Biology*

Venarsky M.P., Stewart-Koster B., Hunt R.J., Jardine T.D. & Bunn S.E. (2020). Spatial and temporal variation of fish community biomass and energy flow throughout a tropical river network. *Freshwater Biology* 65, 1782–1792

Waltham N.J. & Schaffer J. (2021). Will fencing floodplain and riverine wetlands from feral pig damage conserve fish community values? *Ecology and Evolution*

Ward D.P., Petty A., Setterfield S.A., Douglas M.M., Ferdinands K., Hamilton S.K., et al. (2014). Floodplain inundation and vegetation dynamics in the Alligator Rivers region (Kakadu) of northern Australia assessed using optical and radar remote sensing. *Remote Sensing of Environment* 147, 43–55. https://doi.org/10.1016/j.rse.2014.02.009

Webb G.J.W., Manolis S.C. & Buckworth R. (1983). Crocodylus johnstoni in the McKinlay River Area N. T, II.* Dry-Season Habitat Slection and an Estimate of the Total Population Size. *Wildlife Research* 10, 373–382

Webster I.T., Rea N., Padovan A. V, Dostine P., Townsend S.A. & Cook S. (2005). An analysis of primary production in the Daly River, a relatively unimpacted tropical river in northern Australia. *Marine and freshwater research* 56, 303–316

Whitehead P.J., Wilson B.A. & Bowman D. (1990). Conservation of coastal wetlands of the Northern Territory of Australia: the Mary River floodplain. *Biological Conservation* 52, 85–111

4. Case study: Tropical freshwater food webs – spatial and conceptual gaps in our understanding of their ecology and management

Ryan M. Burrows,[1,2] Michael M. Douglas,[2,3] Stuart E. Bunn,[1] Bradley J. Pusey,[2,3] Samantha Setterfield,[2,3] Erica A. Garcia,[2] Mark J. Kennard[1]

[1]Australian Rivers Institute, Griffith University, Brisbane, Australia
[2]Research Institute for the Environment and Livelihoods, Charles Darwin University, Darwin, Australia
[3]School of Biological Sciences, University of Western Australia, Perth, Australia

Manuscript in preparation.

4.1 Abstract

Tropical rivers and their floodplains are under increasing threat from human modification. Less than 3% of all published research in freshwater ecology has focused on tropical regions, and this lack of research effort potentially inhibits our ability to predict how human modifications will affect them. Tropical freshwater food-web research is biased towards regions (i.e. South America and Australia) that are currently least at threat from human modification. We argue that tropical freshwater management actions and our scientific understanding of them are not consistent. For instance, tropical freshwaters are becoming increasingly disconnected but research overwhelming supports the ecological importance of temporal, longitudinal and lateral hydrological connectivity. Finally, surface-water ecosystems are vertically connected to groundwater, but we know little of the ecological role of groundwater-surface water interactions for tropical aquatic food webs. Here, we outline a set of general principles describing river and wetland food webs to enable better management of freshwater ecosystems in the tropics.

4.2 Food webs in tropical freshwater ecosystems

Food webs are an integrative way of exploring ecosystems because they describe the biotic connections and energy transfer within and between ecosystems. Food-web studies allow us to better understand the complexity of ecosystems and unravel the non-linear and interactive effects of environmental change. This is because they combine aspects of community ecology and ecosystem ecology (Thompson et al. 2012). Ultimately, food webs describe fundamental aspects of ecosystems and a better understanding of their structure and function will help us predict how environmental change impacts ecosystems.

Some of Earth's most productive freshwater ecosystems are situated in the tropics. Kakadu National Park (northern Australia), the Okavango Delta (Botswana), the Pantanal (Brazil), and Tonlé Sap (Cambodia) contain critical tropical freshwater environments that support a high degree of biodiversity and provide resources for human populations. For example, Kakadu National Park is home to one-quarter of Australia's freshwater and estuarine fish species (Pusey et al. 2016) and the Traditional Owners (the Bininj and Mungguy people) have lived on, cared for, and developed a strong cultural connection to the region's rivers and wetlands for thousands of years. Further, Tonlé Sap in the Mekong River watershed is a biodiversity hotspot, considered one of the most productive aquatic environments on Earth, and supports the livelihoods of 1.7 million people (Lamberts, 2006). From these few examples, it is clear that ecologically diverse and productive tropical freshwater food webs are critical for the functioning of natural ecosystems and the cultural practices and economic livelihoods of many communities.

Despite their ecological, cultural and economic importance, freshwater food webs in Earth's tropical zone remain comparatively understudied. Less than 3% of papers published in freshwater ecology since 1950 were conducted in tropical regions (see supplementary material for search procedure). However, tropical rivers account for more than 50% of the total river length, and the tropical zone, which is expanding due to climate change (Seidel et al. 2008), covers 19% of the Earth's landmass (Peel et al. 2007). In contrast, the arid region covers 30% of Earth's land mass (Peel et al. 2007) but accounts for more than 10% of all publications in freshwater ecology since 1950. This lack of research inhibits our ability to predict how human modification of tropical freshwaters will affect their ecological functioning.

Freshwater ecosystems are highly vulnerable to direct and indirect human-induced changes and are considered some of the most threatened ecosystems on Earth (Dudgeon, 2000; Reid et al. 2019). Increasing nutrient and pharmaceutical loads, reduced surface-flow persistence due to groundwater extraction, the construction of river impoundments, and the introduction of non-endemic species all cause major changes to the structure and functioning of freshwater ecosystems globally (Reid et al. 2019). Freshwater ecosystems in the tropical region face increasing human-induced threats. The Amazon and Congo river basins contain some of the largest stretches of free-flowing rivers (Grill et al. 2019) but numerous river impoundments are planned, particularly in the Amazon basin (Winemiller et al. 2016; Latrubesse et al. 2017). Further, southern and south-eastern Asia contain some of the most disconnected river systems (Grill et al. 2019). The tropics are predicted to contain more than half of the world's population by 2050 (State of the Tropics, 2019). Economic development combined with this growing population will place an ever-growing pressure on Earth's tropical freshwater ecosystems.

We review the global literature on tropical freshwater food webs to identify the spatial and conceptual gaps in our understanding of them. We focus on published scientific research conducted in predominately undisturbed systems because they describe the hydro-ecological patterns and processes necessary to maintain healthy and productive tropical freshwater ecosystems. We used 5 previously published general principles published in Douglas et al. (2005) that describe the food webs and related ecosystem processes of Australian tropical freshwaters to structure the review process (see Box 4.1). As the human population and economic development continues to expand in Earth's tropical region, there is an urgent need for a broad, rigorous and scientifically supported understanding of the structure and function of tropical freshwater food webs to inform future management decisions and ensure that human-induced changes do not adversely impact Earth's tropical freshwaters.

Box 4.1. Principles describing freshwater food-web dynamics in Australia's tropics and brief method of review.

Despite the general lack of research in tropical freshwaters, there have been concerted efforts to better understand and summarise the eco-hydrological patterns and processes underlying how tropical freshwater ecosystems work (see Pettit et al. 2017). Drawing on national and global literature, Douglas et al. (2005) proposed 5 general principles that describe freshwater food webs and their related ecosystem processes in tropical rivers and floodplains of northern Australia. The 5 principles are:

Principle 1. Seasonal hydrology is the primary driver of aquatic food-web structure and ecosystem processes.

Principle 2. Hydrological connectivity is intact and underpins important lateral and longitudinal food-web subsidies.

Principle 3. River and wetland food webs are strongly dependent on algal productivity.

Principle 4. A few common macroconsumer species have a strong influence on benthic food webs.

Principle 5. Omnivory is widespread and food webs are short.

These 5 general principles were formulated using the then-limited understanding of Australian and global tropical freshwater food webs. However, since the publication of Douglas et al. (2005) there has been a considerable global research effort focusing on freshwater food-web dynamics (Figure 4-1). We conducted the review using search terms describing key aspects of each general principle (see Section 4.14). We included all tropical freshwater research that incorporated aspects of food-web structure and function and the related ecosystem processes of organisms. We excluded research that had no connection to freshwater biota, such as geochemical and hydrological research. For each relevant study we recorded (1) which principle(s) was explicitly or implicitly assessed, (2) the study's location using the United Nations Geoscheme, (3) the methods used, (4) the organisms assessed, and (5) the aquatic system(s) studied (riverine, lacustrine, palustrine, subterranean, estuarine).

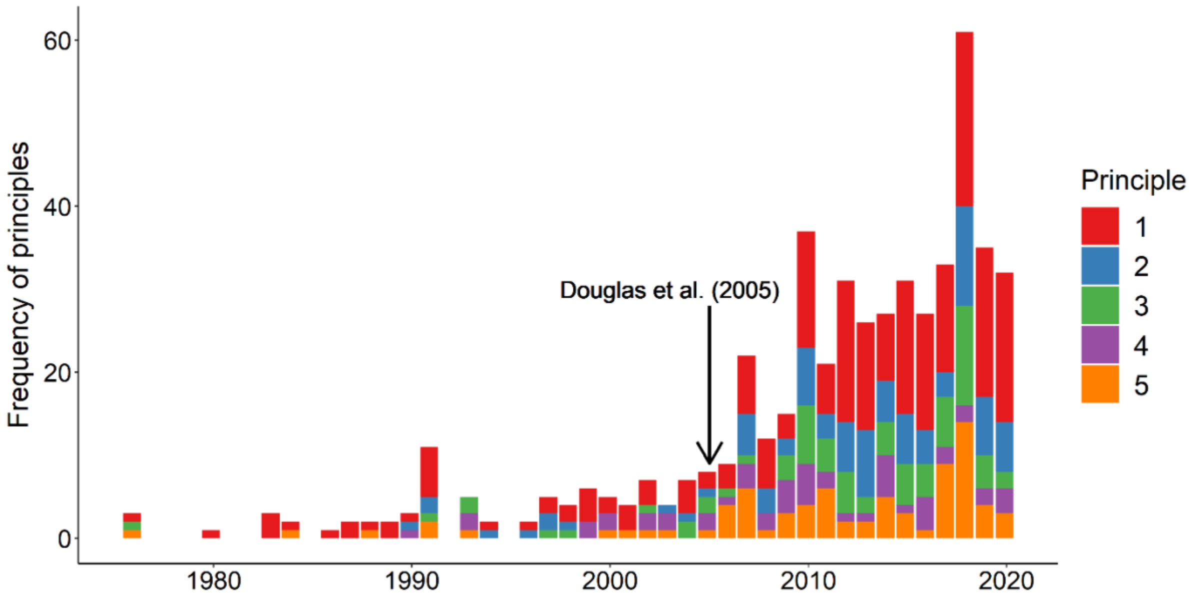

Figure 4-1. The frequency that each of the 5 principles outlined in Douglas et al. (2005) was incorporated into studies on tropical freshwater food webs. The date of publication of Douglas et al. (2005) is indicated by an arrow.

4.3 Geographical variation in tropical freshwater food-web research

Our understanding of tropical aquatic food webs is biased towards certain regions. More than half (58%) of the 369 studies included in this review have been undertaken in just 2 regions – South America (32%) and Australia (25%) (Figure 4-2). Further, the Australian research is biased toward its wet-dry tropical region (Figure 4-2) which is currently less threatened by water-resource development compared with many other regions (Vörösmarty et al. 2010; Collen et al. 2014), although it may be so in the near future (Joint Select Committee on Northern Australia, 2014). In contrast, there has been much less research from south-eastern Asia, southern Asia, eastern Africa, Central America and the Caribbean – these regions individually contribute between 5–8% of total studies undertaken (Figure 4-2). River networks in many of these regions are experiencing large-scale hydrologic modification, through river impoundments and extensive groundwater extraction, as well as large increases in human population (Döll et al. 2009; Zarfl et al. 2015). These changes have led to much of these regions experiencing the tandem threats of human-water scarcity and freshwater biodiversity losses (Vörösmarty et al. 2010). In south-eastern Asia, impoundments are being constructed on many large and regionally important rivers such as the Mekong and Ayeyarwady (Zarfl et al. 2015). The productivity of these river systems, including some of the most recognisable and economically important on Earth (i.e. Tonlé Sap), are thought to be dependent on continued hydrological connectivity (Arias et al. 2014). Southern Asia (mainly India) and Central America (i.e. Mexico) have some of the least sustainable levels of groundwater extraction globally, which is mostly for irrigation (Dalin et al. 2017). While there has been a recent increase in the number of studies undertaken in south-eastern Asia, southern Asia and Central America (Figure 4-3), substantially more is needed in order to understand how freshwater food webs are, and will be, impacted by current and planned hydrological modification.

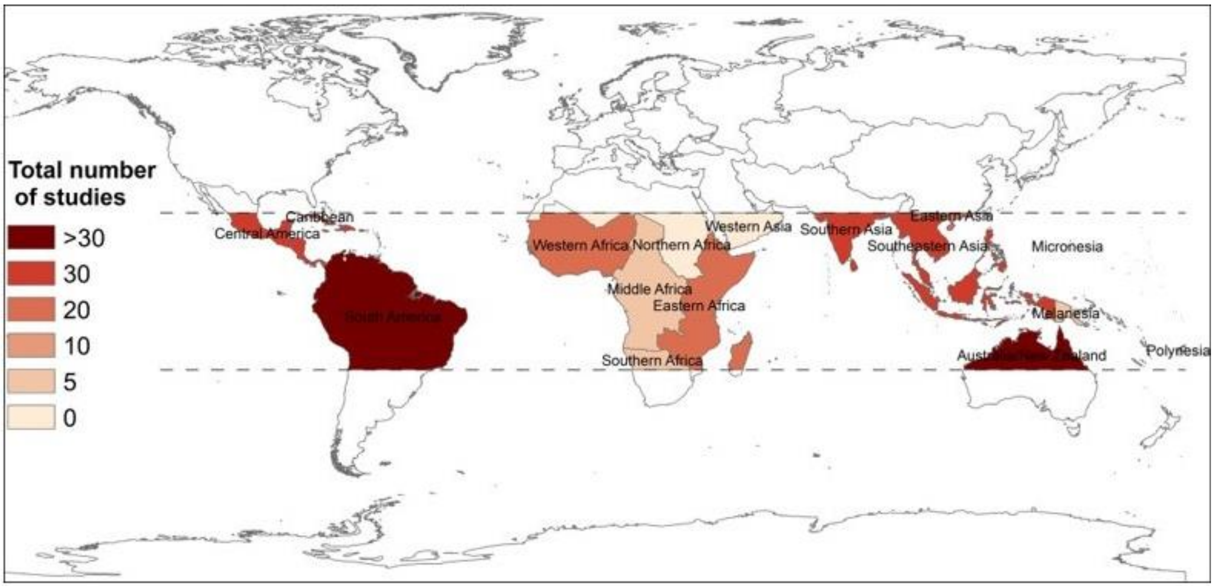

Figure 4-2. The total number of published studies in each UN georegion that addressed the aspects of tropical freshwater food webs we investigated in this review. Only the regions contained within the tropical zone are shown. We delimited the tropical zone in latitude by the Tropic of Cancer (23°26'12.1" N) and the Tropic of Capricorn (23°26'12.1" S).

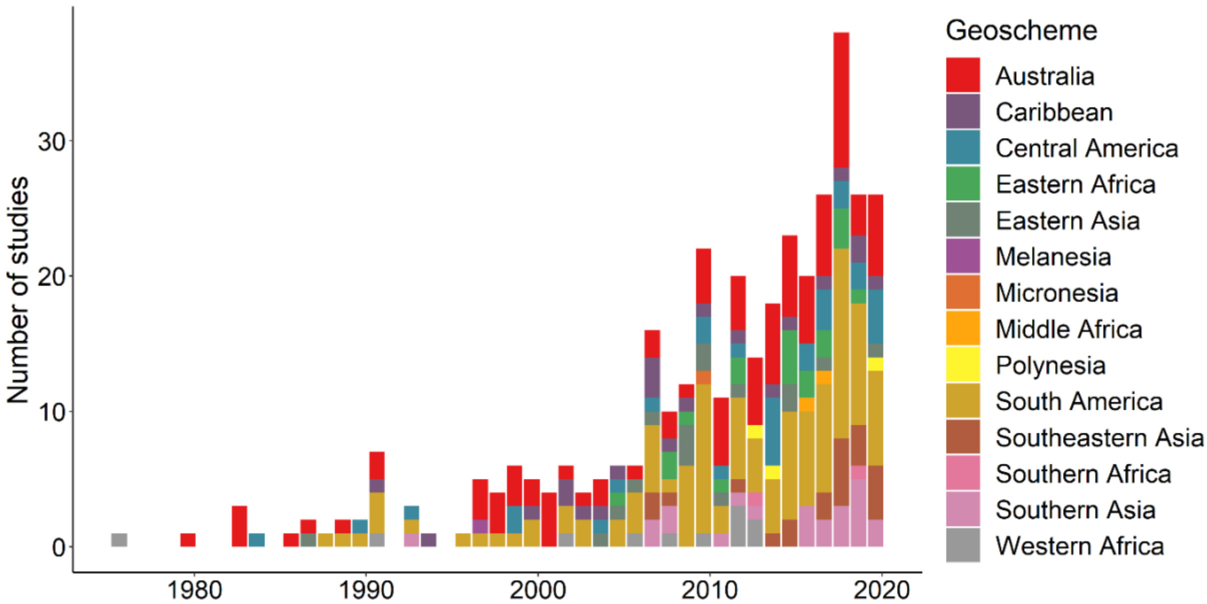

Figure 4-3. The number of aquatic food-web studies conducted in each UN georegion since 1950.

4.4 Quantity, quality and potential transferability of aquatic food-web research in northern Australia

The number of aquatic food-web studies conducted in the wet-dry tropical region of northern Australia has increased markedly in the last decade (Figure 4-4). However, much of this research has been concentrated in just a few river basins, primarily the Daly, East and South Alligator, and Mitchell-Coleman River basins (Figure 4-4).

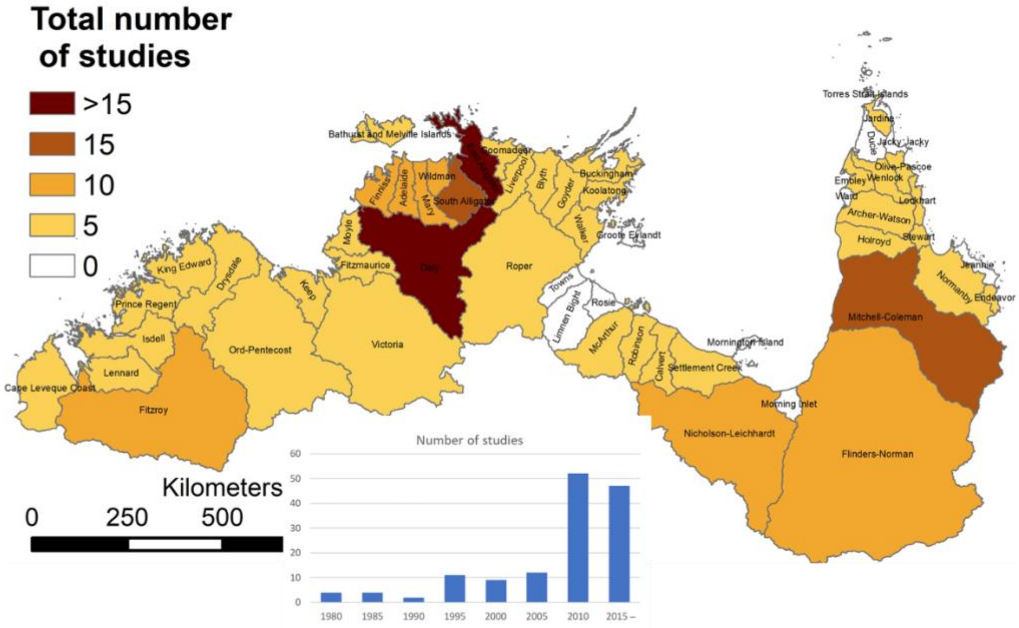

Figure 4-4. The number of aquatic food-web studies conducted in each river basin of northern Australia. Inset plot shows changes in the number of food-web studies over time in northern Australia (total = 104 studies).

The quantity, scale and scope of this research has implications for the potential transferability of the research beyond where (and when) it was conducted. An assessment of the degree of spatial and temporal representation and replication, as well as the lines of evidence (single or multiple approaches) used in the research can be used to infer the potential quality of the research and likely transferability. The majority (45%) of food web-studies in northern Australia were conducted in a single river or stream, although a substantial proportion (37%) were conducted over multiple river basins (Figure 4-5). Spatial replication was generally high across studies, with 62% of studies sampling > 3 replicate sites within each stream/river included in the study (Figure 4-5). Temporal representation and replication of samples was also relatively high, with the majority (~ 45%) of studies sampling over multiple seasons and/or years and having 3 or more replicate samples per sampling period (Figure 4-5). In addition, more than 70% of studies used multiple lines of evidence (i.e. multiple analytical methods) in the conduct of the study. Combining these measures of study scale, scope and methodology to estimate of the overall quality of evidence supporting aquatic food-web research in northern Australia revealed that ~65% of studies could be considered to have moderate to strong evidence (i.e. scoring 15 or more out of a maximum of 25) (Figure 4-5).

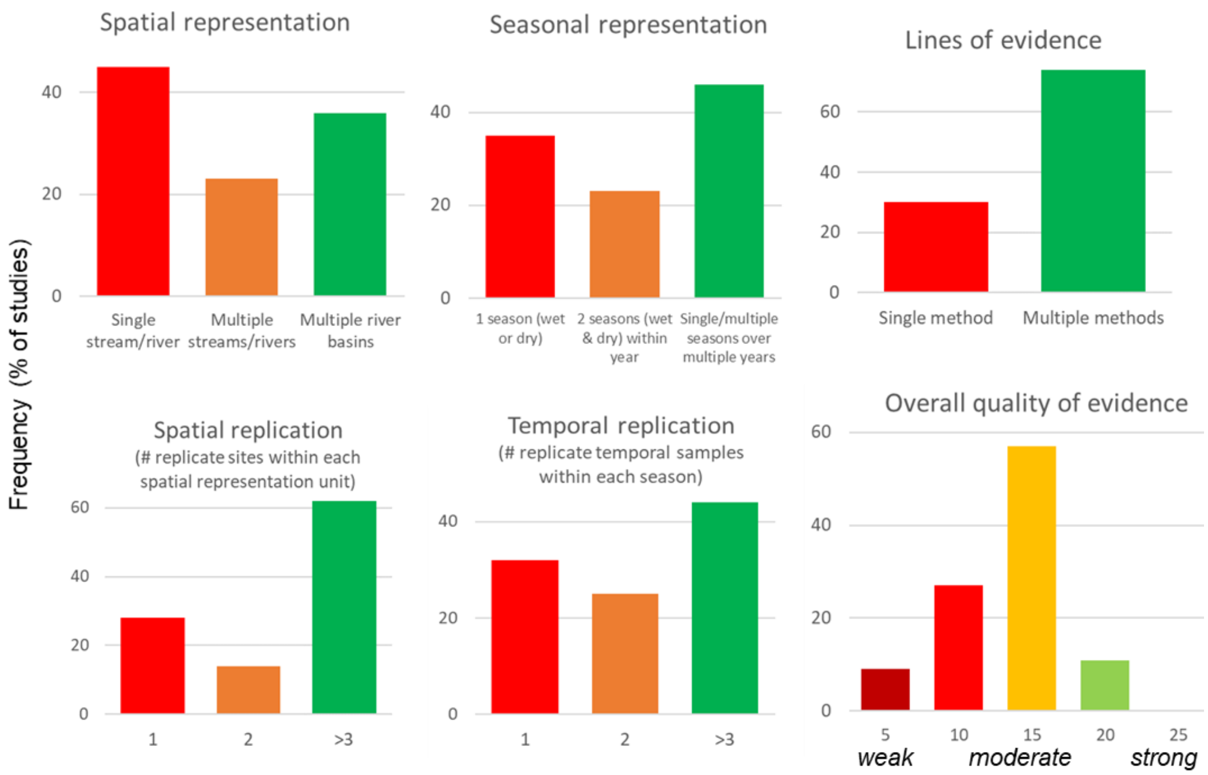

Figure 4-5. Indicators of the potential transferability of research on aquatic food webs in northern Australia defined in terms of the degree of spatial and temporal representation and replication, as well as the lines of evidence (single or multiple approaches) used in the research. This information was used to score the quality of evidence for each criterion (ordinal scale of 1 to 5) and summed to generate an estimate of the overall quality of evidence for each study (maximum score = 25).

4.5 Hydrologic seasonality underpins important ecological processes and food-web structure

One of the most striking findings of this review was the overwhelming focus on the ecological implications of seasonal change for particular aspects of tropical freshwater systems, with almost 60% of studies (220 papers) associated with Principle 1 (Figure 4-1, Figure 4-6). Importantly, over 89% of these studies showed support for this principle, with only 4% of studies refuting the principle (Figure 4-6). In many tropical regions, particularly within the Inter-tropical Convergence Zone, monsoonal rainfall leads to large seasonal changes in surface-water hydrology. Strong hydrological seasonality is a key factor influencing hydro-ecological processes in tropical (Junk, Bayley & Sparks, 1989) and temperate systems (Tockner et al. 2000) as well as in various terrestrial (Oliveras and Malhi, 2016) and coastal marine (Cloern and Jassby, 2008) ecosystems. The degree of hydrological seasonality varies throughout the tropics, with minimal seasonality in precipitation close to the equator. However, most tropical regions experience seasonality in precipitation, with key examples of wet-dry tropical climates being northern Australia, southern India and Bangladesh, south-eastern Asia, and large parts of South America.

Perhaps one of the most important aspects of seasonal-hydrological change is overbank flooding which predictably inundates vast regions of tropical forest and savanna each year

(Junk and Welcomme, 1990). The flood-pulse concept (FPC) describes the importance of this hydrological phenomena for the ecology and biogeochemistry of riverine landscapes (Junk et al. 1989). Seasonal inundation of river channels and floodplains has been identified to be important for the persistence and ecological health of freshwater environments (Leigh et al. 2010). Further, seasonal changes in hydrology alter the delivery of important and/or limiting resources for primary and secondary production (Holtgrieve et al. 2013). In terms of aquatic food webs, these seasonal changes in the hydrology and physicochemistry of systems shape riverine and floodplain population structure and composition (Cotner et al. 2006; Winemiller et al. 2014; Kopij and Paxton, 2018), consumer diet (Costa-Pereira et al. 2017; Heng et al. 2018), as well as the reproductive dynamics and migration of many species such as waterbirds (Whitehead and Saalfeld, 2000) and fish (Stoffels et al. 2016). Additionally, warmer water temperatures and greater freshwater habitats during high-water periods of more seasonal tropical systems, can also increase the growth, availability and consumption of more energetic food items (i.e. algae) that may benefit aquatic consumer populations (Winemiller, 2004; Kloh et al. 2018). The social and economic importance of seasonal changes in hydrology cannot be understated, with many human populations reliant on the large increases in aquatic consumer (i.e. fish, macroinvertebrate and waterbird) populations over natural hydrological cycles (McIntyre et al. 2016).

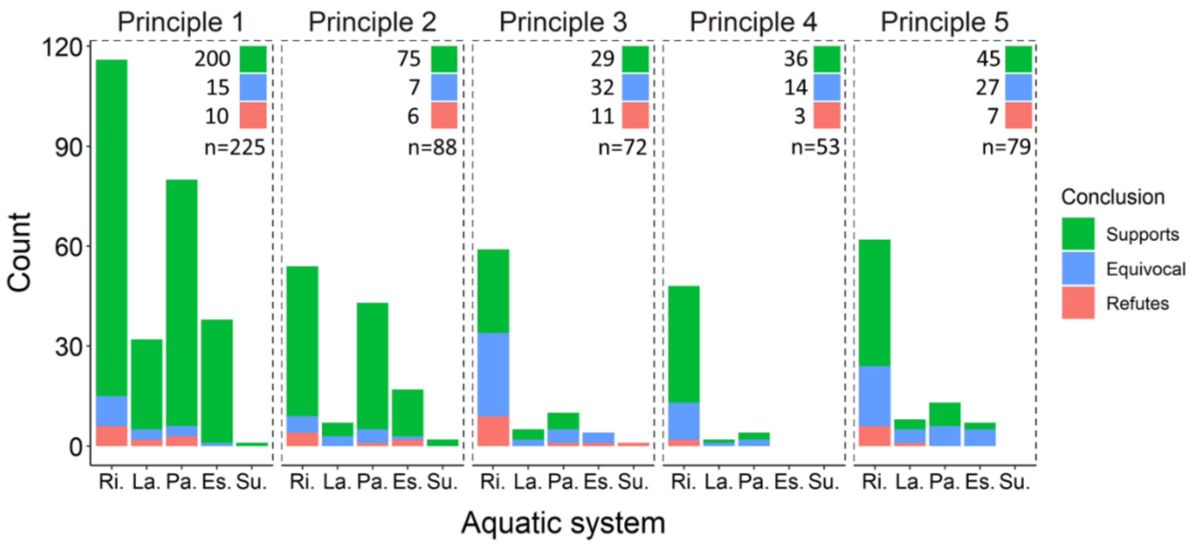

Figure 4-6. Bar plot displaying the level of support (supports, equivocal or refutes) for each principle and aquatic system from relevant studies included in our literature review. The total number of studies associated with each principle are given as well as the number of studies for each level-of-support category. Ri. = Riverine, La. = Lacustrine, Pa. = Palustrine, Es. = Estuarine, Su. = Subterranean.

4.6 Hydrological connectivity maintains important food-web subsidies, but rivers are becoming disconnected

Hydrological connectivity is vital for many fundamental ecosystem processes and functions that are characteristic of healthy freshwater ecosystems (Pringle, 2003). Research from tropical freshwater ecosystems gathered in this review supports this notion, with over 85% of the 88 papers related to Principle 2 providing support for the importance of hydrological connectivity for lateral and longitudinal food-web subsidies (Figure 4-6). Less than 7% of research refuted Principle 2 (Figure 4-6). Hydrological connectivity along lateral, longitudinal, vertical and temporal dimensions regulates the transfer of physical and chemical resources across ecosystem boundaries, stimulating numerous ecosystem processes that shape the structure and function of all fluvial systems (Ward, 1989). A strong lateral hydrological connectivity is hypothesised to be one of the main reasons why many large tropical riverine landscapes remain productive (Junk et al. 1989; Winemiller, 2004). Indeed, in tropical regions with a strong wet-dry climate such as northern Australia, wet-season inundation of river floodplains has been linked to an increase in lateral food-web subsidies (Jardine et al. 2012; Jardine et al. 2017). Longitudinal hydrological connections also drive important food-web subsidies for river channels and estuarine ecosystems. During the wet season, the delivery of limiting resources contributes to enhanced phytoplankton production (Srichandan et al. 2019) and biomass (Rajaneesh et al. 2018) as well as bacterial activity (Gawade et al. 2017) in estuaries. Additionally, seasonal hydrological pulses are associated with the longitudinal migration of amphidromous shrimp (Novak et al. 2017) and fish (Stoffels et al. 2016), and are thought to shape the genetic structure of large aquatic predators (largetooth sawfish; Feutry et al. 2015).

The role of vertical hydrological connectivity for food-web subsidies is virtually unknown in tropical systems. This is despite knowing that many rivers, lakes and wetlands are connected to groundwater (Winter, 1999) with much research quantifying the hydrological and physicochemical linkages between groundwater and surface waters. In the Okavango Delta, 90% of the annual total surface-water loss from the floodplain is to groundwater (Ramberg et al. 2006). This groundwater is eventually transferred to adjacent dryland ecosystems where it is thought to support the spatial extent of dryland vegetation in the region and may continue to do so during dry periods (Ramberg et al. 2006). In tropical streams of the Kimberley region of Australia, ancient organic carbon originating from subterranean food-web metabolism is highly bioavailable to stream microbial communities (Fellman et al. 2014). Further, vegetation along the Daly River in northern Australia displays a high degree of groundwater dependence, especially during the dry season (O'Grady et al. 2006). It is clear that vertical hydrological connectivity can play a central role in determining the persistence and productivity of freshwater and connected-terrestrial environments, particularly during dry periods. In this way, vertical connectivity may be as important for tropical food-web subsidies as lateral and longitudinal connectivity.

The delivery of food-web subsidies for tropical freshwater ecosystems along lateral, longitudinal and vertical hydrological flow-paths is largely dependent on the continuation of natural flow regimes. Hydrological connectivity is very important for large river systems where flow-mediated food-web subsidies underpin ecosystem productivity, including the provision of food resources for human populations (i.e. Mekong River connection to Tonle Sap). Very few large free-flowing rivers remain, but many of them exist within tropical regions (Grill et al. 2019). These large free-flowing and connected rivers exist within the Amazon and Orinoco basins in South America, the Congo Basin in Africa, and the Irrawaddy and Salween basins in south-eastern Asia (Grill et al. 2019). Additionally, parts of the Brahmaputra (India and Bangladesh) river is also considered to have a ‘good’ connectivity status (Grill et al. 2019). However, dam construction, water-diversion schemes, and groundwater extraction threaten the continued hydrological connectivity of many of these river systems and this may have ramifications for ecosystem productivity and the provision of food resources for millions of people (Kummu and Sarkkula, 2008; Holtgrieve et al. 2013; Sabo et al. 2017).

4.7 There is no clear consensus on which resource pathway fuels food-web production

Determining the dominant source pathways underpinning food-web production in tropical freshwater ecosystems is difficult. This difficulty is reflected in the equivocal support for the notion that freshwater food webs are strongly supported by algal production (i.e. Principle 4). A greater percentage of studies either refuted (15%) or indicated equivocal support (45%) for this principle than supported it (40%) (Figure 4-6). We have several explanations for the equivocal support for Principle 3. First, tropical freshwater ecosystems are diverse, encompassing a variety of channel sizes, vegetation types, and lateral, longitudinal and vertical hydrological characteristics. This diversity likely influences which energy sources are most available and important for aquatic food webs through space (throughout catchments and among regions) and time (between wet and dry periods). For instance, tropical streams and rivers draining wet rainforest are often heavily shaded and receive large inputs of allochthonous material (seeds, fruits, terrestrial insects, etc.) which often leads to a greater energetic importance of external food sources (Correa et al. 2007). In contrast, tropical rivers and floodplains within many wet-dry tropical regions, such as in northern Australia for which the original principles were proposed, have comparatively less shading and a high availability of incident light (Townsend et al. 2011). Freshwater food webs in these regions can be strongly dependent on algal production, particularly microalgae (Jardine et al. 2013; Pettit et al. 2017), although algal production in many of these systems can be constrained by low nutrient availability (Townsend et al. 2011). Additionally, the existence of seasonal floodplain inundation in an aquatic system can increase the reliance on allochthonous food-web subsidies during flood periods (Jardine et al. 2012; Jardine et al. 2017). Not all tropical aquatic ecosystems are the same and this diversity likely leads to physical constraints on the dominance of certain energy pathways.

Second, unravelling the important resources fuelling aquatic food webs is difficult due to the variety of methods available and the complexity and dynamic nature of organisms, populations and entire food webs. The diet of consumers and the dominant resource pathways of aquatic food webs can be investigated with a variety of methods including stomach-contents analysis, feeding behaviour observations, and biogeochemical tracers such as stable isotopes and fatty acids (Fry, 2006). A combination of methods is generally thought to be the most rigorous way of understanding the diet and resource pathways of aquatic food webs (Fry, 2006); however, studies rarely employ more than one method. We emphasise that the use of one method can potentially bias the outcome, and a brief analysis of the data relating to Principle 3 in this review highlights this. A study was 4.4 times more likely to support the notion that river and wetland food webs are strongly dependent on algal production if the study used biogeochemical tracers as their dominant method (Chi-square test; P-value < 0.001). We cannot ascertain whether biogeochemical tracers lead to a more or less true outcome. Nevertheless, their use does bias the outcome toward supporting the role of algal production for tropical aquatic food webs. Finally, sampling once in time and/or space may not capture the full variety of important food resources because different resources can be important, as well as more available, at different stages of an individual's life cycle and/or hydrological periods. For example, Jardine et al. (2015) highlights that attributing food-web production to a single-source pathway is problematic because it overlooks the important role external subsidies, which may subtly vary in space and time, have for sustaining viable populations.

4.8 The structure and trophic interactions of tropical freshwater food webs are highly context dependent

Large-bodied macroconsumer species, such as fish and shrimp, are thought to exert a disproportionately large influence on the structure and functioning of tropical benthic environments (Pringle et al. 1999; Crowl et al. 2001; Flecker and Taylor, 2004) as described in Principle 4. Further, fish communities in tropical rivers are thought to be proportionally more omnivorous compared to those in temperate rivers (González-Bergonzoni et al. 2012), leading to short, diffuse and interconnected food webs (Principle 5; (Pusey et al. 2010)). Most research supported aspects of these principles (60% support for Principle 4 and 55% support for Principle 5), but there remains a relatively high level of studies providing 'equivocal' or 'refuting' evidence (Figure 4-6).

Spatial and temporal variation in hydro-ecological characteristics (i.e. Principle 1 and 2) can alter many aspects of freshwater food-web structure and the top-down effects consumers exert (Winemiller et al. 2014). In this way, the detection of food-web changes may vary depending on when (i.e. dry season or wet season) and where (i.e. low or high seasonal variation in hydrology) the study was conducted. For instance, strongest top-down influences of consumers on tropical freshwater food webs are often detected during the dry season when water levels fall and predators and prey become concentrated (Winemiller et al. 2006; Winemiller et al. 2014). Further, omnivory is often reported in highly seasonal river floodplains due to the high variability in resource availability as freshwater habitats expand and contract (Blanchette et al. 2013; Warfe et al. 2013; Heng et al. 2018). Seasonal floodplain inundation has also been suggested to drive variability in food chain length. For example, Warfe et al (2013) hypothesised that the absence of short food chains (food chain length averaged 4.5) in floodplains of northern Australia was due to annual flooding which 'opens' freshwater food webs, allowing consumers to be part of more regional food chains, confounding empirical links of food-web characteristics to local environmental factors.

4.9 A holistic understanding of tropical aquatic food webs is required

The management of tropical freshwaters will likely be best informed by holistic studies encompassing ecological information from multiple food-web components (see Box 4.2) and aquatic systems (i.e. rivers, floodplains, lakes, estuaries) and recognising the temporal variation in the hydro-ecological connections between systems. Hydrological connectivity is known to be particularly important because it links riverine, lacustrine and subterranean aquatic systems with floodplains and estuaries, and this connectivity is critical for maintaining ecosystem productivity and integrity (Pringle, 2003). We found that over 82% of studies conducted research in just one aquatic system type (Figure 4-7a), with most of these studies (63%) focused entirely on riverine systems (Figure 4-7b). Further, less than 2% of studies included 3 aquatic systems (Figure 4-7a), with all these systems being rivers, lakes and their floodplains. Many of the original principles in Douglas et al. (2005) were formed with this 'hydrological connectedness' in mind, particularly wet-season hydrological connectivity between rivers and their floodplains. However, only 34 studies (9.2%) of the surveyed literature incorporated research of rivers and their floodplains. Additionally, we know that diadromous fish species require unimpeded movement between freshwater and marine environments during their life cycles (Drouineau et al. 2018; Dias et al. 2019), yet only 13 studies (3.5%) incorporated both riverine and estuarine environments. It is important to know that the inclusion of multiple aquatic systems in one study is not evidence of relevant research connecting them, so our findings almost certainly underestimate the degree of whole-system research on tropical aquatic food webs. All-in-all, the small number of studies incorporating multiple aquatic systems points to a lack of understanding of tropical aquatic food webs at large spatial and conceptual scales.

One of the most striking findings was the lack of research focusing on subterranean freshwater ecosystems and their links to surface-water ecosystem dynamics. We identified only 2 studies investigating aspects of subterranean-freshwater food webs (Figure 4-7b). Further, only one study incorporated 2 aquatic systems (subterranean and estuarine systems). The paucity of subterranean research included in our review dataset, and research linking subterranean with surface-water environments, is likely related to 2 main reasons. First, we know that many well-established ecological patterns and processes applied to surface-water ecosystems do not necessarily describe subterranean ecosystems (Gibert and Deharveng, 2002). The principles at the centre of this review were developed on surface-water food-web research, and it is likely that these principles, and the literature search terms, may not adequately capture ecological patterns and processes of subterranean food webs. Second, it is probable that the paucity of subterranean freshwater food-web research in our review reflects the paucity of subterranean ecological research more generally (Larned, 2012).

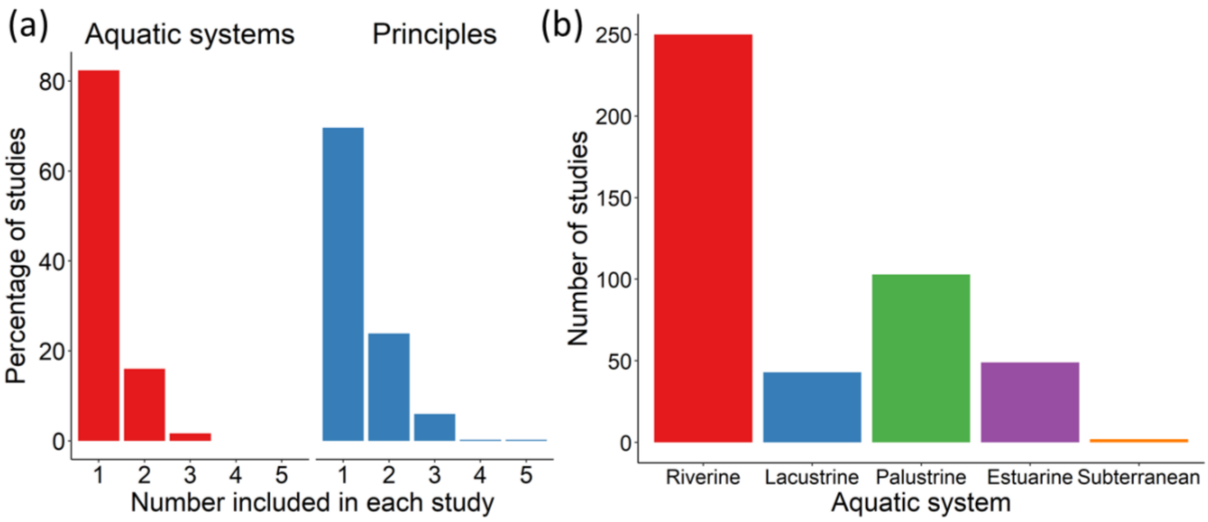

Figure 4-7. The (a) percentage of studies incorporating single or multiple aquatic systems and principles and (b) the number of studies including riverine, lacustrine, palustrine, estuarine and/or subterranean aquatic systems.

Box 4.2. Representation of different food-web components in global tropical food web research.

Fish, macroinvertebrates, and algae were collectively incorporated into 84% of the research (Figure 4-8). Fish were the most studied component of research on tropical aquatic food webs and were studied in more than one-third (35%) of all studies. The focus on fish is likely due to the ecological, economical and social importance of freshwater fish globally (Lynch et al. 2016). Macroinvertebrates (including molluscs) and algae (benthic, filamentous and/or phytoplankton) were each included in just under one-quarter of studies. Further, algae are major contributors to the productivity of aquatic ecosystems, especially in the tropics, due to their role in assimilating and mediating energy and nutrients fluxes throughout trophic levels of food webs (Jardine et al. 2013). We suggest that the ecological importance of macroinvertebrates and algae partly explain why they were incorporated in almost 50% of the studies.

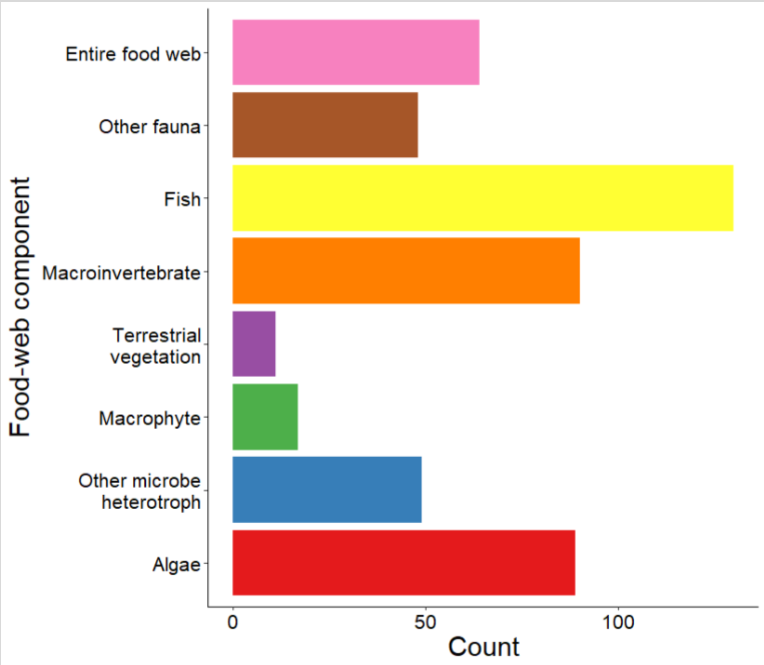

Figure 4-8. The number of times each food-web component was included in the studies included in this review.

4.10 Emerging themes and dealing with rapid hydrological change in the Anthropocene

Freshwater ecosystems have, for some time, been the most threatened ecosystems on our planet (Carpenter et al. 2011). Global change has undoubtably been most focused on freshwater environments due to the crucial role of freshwater resources for human development. The rapid changes experienced by many tropical freshwaters have led to evolving research opportunities and knowledge gaps over time. We outline 2 important and emerging themes related to tropical freshwater food webs below.

4.10.1 Groundwater-surface water interactions – underappreciated role in food webs

Freshwater ecosystems are not only hydrologically connected along longitudinal and lateral flow paths but also vertically through groundwater-surface water interactions (Ward, 1989). Groundwater contains 97% of all unfrozen water on Earth, compared to less than 2% contained in surface freshwater environments, and groundwater inputs ensure many aquatic environments persist during dry conditions (Alley et al. 2002). Although subterranean ecosystems are known to harbour a diverse array of aquatic fauna (Danielopol et al. 2000), the ecology of subterranean ecosystems remains relatively unknown (Gibert and Deharveng, 2002). However, it is becoming increasingly clear that groundwater-surface water interactions play a key role in shaping aquatic food-web structure and ecosystem function (Burrows et al. 2018; Mazumder et al. 2019; Tang et al. 2019). Despite knowing the intrinsic value of subterranean ecosystems as well as the importance of groundwater-surface water interactions for surface-water hydrology, ecology and biogeochemical processes, less than half of 1% of research in our review focused on subterranean ecosystems. Precipitation patterns in many tropical regions are changing due to climate change and this is expected to lead to reduced rainfall in many regions (Zhang and Fueglistaler, 2019). A reduction in rainfall may lead to an increased reliance on baseflow for sustaining surface-water environments. On top of this, population growth in the tropics is already reducing groundwater levels, potentially threatening the persistence of surface-water environments over seasonal and interannual time periods. Given these changes to the relative importance of vertical hydrological connectivity in tropical freshwaters, it is imperative that research focuses on better understanding the implications of changes in groundwater-surface water interactions.

4.10.2 Many human communities rely on healthy tropical freshwater food webs

Local and regional economies, the sustenance of communities, and the cultural values of many people are linked to healthy tropical freshwater food webs. These freshwater-human links will only intensify as human populations in the topics develop and expand. A major challenge will be to balance the economic and cultural needs of human communities with the requirement to maintain important aspects of food-web structure and function. Meeting this challenge in the tropical zone will require a better understanding of (1) the sustainable levels of human uses of freshwater ecosystems and (2) the economic and cultural impacts of the continued degradation to freshwater food webs.

4.11 Reimagined principles to support the better management of tropical freshwater food webs

Integrating various information pieces into general principles that describe ecological patterns and processes is an important objective of scientists and environmental stewards. This is because general principles provide a streamlined ecological understanding that can be tested and more easily used to guide the development and execution of best-practice environmental-management strategies. However, a key challenge is to ensure that general principles adequately represent general ecological patterns and processes: if they do, then principles will have a high inferential strength and broader applicability. We found global support for 4 out of the 5 general principles describing tropical freshwater food webs that were proposed in Douglas et al. (2005). Further, although these general principles were developed to reflect the food-web patterns and processes in mainly riverine and palustrine systems, we show that they also adequately describe freshwater food webs in lacustrine and estuarine systems.

A major shortcoming of the present principles is that they are supported by few data in some aquatic systems, particularly subterranean environments. Furthermore, we recognise that aquatic ecosystems in the tropics are highly diverse and certain principles will not entirely describe food-web structure and function in all locations. We postulate that this may explain the lack of support for Principle 3 (River and wetland food webs are strongly dependent on algal productivity), as outlined in detail in the text above. To overcome these shortcomings, we have revised some of these general principles (see Box 4.3) with the hope that future research efforts will address these research gaps. Major changes include (1) the addition of vertical hydrological connectivity as an important factor underpinning freshwater food-web subsidies and (2) the recognition that algae production may not be the most important energy source for all tropical freshwater food webs.

Box 4.3. Revised principles describing freshwater food web dynamics in Australia's tropics.

Principle 1. Seasonal hydrology is the primary driver of aquatic food-web structure and ecosystem processes.

Principle 2. Hydrological connectivity underpins important lateral, longitudinal, and vertical food-web subsidies.

Principle 3. River and wetland food webs are strongly dependent on algal productivity, but other energy sources may be important under some circumstances .

Principle 4. A few common macroconsumer species have a strong influence on benthic food webs.

Principle 5. Omnivory is widespread and food webs are short.

4.12 Conclusions

Freshwater food webs are an integral component of Earth's tropics that need to function well if we want them to continue to support and maintain the many ecological and economic services that they provide. We conducted a rigorous literature review of 369 studies and found broad scientific support for 5 general principles that describe the structure and function of tropical freshwater food webs. We uncovered the following interesting themes in the evidence base: (1) large evidence bias were found in South America and Australia, with many regions that are arguably most at threat from human impacts were the least studied; (2) seasonal hydrology was incorporated in to most studies and was found to underpin many important aspects of freshwater food webs and ecosystem processes; (3) hydrological connectivity was vital for many species, but the role that vertical hydrological connectivity plays is virtually unknown; (4) there is no clear consensus on which resource pathway fuels food-web production; (5) our understanding of freshwater food-web dynamics is largely based on studies incorporating one aquatic system and a handful of species (e.g. fish, macro-invertebrates, primary producers). Although scientists still have much to learn about tropical freshwater food webs, we hope that these 5 general principles can be used to inform future management decisions and ensure that human-induced changes do not adversely impact Earth's tropical freshwaters.

4.13 References

Alley, W.M., Healy, R.W., LaBaugh, J.W., Reilly, T.E., 2002. Flow and Storage in Groundwater Systems. *Science*, 296, 1985-1990. doi:10.1126/science.1067123

Arias, M.E., Cochrane, T.A., Kummu, M., Lauri, H., Holtgrieve, G.W., Koponen, J., Piman, T., 2014. Impacts of hydropower and climate change on drivers of ecological productivity of Southeast Asia's most important wetland. *Ecological Modelling*, 272, 252-263. doi:10.1016/j.ecolmodel.2013.10.015

Blanchette, M.L., Davis, A.M., Jardine, T.D., Pearson, R.G., 2013. Omnivory and Opportunism Characterize Food Webs in a Large Dry-Tropics River System. *Freshwater Science*, 33, 142-158, 117.

Burrows, R.M., Rutlidge, H., Valdez, D.G., Venarsky, M., Bond, N.R., Andersen, M.S., Fry, B., Eberhard, S.M., Kennard, M.J., 2018. Groundwater supports intermittent-stream food webs. *Freshwater Science*, 37, 42-53. doi:10.1086/696533

Carpenter, S.R., Stanley, E.H., Zanden, M.J.V., 2011. State of the World's Freshwater Ecosystems: Physical, Chemical, and Biological Changes. *Annual Review of Environment and Resources*, 36, 75-99. doi:10.1146/annurev-environ-021810-094524

Cloern, J.E., Jassby, A.D., 2008. Complex seasonal patterns of primary producers at the land–sea interface. *Ecology Letters*, 11, 1294-1303. doi:10.1111/j.1461-0248.2008.01244.x

Collen, B., Whitton, F., Dyer, E.E., Baillie, J.E.M., Cumberlidge, N., Darwall, W.R.T., Pollock, C., Richman, N.I., Soulsby, A.-M., Böhm, M., 2014. Global patterns of freshwater species diversity, threat and endemism. *Global Ecology and Biogeography*, 23, 40-51. doi:10.1111/geb.12096

Correa, S.B., Winemiller, K.O., LóPez-Fernández, H., Galetti, M., 2007. Evolutionary Perspectives on Seed Consumption and Dispersal by Fishes. *Bioscience*, 57, 748-756. doi:10.1641/b570907

Costa-Pereira, R., Tavares, L.E.R., de Camargo, P.B., Araújo, M.S., 2017. Seasonal population and individual niche dynamics in a tetra fish in the Pantanal wetlands. *Biotropica*, 49, 531-538. doi:10.1111/btp.12434

Cotner, J.B., Montoya, J.V., Roelke, D.L., Winemiller, K.O., 2006. Seasonally variable riverine production in the Venezuelan llanos. *Journal of the North American Benthological Society*, 25, 171-184. doi:10.1899/0887-3593(2006)25[171:Svrpit]2.0.Co;2

Crowl, T.A., McDowell, W.H., Covich, A.P., Johnson, S.L., 2001. FRESHWATER SHRIMP EFFECTS ON DETRITAL PROCESSING AND NUTRIENTS IN A TROPICAL HEADWATER STREAM. *Ecology*, 82, 775-783. doi:10.1890/0012-9658(2001)082[0775:Fseodp]2.0.Co;2

Dalin, C., Wada, Y., Kastner, T., Puma, M.J., 2017. Groundwater depletion embedded in international food trade. *Nature*, 543, 700-704. doi:10.1038/nature21403

Danielopol, D.L., Pospisil, P., Rouch, R., 2000. Biodiversity in groundwater: a large-scale view. *Trends in Ecology & Evolution*, 15, 223-224. doi:10.1016/S0169-5347(00)01868-1

Dias, B.S., Frisk, M.G., Jordaan, A., 2019. Opening the tap: Increased riverine connectivity strengthens marine food web pathways. *PLOS ONE*, 14, e0217008. doi:10.1371/journal.pone.0217008

Douglas, M.M., Bunn S.E., Davies P.M. (2005) River and wetland food webs in Australia's wet–dry tropics: general principles and implications for management. *Marine and Freshwater Research* 56, 329-342.

Döll, P., Fiedler, K., Zhang, J., 2009. Global-scale analysis of river flow alterations due to water withdrawals and reservoirs. *Hydrol. Earth Syst. Sci.*, 13, 2413-2432. doi:10.5194/hess-13-2413-2009

Drouineau, H., Carter, C., Rambonilaza, M., Beaufaron, G., Bouleau, G., Gassiat, A., Lambert, P., le Floch, S., Tétard, S., de Oliveira, E., 2018. River Continuity Restoration and Diadromous Fishes:

Much More than an Ecological Issue. *Environmental Management*, 61, 671-686. doi:10.1007/s00267-017-0992-3
Dudgeon, D., 2000. Large-Scale Hydrological Changes in Tropical Asia: Prospects for Riverine Biodiversity: The construction of large dams will have an impact on the biodiversity of tropical Asian rivers and their associated wetlands. *Bioscience*, 50, 793-806. doi:10.1641/0006-3568(2000)050[0793:Lshcit]2.0.Co;2
Fellman, J.B., Spencer, R.G.M., Raymond, P.A., Pettit, N.E., Skrzypek, G., Hernes, P.J., Grierson, P.F., 2014. Dissolved organic carbon biolability decreases along with its modernization in fluvial networks in an ancient landscape. *Ecology*, 95, 2622-2632. doi:10.1890/13-1360.1
Feutry, P., Kyne, P.M., Pillans, R.D., Chen, X., Marthick, J., Morgan, D.L., Grewe, P.M., 2015. Whole mitogenome sequencing refines population structure of the Critically Endangered sawfish Pristis pristis. *Marine Ecology Progress Series*, 533, 237-244.
Flecker, A.S., Taylor, B.W., 2004. TROPICAL FISHES AS BIOLOGICAL BULLDOZERS: DENSITY EFFECTS ON RESOURCE HETEROGENEITY AND SPECIES DIVERSITY. *Ecology*, 85, 2267-2278. doi:10.1890/03-0194
Fry, B., 2006. Stable isotope ecology.
Gawade, L., Sarma, V.V.S.S., Rao, Y.V., Hemalatha, K.P.J., 2017. Variation of Bacterial Metabolic Rates and Organic Matter in the Monsoon-Affected Tropical Estuary (Godavari, India). *Geomicrobiology Journal*, 34, 628-640. doi:10.1080/01490451.2017.1326989
Gibert, J., Deharveng, L., 2002. Subterranean Ecosystems: A Truncated Functional Biodiversity: This article emphasizes the truncated nature of subterranean biodiversity at both the bottom (no primary producers) and the top (very few strict predators) of food webs and discusses the implications of this truncation both from functional and evolutionary perspectives. *Bioscience*, 52, 473-481. doi:10.1641/0006-3568(2002)052[0473:Seatfb]2.0.Co;2
González-Bergonzoni, I., Meerhoff, M., Davidson, T.A., Teixeira-de Mello, F., Baattrup-Pedersen, A., Jeppesen, E., 2012. Meta-analysis Shows a Consistent and Strong Latitudinal Pattern in Fish Omnivory Across Ecosystems. *Ecosystems*, 15, 492-503. doi:10.1007/s10021-012-9524-4
Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F., Babu, S., Borrelli, P., Cheng, L., Crochetiere, H., Ehalt Macedo, H., Filgueiras, R., Goichot, M., Higgins, J., Hogan, Z., Lip, B., McClain, M.E., Meng, J., Mulligan, M., Nilsson, C., Olden, J.D., Opperman, J.J., Petry, P., Reidy Liermann, C., Sáenz, L., Salinas-Rodríguez, S., Schelle, P., Schmitt, R.J.P., Snider, J., Tan, F., Tockner, K., Valdujo, P.H., van Soesbergen, A., Zarfl, C., 2019. Mapping the world’s free-flowing rivers. *Nature*, 569, 215-221. doi:10.1038/s41586-019-1111-9
Heng, K., Chevalier, M., Lek, S., Laffaille, P., 2018. Seasonal variations in diet composition, diet breadth and dietary overlap between three commercially important fish species within a flood-pulse system: The Tonle Sap Lake (Cambodia). *PLOS ONE*, 13, e0198848. doi:10.1371/journal.pone.0198848
Holtgrieve, G.W., Arias, M.E., Irvine, K.N., Lamberts, D., Ward, E.J., Kummu, M., Koponen, J., Sarkkula, J., Richey, J.E., 2013. Patterns of Ecosystem Metabolism in the Tonle Sap Lake, Cambodia with Links to Capture Fisheries. *PLOS ONE*, 8, e71395. doi:10.1371/journal.pone.0071395
Jardine, T.D., Pusey, B.J., Hamilton, S.K., Pettit, N.E., Davies, P.M., Douglas, M.M., Sinnamon, V., Halliday, I.A., Bunn, S.E., 2012. Fish mediate high food web connectivity in the lower reaches of a tropical floodplain river. *Oecologia*, 168, 829-838. doi:10.1007/s00442-011-2148-0
Jardine, T.D., Hunt, R.J., Faggotter, S.J., Valdez, D., Burford, M.A., Bunn, S.E., 2013. Carbon from periphyton supports fish biomass in waterholes of a wet–dry tropical river. *River Research and Applications*, 29, 560-573. doi:10.1002/rra.2554
Jardine, T.D., Woods, R., Marshall, J., Fawcett, J., Lobegeiger, J., Valdez, D., Kainz, M.J., 2015. Reconciling the role of organic matter pathways in aquatic food webs by measuring multiple tracers in individuals. *Ecology*, 96, 3257-3269. doi:10.1890/14-2153.1

Jardine, T.D., Rayner, T.S., Pettit, N.E., Valdez, D., Ward, D.P., Lindner, G., Douglas, M.M., Bunn, S.E., 2017. Body size drives allochthony in food webs of tropical rivers. *Oecologia*, 183, 505-517. doi:10.1007/s00442-016-3786-z

Joint Select Committee on Northern Australia, 2014. Pivot North: Inquiry into the Development of Northern Australia: Final Report. The Parliament of the Commonwealth of Australia, Canberra, Australia.

Junk, W.J., Bayley, P.B., Sparks, R.E., 1989. The flood-pulse concept in river-floodplain systems. Dodge, D.P. (Ed.), Proceedings of the International Large River Symposium (LARS). NRC research press, pp. 110-127.

Junk, W.J., Welcomme, R.L., 1990. Floodplains. In: Patten, B.C. (Ed.), Wetlands and Shallow Continental Water Bodies. SPB Academic Publishing, The Hague, pp. 491-524.

Kloh, J.S., Figueredo, C.C., Eterovick, P.C., 2018. You are what, where, and when you eat: seasonal and ontogenetic changes in a tropical tadpole’s diet. 39, 445. doi:10.1163/15685381-17000209

Kopij, G., Paxton, M., 2018. Seasonal Changes in the Diversity and Numbers of Waterbirds in a Tropical River in Southern Africa. *Polish Journal of Ecology*, 66, 257-269, 213.

Kummu, M., Sarkkula, J., 2008. Impact of the Mekong River Flow Alteration on the Tonle Sap Flood Pulse. *Ambio*, 37, 185-192.

Lamberts, D., 2006. The Tonle Sap Lake as a Productive Ecosystem. *International Journal of Water Resources Development*, 22, 481-495. doi:10.1080/07900620500482592

Larned, S.T., 2012. Phreatic groundwater ecosystems: research frontiers for freshwater ecology. *Freshwater Biology*, 57, 885-906. doi:10.1111/j.1365-2427.2012.02769.x

Latrubesse, E.M., Arima, E.Y., Dunne, T., Park, E., Baker, V.R., d’Horta, F.M., Wight, C., Wittmann, F., Zuanon, J., Baker, P.A., Ribas, C.C., Norgaard, R.B., Filizola, N., Ansar, A., Flyvbjerg, B., Stevaux, J.C., 2017. Damming the rivers of the Amazon basin. *Nature*, 546, 363-369. doi:10.1038/nature22333

Leigh, C., Sheldon, F., Kingsford, R.T., Arthington, A.H., 2010. Sequential floods drive booms and wetland persistence in dryland rivers: a synthesis. *Marine and Freshwater Research*, 61, 896-908. doi:10.1071/MF10106

Mazumder, D., Saintilan, N., Hollins, S., Meredith, K., Jacobsen, G., Kobayashi, T., Wen, L., 2019. Carbon Uptake in Surface Water Food Webs Fed by Palaeogroundwater. *Journal of Geophysical Research: Biogeosciences*, 124, 1171-1180. doi:10.1029/2018jg004925

McIntyre, P.B., Reidy Liermann, C.A., Revenga, C., 2016. Linking freshwater fishery management to global food security and biodiversity conservation. *Proceedings of the National Academy of Sciences*, 113, 12880-12885. doi:10.1073/pnas.1521540113

Novak, P.A., Garcia, E.A., Pusey, B.J., Douglas, M.M., 2017. Importance of the natural flow regime to an amphidromous shrimp: a case study. *Marine and Freshwater Research*, 68, 909-921. doi:10.1071/MF16034

O'Grady, A.P., Eamus, D., Cook, P.G., Lamontagne, S., 2006. Groundwater use by riparian vegetation in the wetdry tropics of northern Australia. *Australian Journal of Botany*, 54, 145-154. doi:10.1071/BT04164

Oliveras, I., Malhi, Y., 2016. Many shades of green: the dynamic tropical forest–savannah transition zones. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 371. doi:20150308

Peel, M.C., Finlayson, B.L., McMahon, T.A., 2007. Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences*, 11, 1633-1644. doi:10.5194/hess-11-1633-2007

Pettit, N., Warfe, D., Close, P., Pusey, B., Dobbs, R., Davies, C., Valdez, D., Davies, P., 2017. Carbon sources for aquatic food webs of riverine and lacustrine tropical waterholes with variable groundwater influence. *Marine and Freshwater Research*, 68, 442-451. doi:10.1071/MF15365

Pringle, C., 2003. What is hydrologic connectivity and why is it ecologically important? *Hydrological Processes*, 17, 2685-2689. doi:10.1002/hyp.5145

Pringle, C.M., Hemphill, N., McDowell, W.H., Bednarek, A., March, J.G., 1999. LINKING SPECIES AND ECOSYSTEMS: DIFFERENT BIOTIC ASSEMBLAGES CAUSE INTERSTREAM DIFFERENCES IN ORGANIC MATTER. *Ecology*, 80, 1860-1872. doi:10.1890/0012-9658(1999)080[1860:Lsaedb]2.0.Co;2

Pusey, B.J., Arthington, A.H., Stewart-Koster, B., Kennard, M.J., Read, M.G., 2010. Widespread omnivory and low temporal and spatial variation in the diet of fishes in a hydrologically variable northern Australian river. *Journal of Fish Biology*, 77, 731-753. doi:10.1111/j.1095-8649.2010.02712.x

Pusey, B.J., Kennard, M.J., Larson, H.K., Alsop, Q., Hammer, M., Buckle, D.J., 2016. Estuarine fishes of the South Alligator River, Kakadu National Park, northern Australia. *Marine and Freshwater Research*, 67, 1797-1812. doi:10.1071/MF15221

Rajaneesh, K.M., Mitbavkar, S., Anil, A.C., 2018. Dynamics of size-fractionated phytoplankton biomass in a monsoonal estuary: Patterns and drivers for seasonal and spatial variability. *Estuarine, Coastal and Shelf Science*, 207, 325-337. doi:10.1016/j.ecss.2018.04.026

Ramberg, L., Wolski, P., Krah, M., 2006. Water balance and infiltration in a seasonal floodplain in the Okaying Delta Botswana. *Wetlands*, 26, 677-690. doi:10.1672/0277-5212(2006)26[677:WBAIIA]2.0.CO;2

Reid, A.J., Carlson, A.K., Creed, I.F., Eliason, E.J., Gell, P.A., Johnson, P.T.J., Kidd, K.A., MacCormack, T.J., Olden, J.D., Ormerod, S.J., Smol, J.P., Taylor, W.W., Tockner, K., Vermaire, J.C., Dudgeon, D., Cooke, S.J., 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews*, 94, 849-873. doi:10.1111/brv.12480

Sabo, J.L., Ruhi, A., Holtgrieve, G.W., Elliott, V., Arias, M.E., Ngor, P.B., Räsänen, T.A., Nam, S., 2017. Designing river flows to improve food security futures in the Lower Mekong Basin. *Science*, 358, eaao1053. doi:10.1126/science.aao1053

Seidel, D.J., Fu, Q., Randel, W.J., Reichler, T.J., 2008. Widening of the tropical belt in a changing climate. *Nature Geoscience*, 1, 21-24. doi:10.1038/ngeo.2007.38

Srichandan, S., Baliarsingh, S.K., Prakash, S., Lotliker, A.A., Parida, C., Sahu, K.C., 2019. Seasonal dynamics of phytoplankton in response to environmental variables in contrasting coastal ecosystems. *Environmental Science and Pollution Research*, 26, 12025-12041. doi:10.1007/s11356-019-04569-5

State of the Tropics, 2019. Health in the Tropics.

Stoffels, R.J., Rehwinkel, R.A., Price, A.E., Fagan, W.F., 2016. Dynamics of fish dispersal during river-floodplain connectivity and its implications for community assembly. *Aquatic Sciences*, 78, 355-365. doi:10.1007/s00027-015-0437-0

Tang, T., Guo, S., Tan, L., Li, T., Burrows, R.M., Cai, Q., 2019. Temporal Effects of Groundwater on Physical and Biotic Components of a Karst Stream. *Water*, 11, 1299.

Thompson, R.M., Brose, U., Dunne, J.A., Hall Jr, R.O., Hladyz, S., Kitching, R.L., Martinez, N.D., Rantala, H., Romanuk, T.N., Stouffer, D.B., Tylianakis, J.M., 2012. Food webs: reconciling the structure and function of biodiversity. *Trends in Ecology & Evolution*, 27, 689-697. doi:10.1016/j.tree.2012.08.005

Townsend, S.A., Webster, I.T., Schult, J.H., 2011. Metabolism in a groundwater-fed river system in the Australian wet/dry tropics: tight coupling of photosynthesis and respiration. *Journal of the North American Benthological Society*, 30, 603-620. doi:10.1899/10-066.1

Vörösmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S.E., Sullivan, C.A., Liermann, C.R., Davies, P.M., 2010. Global threats to human water security and river biodiversity. *Nature*, 467, 555-561. doi:10.1038/nature09440

Ward, J.V., 1989. The Four-Dimensional Nature of Lotic Ecosystems. *Journal of the North American Benthological Society*, 8, 2-8. doi:10.2307/1467397

Warfe, D.M., Jardine, T.D., Pettit, N.E., Hamilton, S.K., Pusey, B.J., Bunn, S.E., Davies, P.M., Douglas, M.M., 2013. Productivity, Disturbance and Ecosystem Size Have No Influence on Food Chain Length in Seasonally Connected Rivers. *PLOS ONE*, 8. doi:10.1371/journal.pone.0066240

Whitehead, P.J., Saalfeld, K., 2000. Nesting phenology of magpie geese (Anseranas semipalmata) in monsoonal northern Australia: responses to antecedent rainfall. *Journal of Zoology*, 251, 495-508. doi:10.1111/j.1469-7998.2000.tb00805.x

Winemiller, K.O., 2004. Floodplain river food webs: generalizations and implications for fisheries management. In: Welcomme, R., Petr, T. (Eds.), Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries. RAP Publication Regional Office for Asia and the Pacific, Bangkok, Thailand, pp. 285-309.

Winemiller, K.O., Montoya, J.V., Roelke, D.L., Layman, C.A., Cotner, J.B., 2006. Seasonally varying impact of detritivorous fishes on the benthic ecology of a tropical floodplain river. *Journal of the North American Benthological Society*, 25, 250-262, 213.

Winemiller, K.O., Montaña, C.G., Roelke, D.L., Cotner, J.B., Montoya, J.V., Sanchez, L., Castillo, M.M., Layman, C.A., 2014. Pulsing hydrology determines top-down control of basal resources in a tropical river–floodplain ecosystem. *Ecological Monographs*, 84, 621-635. doi:10.1890/13-1822.1

Winemiller, K.O., McIntyre, P.B., Castello, L., Fluet-Chouinard, E., Giarrizzo, T., Nam, S., Baird, I.G., Darwall, W., Lujan, N.K., Harrison, I., Stiassny, M.L.J., Silvano, R.A.M., Fitzgerald, D.B., Pelicice, F.M., Agostinho, A.A., Gomes, L.C., Albert, J.S., Baran, E., Petrere, M., Zarfl, C., Mulligan, M., Sullivan, J.P., Arantes, C.C., Sousa, L.M., Koning, A.A., Hoeinghaus, D.J., Sabaj, M., Lundberg, J.G., Armbruster, J., Thieme, M.L., Petry, P., Zuanon, J., Vilara, G.T., Snoeks, J., Ou, C., Rainboth, W., Pavanelli, C.S., Akama, A., Soesbergen, A.v., Sáenz, L., 2016. Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. *Science*, 351, 128-129. doi:10.1126/science.aac7082

Winter, T.C., 1999. Relation of streams, lakes, and wetlands to groundwater flow systems. *Hydrogeology Journal*, 7, 28-45. doi:10.1007/s100400050178

Zarfl, C., Lumsdon, A.E., Berlekamp, J., Tydecks, L., Tockner, K., 2015. A global boom in hydropower dam construction. *Aquatic Sciences*, 77, 161-170. doi:10.1007/s00027-014-0377-0

Zhang, Y., Fueglistaler, S., 2019. Mechanism for Increasing Tropical Rainfall Unevenness With Global Warming. *Geophysical Research Letters*, 46, 14836-14843. doi:10.1029/2019gl086058

4.14 Supplementary material

4.14.1 Review protocol

We undertook a comprehensive ‘rapid review’ procedure to assess the veracity of the 5 principles for tropical aquatic food webs. Rapid reviews are a valuable form of evidence synthesis for highly focussed questions (Cook et al. 2017). While there is no single way of performing a rapid review, we used a structured approach that included a systematic literature search with clear inclusion criteria and an assessment of the strength of evidence supporting each general principle.

4.14.2 Search strategy, data inclusion and extraction

We conducted the literature search in SCOPUS by searching research titles, abstracts and keywords for terms describing the climate (‘tropic*’), environment (‘aquatic’, ‘fresh*’, ‘floodplain’, ‘wetland*’, ‘river*’, ‘stream*’), research focus area (‘food web’, ‘food-web’, ‘foodweb’, ‘diet’, ‘trophic’, ‘connectivity’, ‘top-down’, ‘macroconsumer*’, ‘subsid*’, ‘food chain’, ‘food-chain’, ‘ecosystem proces*’, ‘isotop*’) and subject area (‘Agricultural and Biological Sciences’, ‘Environmental Sciences’, ‘Earth and Planetary Sciences’, ‘Biochemistry, Genetics and Molecular Biology’). Additionally, we excluded a number of subject areas such as ‘Arts’, ‘Medical’, ‘Dental’. We limited the search period to the period between 1 January 1950 and 30 June 2019. The full list of terms and rules used in the SCOPUS search is available in Table 4-1.

The SCOPUS search produced 2,825 research items, of which 369 were considered to relate to one or more of the 5 general principles. We included research items only if they satisfied the following conditions:

- The research findings had direct implications for one or more of the 5 general principles (see Table 4-2 for supporting evidence for each principle).
- The article language was English or a summary in English was available with sufficient detail to extract the required information.
- The article was not a review article.
- The study was conducted within Earth’s tropical zone (i.e. having a latitude below 23°26′12.2″ N and 23°26′12.2″ S).
- The research was not contained within heavily altered environments (i.e. reservoirs or urban catchments).
- The research primarily focused on endemic species.

For each study we recorded:

- The general principle(s) that the research assessed and the level of support for each principle based on the findings (Support, Equivocal, or Refutes).
- The United Nations Geoscheme(s) which encompasses the study system.
- The response variables included in the study (algae, other microbe/heterotroph, macrophyte, terrestrial vegetation, invertebrate [including mollusc], fish, other fauna [amphibian, reptile, bird, mammal or arachnid], or entire food web).
- The dominant method(s) deployed (stable isotopes, fatty acids, biogeochemistry, diet, autotrophic or heterotrophic activity, genetics, morphology/condition/growth rate, otolith analysis, fauna/flora movement, biomass/cover/abundance, community

composition/structure, reproductive success/dynamics, feeding behaviour, material flux, trophic position/structure).

- The aquatic environment (riverine, lacustrine, palustrine, estuarine, subterranean).

SCOPUS search for ‘freshwater ecology’ research

We determined the total number of published ‘freshwater ecology’ research between from 1950 onward and investigated what proportion of this research was related to tropical ecosystems. We split all SCOPUS searches into two time periods (1950–99 and 2000 until the date of the SCOPUS search) to investigate any recent temporal changes in the study of freshwater ecology in the tropics. We adjusted our search terms to obtain information on the total number of studies in freshwater ecology globally, the total number of studies associated with the tropics, and the total number of studies associated with dryland ecosystems. We chose to compare the total number of ‘freshwater ecology’ studies in tropical and dryland ecosystems to investigate relative differences in the research effort among these regions. We used the following search terms and recorded the total number of research items:

- ALL (‘freshwater’ AND ‘ecology’)
- ALL (‘freshwater’ AND ‘ecology’ AND ‘tropic’ AND NOT ‘subtropic*’ OR ‘subtrop*’)
- ALL (‘freshwater’ AND ‘ecology’ AND dryland OR desert OR arid OR ‘semi-arid’)

Table 4-1. Terms used in SCOPUS to search for studies to include in the literature review.

Climate	Environment	Research focus area	Limit to	Exclude
tropic*	aquatic	food web	Agriculture and Biological Sciences	Arts
	fresh*	food-web	Environmental Sciences	Medical
	floodplain	foodweb	Earth and Planetary Sciences	Engineering
	wetland*	diet	Biochemistry, Genetics and Molecular Biology	Pharmacology, Toxicology, Pharmaceutics
	river*	trophic		Veterinary
	stream*	connectivity		Decision sciences
		top-down		Computer science
		macroconsumer*		Neuroscience
		subsid*		Nursing
		food chain		Materials science
		food-chain		Business, management and accounting
		ecosystem proces*		Economics, econometrics and finance
		isotopo*		Dentistry
				Health professions

Table 4-2. The criteria used to determine if a study is related to one or more of the general principles outlined in Douglas et al. (2005) and thus should be included in the review. Although the criteria are written to support each principle, we recorded evidence that supported, refuted or was equivocal in relation to each principle.

Principle	The principle and the criteria for inclusion
1.	The seasonal hydrology is a strong driver of ecosystem processes and food-web structure 1. Hydrology shapes seasonal variation in food-web structure, biogeochemistry, and/or the ecosystem processes of microbial, vertebrate or invertebrate species. 2. Seasonal hydrology is linked to variation in food-web structure, biogeochemistry, and/or the ecosystem processes of microbial, vertebrate or invertebrate species. 3. Seasonal shift in, or seasonal hydrology is likely a main reason influencing, variation in ecosystem processes and/or the activity, diet, biogeochemical character, abundance, biomass and/or community structure of a species.
2.	Hydrological connectivity is largely intact and underpins important lateral and longitudinal food-web subsidies 1. Hydrological connectivity mediates the lateral and longitudinal flux of resources which contributes to the energetic base of species, aquatic food webs and/or ecosystem process(es). 2. Hydrological connectivity is associated with variation in the resource availability, activity, movement, life history, diet, biogeochemical character, abundance, biomass and/or community structure of a species.
3.	River and wetland food webs are strongly dependent on algal production 1. Biogeochemical values of many food-web components indicate algal resources are the most important carbon source. 2. Dietary studies (i.e. stomach content/feeding trials) and/or biogeochemical values of a/many primary and/or secondary consumer(s).
4.	A few common macroconsumer species have a strong influence on benthic food webs 1. Macroconsumer(s) exert disproportionally large influence (i.e. top-down control) on benthic food web structure (i.e. on species abundance and community composition) or benthic ecosystem processes and biogeochemistry (i.e. sediments, detritus, nutrient demand and processing).
5.	Omnivory is widespread and food chains are short 1. Omnivory is common for most primary and secondary consumers. 2. Trophic levels in the entire food web assessed indicating short or long food chains. 3. Omnivory is common for some primary and/or secondary consumers. 4. Sampled consumer(s) determined to have a low (e.g. < 3) trophic level. 5. Omnivory is thought to be an important determinant of species abundance or presence.

5. Ecohydrological risks from hydrologic alteration and other threats

5.1 Hydrologic alteration

The maintenance of the natural flow regime is critical to the integrity of aquatic ecosystems. Changes in natural patterns of river flow due to human activities is regarded as one of the most serious and ongoing threats to ecological sustainability of rivers and their associated floodplain wetlands in many parts of the world (Bunn and Arthington, 2002; Dudgeon et al. 2006; Vörösmarty et al. 2010). Human activities that alter natural patterns of river flows include:

- water-resource development (e.g. dams and weirs used for irrigation, hydropower, etc)
- surface and groundwater extraction for agriculture and human consumption
- interbasin transfers of water (e.g. associated with irrigation or hydropower)
- land use change (i.e. loss of vegetation cover, agriculture, urbanisation, mining, etc)
- anthropogenic climate change.

Particular attributes of the flow regime are affected in a variety of ways by these different sources of hydrologic alteration and are briefly summarised below.

5.1.1 Changes to high flows

Large dams typically dampen flood peaks, reducing the frequency, extent, and often the duration of floodplain inundation. Reduction in the size, number, and duration of floods decreases the area and depth of floodplains, the period in which biota may freely move between the main channel and the floodplain, and the duration of floodplain waterhole persistence throughout the dry season (Bunn and Arthington, 2002). Given the strong positive relationships between wet-season flows and fisheries production (Loneragan and Bunn, 1999; Welcomme et al. 2006; Crook et al. 2022), a reduction in the magnitude and frequency of flood events is likely to have a marked impact on this important ecosystem service.

A reduction in the magnitude and frequency of smaller, channel-forming flows (i.e. those with a return frequency of 1:1 to 1:2 years) can result in sediment accumulation in river pools, encroachment of riparian vegetation, accumulation of aquatic weeds, and a contraction in river-channel size and overall habitat for biota. This can also lead to changes in the pattern of channel migration, lowering habitat diversification on floodplains and, ultimately, reducing the biological diversity and ecological integrity of floodplain rivers (Ward and Stanford, 1995).

Smaller dams and weirs may not have a great effect on flood dynamics but may be sufficiently large to trap smaller flood events, particularly those that occur late in the dry season when water levels are low. These flow 'pulses' may be critical in maintaining water quality and, hence, the survival of biota, in pools late in the dry season (Bunn et al. 2006).

5.1.2 Changes to low flows

Flow regulation and other anthropogenic disturbances (e.g. land clearing, climate change) can alter the ecologically relevant attributes of low-flow hydrology (Rolls et al. 2012; King et al. 2015). Perennial rivers often have permanent baseflows due to significant shallow groundwater inputs during the dry season. Reductions in low-flow magnitude downstream of dams, or from groundwater extraction that reduces groundwater contributions to surface flow, can reduce the availability and quality of important flow-sensitive habitats, such as shallow, fast-flowing riffles and refugial pools. Reductions in water depth can also affect longitudinal connectivity, as increasingly shallow areas become barriers to migration for a range of biota, including turtles, fish and crustaceans (Rolls et al. 2012; King et al. 2015).

Ecologically important low flows can also be impacted by flow supplementation, when water stored in impoundments in the wet season is delivered down the stream channel during the dry season. This form of supplementation often occurs downstream from storages delivering water for irrigation, when water is released during the dry season when it is most needed by irrigators. However, elevated flows during the dry season can also occur downstream of large-storage hydropower dams. Although elevated baseflows in the dry season may increase longitudinal connectivity and reduce the risk of poor water quality in isolated river pools, there are associated negative effects. Elevated flows during the dry season may inundate key habitats for biota (e.g. nesting sand banks for turtles or productive littoral habitats).

5.1.3 Changes to flow timing and variability

Although temperature regimes influence the life cycles of many stream and river animals, the timing of particular flow events is also important (Bunn and Arthington, 2002). The operation of large storages, especially for irrigation supply but also hydropower, can lead to the dampening and, in some cases, reversal of seasonal flow pulses (Lytle and Poff, 2004). This can disrupt life cycles of aquatic species, where reproductive or migration flow cues are linked to seasonal differences in temperature and food availability. The operation of some hydropower dams can also lead to erratic changes in flow variability, completely masking natural flow cues. Extreme daily variations below peaking power hydroelectric dams have no natural analogue in freshwater systems (Poff et al. 1997). In addition to stranding of aquatic organisms in floodplain habitats, dam operations that lead to rapid drawdown of flood events can lead to mass failure of saturated riverbanks and increased erosion.

5.2 River impoundment and loss of flowing riverine habitat

It is often perceived that the loss of flowing riverine habitat, due to inundation of river channels by impoundments, is balanced by the creation of non-flowing lake habitat. This can be quite misleading, because natural lakes and wetlands often function in a very different way to river storages. Much of the productivity of lakes and wetlands is associated with the littoral margins (Davies et al. 2008; Adame et al. 2017). Large impoundments are generally not operated at a constant water level, and productive littoral areas are rarely sustained. In addition, water levels are usually significantly elevated above natural stream levels, flooding part of the terrestrial-aquatic interface and creating a new littoral zone with steeper banks, less complex aquatic habitat, and different physicochemical conditions for aquatic plants. Moreover, the simple transformation of previously flowing riverine to non-flowing lake habitat within impoundments has major implications for species with an obligate need for flowing riverine habitats (e.g. for spawning, juvenile recruitment, foraging and refuge). Water quality in impoundments is often very different from that in rivers, due to the absence of continual physical mixing. Stratification of the water column may develop as deeper waters become colder and more oxygen-deficient than surface waters (Olden and Naiman, 2010). This can result in much of the reservoir becoming unsuitable habitat for all but the most tolerant of species.

5.3 River fragmentation and loss of connectivity

In addition to the way in which they alter natural flow regimes, dams form barriers to the longitudinal movement of biota and materials (e.g. sediments, nutrients, carbon) along river channels (Wohl, 2017). The disappearance or decline of important migratory fish species often follows river impoundment and the blocking of passage in the system (Bunn and Arthington, 2002). Mainstream dams can have a major negative impact on fisheries resources through 2 main mechanisms: 1) river fragmentation and disruption of fish migrations (in particular, loss of access to breeding sites) and 2) a significant loss of nutrients due to sediment retention by dams, resulting in an overall loss of aquatic primary productivity and energy-sustaining food webs (Baran et al. 2015).

Large dams may also act as barriers to the movement of materials other than biota. For example, fine sediment may be trapped and no longer available for downstream and lateral transport in floodwaters, thus preventing the annual replenishment of floodplain habitats and deltas, vital for natural communities as well as agricultural production. Disruption of floodplain connections (through levee construction, blocking of distributary channels, and converting wetlands for aquaculture) are also significant issues in many tropical floodplain rivers (Dudgeon, 2011). Further examples of potential ecological impacts of water infrastructure (dams and weirs) on northern Australian rivers is summarised in Table 5-1.

Table 5-1. Potential ecological impacts of water infrastructure (dams and weirs) in northern Australian rivers (modified from Pusey and Kennard, 2009).

Source of impact	Mechanism of impact and potential consequences
Change in riverine habitat from flowing to still water conditions within impounded area of dam	May cause a change in native species composition to favour those species capable of utilising deep still water habitats for reproduction, foraging and refuge (e.g. bony bream, fork-tailed catfish) and a decline in species favouring riverine habitat conditions is likely
Water abstraction and/or flow releases from impoundments resulting in artificial fluctuations in water levels within impounded area	Fluctuations in water levels expose previously inundated marginal areas potentially containing fish nesting sites (e.g. aquatic macrophyte beds utilised by small-bodied species); can result in desiccation of fish eggs and larvae
Deterioration in water quality within and downstream of impoundment	Proliferation of blue-green algae and floating aquatic macrophytes, stratification of impounded waters and flow releases from bottom waters can cause degraded water quality conditions (e.g. low dissolved oxygen and temperature); may result in localised fish kills, a change in assemblage structure to favour those species tolerant of poor water quality (e.g. alien species), a decline in sensitive species and potentially interrupt cues for fish migrations and reproduction
Stocking of large predatory fish in impoundments and increased predation by piscivorous birds	Potentially increased predation pressure within and upstream of impoundments and can have long-term implications for food-web structure, species composition and assemblage structure
Decrease in freshwater tidal/brackish water habitat if impoundment located at freshwater/estuarine interface	Can cause reduction in penetration of tidal prism and a decrease in overall amount of spawning and rearing habitat for larvae and juveniles; likely to lead to decrease in recruitment of many important recreational and commercial species (e.g. barramundi, mullet, mangrove jack, threadfin salmon)
Physical barriers to longitudinal movement	May prevent or hinder local and large-scale movements by fully freshwater fish for foraging, spawning and/or dispersal of juveniles
	May prevent or hinder large-scale movements of fish that require access to estuaries by: (1) trapping downstream spawning migrations of adult fish in weir pools thereby preventing access to estuarine and brackish water spawning habitat, and (2) preventing upstream dispersal of juveniles into freshwater habitats for foraging development and growth
	May prevent or hinder movements of predominantly estuarine and marine fish into freshwater habitats for foraging, development and growth
	Barriers result in a decrease in overall amount of freshwater habitat accessible estuarine-dependent fish
	Large numbers of upstream migrating fish may accumulate immediately downstream of barriers waiting for conditions suitable for upstream passage. These fish can be subject to increased levels of predation (by other fish, birds and crocodiles), competition and recreational fishing pressure
Barrier effects dependent on relative position of barrier along river continuum	If located close to river mouth, then impacts likely to be greater than if barrier is located high in catchment (as lower proportion of overall habitat is inaccessible)
Barrier effects likely to be cumulative	With increasing distance upstream, a succession of barriers is likely to progressively filter out species less capable of overcoming barriers; therefore, progressive downstream displacement of species less able to overcome barriers may occur
Barrier effects may be ameliorated by the relative frequency of drown-outs by high flows	However, actual drown-outs that permit fish movement are likely to occur relatively infrequently for larger structures; although many fish will move during high flows (if seasonally appropriate), juveniles of some species may move only during low-flow conditions, therefore, the ability of fish to overcome barriers during drown-outs may be specific to species and size classes
Interbasin transfers of water via pipelines and canals	Increases the risks of translocating native fish between river basins, thereby mixing distinct genetic stocks and threatening evolutionarily significant units. Increased likelihood of translocating noxious alien fish.

5.4 Other threats to freshwater ecosystem integrity

Alterations to the flow regime and the associated effects of water-resource development, through loss of habitat due to impoundment or loss of longitudinal and lateral connectivity, are not the only stressors affecting environmental assets and values associated with rivers and their floodplains (Dudgeon et al. 2006; Vörösmarty et al. 2010). The following sections provide a brief summary of some of these issues.

5.4.1 Thermal alteration

Water temperature directly influences the metabolic rates, physiology and life-history traits of aquatic species and helps determine rates of important ecological processes, such as nutrient cycling and productivity (Olden and Naiman, 2010). Deep impoundments are prone to thermal stratification, and water released from the lower strata of dams is often much colder (and poorer in water quality – including lower oxygen) than ambient surface waters (Bobat, 2015). Water releases from reservoirs tend to moderate downstream thermal regimes, causing lower temperatures in the spring and summer months, higher temperatures in winter, and a dampened seasonal signal (Olden and Naiman, 2010). Such releases can make many kilometres of river downstream unsuitable habitat for riverine plants and animals and inhibit critical life-cycle processes (e.g. fish spawning).

5.4.2 Changes in sediment regimes

The role of dams in sediment sequestration is well established (Vörösmarty et al. 2003). However, the implication of this process in major rivers across Asia has been profound, with recent delta shrinkage and reductions in the rate of aggradation (Dudgeon, 2011; Syvitski and Kettner, 2011). This is likely to compound the effects of sea-level rise on river deltas and alter the spatial and temporal patterns of inundation on floodplains. It is not clear how sediment sequestration by impoundments and associated nutrient reduction will interact with the other effects of dams (e.g. flow alteration, barriers to connectivity) and thereby influence aquatic biodiversity and fisheries production.

5.4.3 Water pollution

Flow regulation seldom occurs in isolation from changes in catchment land use, with intensive agriculture and urbanisation, mining and industry also having wide-ranging and cascading effects on river ecosystems (Allan, 2004; Vörösmarty et al. 2010). Thermal pollution and the associated water quality issues associated with stratification of impoundments are briefly noted in Section 5.4.1. The impact of pollutant loading to river systems (e.g. from industrial or urban sources) can be ameliorated by flow. As noted above (Section 5.1.2), reduction in baseflows can be associated with water quality problems, and this is, undoubtedly, compounded by diffuse and non-point source pollution.

5.4.4 Climate change

In tropical regions of the world, climate change is having negative impacts across the water, agriculture and environment sectors (Dudgeon, 2011; Wong et al. 2014). This is especially so in low-lying river basins which can be affected by extremes of temperature, rainfall and rising sea levels (Keskinen et al. 2010; Kano et al. 2016). In terms of fishery resources, climate effects are likely to lead to: 1) reduced availability of wild fish stocks due to degraded water quality, new predators and pathogens, and changed abundance of food available to the fishery species; 2) changes in fish migration and recruitment patterns and success due to changes in the seasonal timing and intensity of rainfall-runoff events; 3) reduced wild fish stocks, intensified competition for fishing areas, and more migration by fisherpeople; and 4) alteration to freshwater capture fisheries due to saline influence.

5.5 References

Adame M.F., Pettit N., Valdez D., Ward D., Burford M. & Bunn SS.E. (2017). Epiphyton contribution to the primary production of a tropical floodplain wetland. *Biotropica* 49: 461-471.

Allan J.D. (2004). Landscape and riverscapes: The influence of land use on river ecosystems. *Annual Reviews of Ecology, Evolution and Systematics* 35: 257-284.

Baran E., Guerin E. & Nasielski J. (2015). Fish, sediment and dams in the Mekong. Penang, Malaysia: WorldFish, and CGIAR Research Program on Water, Land and Ecosystems (WLE). 108. Available at: https://wle.cgiar.org/cgspace/resource/10568-71117.

Bobat A. (2015). Thermal Pollution Caused by Hydropower Plants. In: Bilge, A., A. Toy, and M. Günay (eds). Energy Systems and Management. Springer Proceedings in Energy. Springer, Cham.

Bunn S.E. & Arthington A.H. (2002). Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* 30: 492-507.

Bunn S.E., Thoms M.C., Hamilton S.K. & Capon S.J. (2006). Flow variability in dryland rivers: boom, bust and the bits in between. *River Research and Applications* 22: 179-186.

Crook D.A., Morrongiello J.R., King A.J., Adair B.J., Grubert M.A., Roberts B.H., Douglas M.M. & Saunders T.M. (2022). Environmental drivers of recruitment in a tropical fishery: monsoonal effects and vulnerability to water abstraction. *Ecological Applications* 32(4): e2563.

Davies P.M., Bunn S.E. & Hamilton S.K. (2008). Primary production in tropical rivers. In: Dudgeon, D. (ed). Tropical Stream Ecology. Academic Press. 24-43.

Dudgeon D. (2011). Asian river fishes in the Anthropocene: threats and conservation challenges in an era of rapid environmental change. *Journal of Fish Biology* 79: 1487-1524.

Dudgeon D., Arthington A.H., Gessner M.O., Kawabata Z., Knowler D., Leveque C., Naiman R.J., Prieur-Richard A.H., Soto D. & Stiassny M.L.J. (2006). Freshwater biodiversity: importance, threats, status, and conservation challenges. *Biological Reviews* 81: 163-182.

Kano Y., D. Dudgeon, S. Nam, H. Samejima, K. Watanabe, C. Grudpan, J. Grudpan, W. Magtoon, P. Musikasinthorn, P. Thanh Nguyen, B. Praxaysonbath, T. Sato, K. Shibukawa, Y. Shimatani, A. Suvarnaraksha, W. Tanaka, P. Thach, D. Dinh Tran, T. Yamashita & K. Utsugi. (2016). Impacts of Dams and Global Warming on Fish Biodiversity in the Indo-Burma Hotspot. *PLoS ONE* 11(8): e0160151.

Keskinen M., Chinvanno S., Kummu M., Nuorteva P., Snidvongs A., Varis O. & Västilä K. (2010). Climate change and water resources in the lower Mekong river basin: Putting adaptation into context. *Journal of Water and Climate Change* 1: 103-117.

King A.J., Townsend S., Douglas M.M. & Kennard M.J. (2015). Implications of water extraction on the low-flow hydrology and ecology of tropical savannah rivers: an appraisal for northern Australia. *Freshwater Science* 34: 741–758.

Loneragan N.R. & Bunn S.E. (1999). River flows and estuarine ecosystems: Implications for coastal fisheries from a review and a case study of the Logan River, southeast Queensland. *Australian Journal of Ecology* 24:431-440.

Lytle D.A. & Poff L.R.. 2004. Adaptation to natural flow regimes. *Trends in Ecology & Evolution*. 19: 94-100.

Olden J.D. & Naiman R.J. (2010). Incorporating thermal regimes into environmental flows assessments: modifying dam operations to restore freshwater ecosystem integrity. *Freshwater Biology* 55: 86-107.

Poff N.L., Allan J.D., Bain M.B., Karr J.R., Prestegaard K.L., Richter B.D., Sparks R.E. & Stromberg J.C. (1997). The natural flow regime: a paradigm for river conservation and restoration. *BioScience*. 47: 769-784.

Pusey B.J. & Kennard M.J. (2009). Chapter 3 – Aquatic ecosystems of northern Australia. In: Stone, P. (ed). “Northern Australia Land and Water Science Review”. Final report to the Northern Australia Land and Water Taskforce. CSIRO Publishing. Available at: http://www.northernaustralia.gov.au/page/water/northern-australia-land-and-water-taskforce.

Rolls R.J., Leigh C. & Sheldon F. (2012). Mechanistic effects of low-flow hydrology on riverine ecosystems: Ecological principles and consequences of alteration. *Freshwater Science* 31: 1163-1186.

Syvitski J.P.M & Kettner A. (2011). Sediment flux and the Anthropocene. *Philosophical Transactions of the Royal Society A* 369: 957-975.

Vörösmarty C., Meybeck M., Fekete B., Sharma K., Green P & Syvitski J.P.M. (2003). Anthropogenic sediment retention: major global-scale impact from the population of registered impoundments. *Global Planetary Change* 39: 169-190.

Vörösmarty C.J., P.B. McIntyre, M.O. Gessner, D. Dudgeon, A. Prusevich, P.A. Green, S. Glidden, S.E. Bunn, C.A. Sullivan, C.A. Reidy & P.M. Davies. (2010). Global threats to human water security and river biodiversity. *Nature* 467: 555-561.

Ward J.V. & Stanford J.A. (1995). Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. *Regulated Rivers: Research and Management* 11: 105-119.

Welcomme RL., Bene C., Brown C.A., Arthington A.H., Dugan P., King J.M. & Sugunan V. (2006). Predicting the water requirements of river fisheries. In: Wetlands and Natural Resource Management (J.T.A. Verhoeven, B. Beltman, R. Bobbink and D.F. Whigham, Eds). Ecological Studies Vol. 190, Springer-Verlag, Berlin, Heidelberg, p. 123-154.

Wohl E. (2017). Connectivity in rivers. *Progress in Physical Geography* 41: 345-362.

Wong P.P., I.J. Losada, J.P. Gattuso, J. Hinkel, A. Khattabi, K.L. McInnes, Y. Saito, and A. Sallenger. (2014). Chapter 5: Coastal systems and low-lying areas. In CB Field, VR Barros, DJ Dokken, K.J. Mach, M.D. Mastrandrea, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea, and L.L. White. (Eds.), Climate change 2014: Impacts, adaptation, and vulnerability. Part A: Global and sectoral aspects. Contribution of working group II to the fifth assessment report of the Intergovernmental Panel on Climate Change. 361-409. NY, USA: Cambridge University Press.

6. Management options to mitigate risks and enhance benefits of water-resource development in northern Australia

General principles, key strategies and example management actions to minimise negative ecohydrological risks of water-resource development and maximise the socioeconomic benefits of healthy rivers are outlined below and in Table 6-1. These relate to:

- strategic planning and management
- environmental flow management
- water infrastructure management
- other measures.

6.1 Strategic water resource planning and management

The following general principles for strategic water-resource planning and management (drawn from OECD, 2006; ICEM, 2008; Pusey and Kennard, 2009; Kennard et al. 2017) may be appropriate for consideration to minimise ecological impacts and maximise socioeconomic benefits of water-resource development in wet-dry tropical rivers of northern Australia:

- Apply precautionary principle to water-resource development proposals because it is usually more cost-effective to prevent environmental harm than it is to restore the damage. The precautionary principle could be applied if:
    - there is a threat of serious or irreversible damage
    - there is scientific uncertainty as to the nature and extent of possible damage
- Include in relevant policies (e.g. relating to environmental impact assessment, water quality management, fisheries management, environmental flow management) specifications for the systematic collection of ecological data and analysis requirements to allow informed evaluation of ecological impacts of water-resource developments and mitigation of risks.
- Improve knowledge base to support decision-making and tradeoff evaluations. Knowledge availability and use could be enhanced through:
    - technical capacity development and training
    - database management
    - data sharing and coordination across government agencies and other stakeholders (e.g. universities)
- Develop policies to ensure that representative river systems/tributaries and those of high ecological value are protected from negative consequences of water-resource development (e.g. by minimising barriers to connectivity, flow alteration, destructive fishing practices and other land use impacts). The choice of rivers for protection can be guided by spatial prioritisation analyses (e.g. Hermoso et al. 2012, 2018) and engagement with key stakeholders.
- Different management actions will likely be needed to achieve the conservation goals (e.g. protection, threat mitigation, rehabilitation); therefore, monetary estimates of management costs should ideally be linked to decision-making, concerning which management actions to implement in which places. The incorporation of realistic and spatially explicit cost estimates for different management actions would allow cost-

benefit trade-offs to identify the most efficient combination of actions, and where they should be spatially prioritised to achieve the conservation goals. Adaptive management plans, where information is gained through well-defined monitoring programs in the early stages of the plan or from previous experiences, can be incorporated in the decision-making process and would greatly improve the cost-efficiency of conservation management.

- Consider environmental offsets or compensation as a strategy to improve environmental outcomes from water-resource development. An environmental offset compensates for unavoidable impacts on significant environmental values (e.g. fisheries production, critical habitat for rare and threatened species) in one area, by investing in environmental management activities in another area over a period of time, to replace those significant environmental values which were lost. Examples of environmental offsets to improve fisheries include improved policing to prevent overfishing, stocking of some species that are in decline, treatment of polluted wastewaters, and river rehabilitation measures. Offsets could be funded as part of the cost of development of a new dam, or by using revenue from hydropower, and could help to compensate for environmental and social impacts of such developments.

6.2 Environmental flow management

Environmental flows can be defined as describing '… the quantity, timing, and quality of freshwater flows and levels necessary to sustain aquatic ecosystems which, in turn, support human cultures, economies, sustainable livelihoods, and well-being.' (Arthington et al. 2018). This includes managing flows to sustain the physical integrity of river-floodplains, water-dependent species (e.g. fish, birds, riparian trees), ecological processes (nutrient and energy flow), ecosystem goods and services from which people benefit (e.g. water purification, fisheries production, tourism values), and cultural and spiritual values. Environmental flow assessments evaluate how much water the river needs, to sustain natural values and processes, recognising that the environment is a legitimate and essential user of water.

Importantly, an environmental flow is not simply a fixed water allocation delivered, for example, as a minimum daily flow, but acknowledges that key attributes of the flow regime (e.g. flow magnitude, frequency, timing, and duration of particular flow events) are also ecologically important (Poff et al. 1997; Bunn and Arthington, 2002). Environmental-flow assessments are, therefore, an important step for decision-makers to evaluate tradeoffs among other, often competing, users of water (e.g. for agriculture, hydropower, urban supply, and industry) (Arthington, 2012). Numerous methods exist to assess environmental water requirements using varying levels of knowledge of the ecohydrology of a river system and its floodplain wetlands/delta (Poff et al. 2017). Ideally, detailed environmental-flow assessments should be undertaken for all existing and future water-resource developments so that the flow requirements of important aquatic biota and risks of hydrological change for aquatic ecosystem services can be evaluated and mitigated. This would guide the choice of appropriate flow mitigation strategies within the River Basin Management planning process.

Following is a series of general principles for environmental-flow management (sourced from Pusey and Kennard, 2009; Kennard et al. 2017, Hortle and So Nam, 2017) that may be appropriate for consideration in rivers of Lao PDR.

- Undertake environmental-flow assessments for all existing and future water-resource developments using appropriate frameworks and methods.
- Implement environmental-flow management practices. For example, water infrastructure (dams and weirs) can be designed and operated to be hydrologically transparent (bounded by infrastructure constraints and reductions in yield for other uses). This means that ecologically important flow events (e.g. floods, flow pulses, baseflows, low flow spells) from upstream can be delivered downstream. This would help to mimic ecologically important components of the flow regime for downstream aquatic ecosystems.
- Dry-season flow releases from dams (e.g. for delivery of water for irrigation purposes) that result in artificially elevated low flows that may drown out important habitats (e.g. nesting banks for turtles) could be avoided by delivering the water through off-stream pipelines, instead of along the river channel, and off-stream storage at the destination.
- Flow releases from dams that result in unnaturally rapid rises and falls in water levels downstream and within impoundments, should be avoided due to the risk of stranding aquatic organisms, disrupting nesting areas, etc.
- Flood harvesting (capture and use of water flowing across a floodplain) and off-stream storage could be used to mitigate the requirement for in-channel storages. Harvesting of floodwaters should only be considered in circumstances where changes to ecologically important components of the natural flood hydrograph (e.g. rates of rise and fall, peak magnitude) can be minimised, and the location of off-stream storages can be situated in areas that avoid habitat for important terrestrial and aquatic biota (e.g. important floodplain wetlands or hotspots of aquatic primary production).
- Groundwater extraction should be carefully assessed to ensure protection of groundwater-dependent ecosystems, especially during the dry season. Over extraction of groundwater can also lead to land subsidence on floodplains and alter the pattern of flood inundation.
- The cumulative effects of riparian extraction of water from streams and rivers (i.e. through direct pumping) can lead to major reductions in low flows and increases in the frequency and duration of dry spells. Similarly, water extraction from isolated waterholes can reduce the duration of persistence and quality of these important dry season refugial habitats. These impacts could be mitigated by setting minimum thresholds for dry season water extraction by riparian users and adequately policing these regulations. Pump offtakes should be positioned well below the water surface to minimise the possibility of removing high-quality surface waters from deep, stratified waterholes. These offtakes could also be screened to avoid potential entrainment of fish.
- For high-priority aquatic habitats (e.g. conservation zones, those known to be critical dry season refugia and/or supporting species of conservation significance), individual site-specific management rules should be established to protect their ecological values, including specification of permissible drawdown depths and rates. Ecological impacts could also be minimised, if riparian extraction was undertaken during high flow conditions rather than during low flow periods. However, this would require suitable storage capacity to be provided off-stream, given that the greatest demand for water is usually at times of low flow (i.e. during the dry season).

6.3 Water infrastructure management

Associated with the general principles for environmental-flow management described in above, the following general principles for water infrastructure management (sourced from Pusey and Kennard, 2009; Kennard et al. 2017; Hortle and So Nam, 2017; Baumgartner et al. 2018) may be appropriate for consideration to minimise ecological impacts in the wet-dry tropical rivers of northern Australia.

- Dams could be fitted with multi-level offtakes to minimise the release of poor-quality water downstream (e.g. release of bottom waters of low temperature and dissolved oxygen). De-stratification measures within impoundments and/or oxygenation of discharges downstream could also be attempted.
- Sediment bypass measures may be used to mitigate clearwater-erosion and substrate changes caused by sediment load deficits downstream of dams and larger weirs. Such measures could include installation of gates on water infrastructure to minimise impedance to sediment transport or removal of accumulated bedload from impoundments and reintroduction downstream.
- Some impoundments provide ideal habitat for growth of invasive aquatic plants. In situations where the problem is severe, it may be feasible to reduce such plant growth by manual harvesting or biological control.
- Maintain the integrity of riparian zones, upstream and downstream of impoundments.
- Inter-basin transfers of water increase the risk of translocation of non-native organisms between catchments. Installation and regular maintenance of effective screens can help prevent such translocations.
- Consider ecologically sensitive spillway design to prevent fish injury (i.e. physical damage or gas bubble trauma due to dissolved gas supersaturation) to reduce risks to fish moving downstream of dams. This issue may be significant downstream of high dams with deep stilling basins below their spillways.
- Installation of effective fish-passage devices (e.g. rock-ramp fishways, fish ladders, fish locks, fish lifts) may be required on some existing and new water infrastructure. Provisions of specific environmental-flow allocations, to render these fish-passage devices effective, should also be ensured. However, it should be noted that fish-passage devices can never fully restore natural fish passage and can, at best, only allow movement of a subset of the fish community.
- Dams and weirs may also impede passage of other aquatic and water-dependent biota (e.g. crustaceans, turtles). It is, therefore, critical that their passage requirements (i.e. in terms of depths, velocity and turbulence in fishways) also be provided for. Trap and transport and/or collection of wild fish and propagation of particular species may also partially offset the risks associated with restrictions to fish passage.

Table 6-1. Hydrological threats from water-resource development and potential risk mitigation measures (adapted from DES 2018).

Water-resource development type	Hydrological threats	Potential risk mitigation measures
Pumping from waterholes during dry spells	• Reduced waterhole persistence time and water quality • Increased rate of water depth change	• No pumping from any waterhole less than 1 m deep and no pumping once waterhole depth falls to 0.5 m below cease-to-flow depth • Set maximum daily rate of take
Flow harvesting (in-channel flows)	• Loss of perennial flow and increased frequency and duration of no-flow spells	• Set minimum passing flow thresholds
	• Reduced frequency and duration of hydrological connectivity and bank-full flows	• Take water only from falling limb of hydrograph and set minimum pumping thresholds
	• Increased rate of recession	• Limit daily rate of take
Flood harvesting	• Reduced frequency, duration and extent of floodplain inundation and aquifer recharge	• Take water only from falling limb of hydrograph and set minimum pumping thresholds
Pumping bed-sand hyporheic water during dry spells	• Reduced pool depth and persistence time	• No pumping from any waterhole less than 1 m deep and no pumping once waterhole depth falls to 0.5 m below cease-to-flow depth • Set maximum daily rate of take
	• Increased rate of dry-season hyporheic water-depth reduction	• Limit daily rate of take
Inter-basin water transfers	• Receiving river experiences seasonal flow reversal and intermittent reaches are converted to perennial reaches.	• Ensure timing coincides with wet-season and dry-season flow patterns and take from receiving river has minimum daily flow thresholds
	• Increased rate of water depth change in both donor and receiving rivers	• Set maximum daily rate of take and ensure releases mimic natural hydrological events
	• Reduced magnitude and duration of flow events, and loss of perennial flow, in donor river	• Take water only from falling limbs of hydrograph and set minimum daily flow and pumping thresholds in donor river
	• Accidental translocation of biological material (pests, diseases, genetic effects)	• Strict controls on biological translocation with strict compliance requirements
Dam operation	• Seasonal reversal with un-natural dry season events created by demand-driven releases which may convert intermittent reaches to perennial reaches • Increased rate of water depth change	• Condition release patterns to mimic natural hydrograph shapes
	• New barriers to movement of biota	• Do not allow in channel infrastructure which will limit free movement of biota, sediments, constituents through river systems. If such structures are allowed, stipulate effective fishways with relevant monitoring requirements
	• Reduced magnitude and duration of flow events and loss of perennial flow	• Condition release patterns to mimic natural hydrograph shapes and protect outflow events
Overall take	• Reduced end of system discharges to estuaries	• Set environmental flow objects (EFOs) and performance indicators (PIs) for change in Mean Annual Flows at end of system
	• Loss of perennial flow	• Set EFOs and PIs for change in perennial low flows
	• Reduced magnitude and duration of flow events	• Set EFOs and PIs for change in medium and high flow events
Groundwater extraction	• Lowering of water table and loss of surface expression of groundwater	• Set cease-to-pump depth thresholds for groundwater
Managed aquifer recharge	• Raising of water table	• Set maximum water-table height thresholds for aquifers

Water-resource development type	Hydrological threats	Potential risk mitigation measures
	• Altered water quality of aquifer e.g. increased nutrient concentrations	• Set water quality thresholds for recharge water such as maximum nutrient concentrations and turbidity
Overland flow harvesting	• Hydrological isolation of floodplains	• Control the area of floodplain isolated by structures in overland flow developments. • Protect key floodplain assets such as DIWA wetlands from overland flow threats

6.4 References

Adame, M.F., N. Pettit, D. Valdez, D. Ward, M. Burford, and S.E. Bunn. 2017. Epiphyton contribution to the primary production of a tropical floodplain wetland. Biotropica 49:461-471.

Allan, J.D. 2004. Landscape and riverscapes: The influence of land use on river ecosystems. Annual Reviews of Ecology, Evolution and Systematics 35:257-284.

Arthington, A.H. 2012. Environmental Flows: Saving Rivers in the Third Millennium. University of California Press: Berkeley.

Arthington, A.H., Bhaduri, A., Bunn, S.E., Jackson, S. et al. 2018. The Brisbane Declaration and Global Action Agenda on Environmental Flows (2018). Frontiers in Environmental Science 6: 45, 2018

Brett, M.T., S.E. Bunn, S. Chandra, A.W.E. Galloway, F. Guo, M.J. Kainz, P. Kankaala, D.C.P. Lau, T.P. Moulton, M.E. Power, J.B. Rasmussen, S.J. Taipale, J.H. Thorp, and J.D. Wehr. 2017. How important are terrestrial organic carbon inputs for secondary production in aquatic ecosystems? Freshwater Biology 62:833-853.

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

Bunn, S.E., M.C. Thoms, S.K. Hamilton, and S.J. Capon. 2006. Flow variability in dryland rivers: boom, bust and the bits in between. River Research and Applications 22:179-186.

Davies, P.M., S.E. Bunn, and S.K. Hamilton. 2008. Primary production in tropical rivers. In: Dudgeon, D. (ed). Tropical Stream Ecology. Academic Press. 24-43.

DES (2018). Cape York Water Plan: Environmental Assessment Report. Department of Environmental and Science, Queensland Government, Brisbane.

Dudgeon, D., A.H. Arthington, M.O. Gessner, Z. Kawabata, D. Knowler, C. Leveque, R.J. Naiman, A.H. Prieur-Richard, D. Soto, and M.L.J. Stiassny. 2006. Freshwater biodiversity: importance, threats, status, and conservation challenges. Biological Reviews 81:163-182.

Hermoso, V., Kennard, M.J. & Linke, S. (2012). Integrating multi-directional connectivity requirements in systematic conservation planning for freshwater systems. Diversity and Distributions 18: 448–458.

Hermoso, V., Cattarino, L., Linke, S. & Kennard, M.J. (2018). Catchment zoning to enhance co-benefits and minimise trade-offs between ecosystem services and biodiversity conservation. Aquatic Conservation: Marine and Freshwater Ecosystems 28: 1004-1014.

Jardine, T.D., N.R. Bond, M.A. Burford, M.J. Kennard, D.P. Ward, P. Bayliss, P.M. Davies, M.M. Douglas, S.K. Hamilton, J.M. Melack, R.J. Naiman, N.E. Pettit, B.J. Pusey, D.M. Warfe, and S.E. Bunn. 2015. Flood rhythm and ecosystem responses in tropical riverscapes. Ecology 96: 684-692.

Junk, W. J., Bayley, P. B. & Sparks, R. E. (1989). The flood pulse concept in river-floodplain systems. pp. 110-27. In Proceedings of the international large river symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

King, A.J., Townsend, S. Douglas, M.M. & Kennard, M.J. 2015. Implications of water extraction on the low-flow hydrology and ecology of tropical savannah rivers: an appraisal for northern Australia. Freshwater Science 34: 741–758.

Loneragan, N.R., and S.E. Bunn. 1999. River flows and estuarine ecosystems: Implications for coastal fisheries from a review and a case study of the Logan River, southeast Queensland. Australian Journal of Ecology 24:431-440.

Lowe-McConnell, R. H. (1975). Fish communities in tropical freshwaters. Longman, London.

Lytle, D.A., and L.R. Poff. 2004. Adaptation to natural flow regimes. TREE. 19: 94-100.

Mackay, S.J., A.H. Arthington, and C.S. James. 2014. Classification and comparison of natural and altered flow regimes to support an Australian trial of the Ecological Limits of Hydrologic Alteration framework. Ecohydrology 7:1485-1507.

Moulton, T.P., M.L. Souza, R.M.L. Silveira, and F.A.M. Krsulovic. 2004. Effects of ephemeropterans and shrimps on periphyton and sediments in a coastal stream (Atlantic forest, Rio de Janeiro, Brazil). Journal of the North American Benthological Society 23: 86-881.

OECD. 2006. Applying Strategic Environmental Assessment: Good Practice Guidance for Development Co-operation. OECD Publishing.

Olden, J.D., and R.J. Naiman. 2010. Incorporating thermal regimes into environmental flows assessments: modifying dam operations to restore freshwater ecosystem integrity. Freshwater Biology 55: 86-107.

Olden, J.D., M.J. Kennard, and B.J. Pusey. 2012. A framework for hydrologic classification with a review of methodologies and applications in ecohydrology. Ecohydrology 5: 503-518.

Pegram, G. Y. Li, T. Le. Quesne, R. Speed, J. Li, and F. Shen. 2013. River basin planning: Principles, procedures and approaches for strategic basin planning. Paris, UNESCO.

Pettit, N.E., R.J. Naiman, D.M. Warfe, T.D. Jardine, M.M. Douglas, S.E. Bunn, and P.M. Davies. 2017. Productivity and connectivity in tropical riverscapes of Northern Australia: Ecological insights for management. Ecosystems 20: 492-514.

Poff N.L., Tharme R.E., Arthington A.H. (2017). Evolution of environmental flows assessment science, principles and methodologies. Chapter 11 in 'Water for the Environment: Policy, Science, and Integrated Management' (A. Horne, A. Webb, M. Stewardson, B. Richter and M. Acreman, Eds.). Elsevier

Poff, N.L., J.D. Allan, M.B. Bain, J.R. Karr, K.L. Prestegaard, B.D. Richter, R.E. Sparks, and J.C. Stromberg. 1997. The natural flow regime: a paradigm for river conservation and restoration. BioScience. 47:769-784.

Pringle, C. 2003. What is hydrologic connectivity and why is it ecologically important? Hydrological Processes 17: 2685-2689.

Pringle, C.M., G.A., Blake, A.P. Covich, K.M. Buzby, and A. Finley. 1993. Effects of omnivorous shrimp in a montane tropical stream: Sediment removal, disturbance of sessile invertebrates and enhancement of understory algal biomass. Oecologia 93: 1-11.

Pusey, B.J., and M.J. Kennard. 2009. Chapter 3 – Aquatic ecosystems of northern Australia. In: Stone, P. (ed). 'Northern Australia Land and Water Science Review'. Final report to the Northern Australia Land and Water Taskforce. CSIRO Publishing. Available at: http://www.northernaustralia.gov.au/page/water/northern-australia-land-and-water-taskforce.

Robins, J., D. Mayer, J. Staunton-Smith, J.I. Halliday, B. Sawynok, and M. Sellin. 2006. Variable growth rates of the tropical estuarine fish barramundi Lates calcarifer (Bloch) under different freshwater flow conditions. Journal of Fish Biology 69: 379-391.

Rolls, R.J., C. Leigh, and F. Sheldon. 2012. Mechanistic effects of low-flow hydrology on riverine ecosystems: Ecological principles and consequences of alteration. Freshwater Science 31: 1163-1186.

Syvitski, J.P.M. and A. Kettner. 2011. Sediment flux and the Anthropocene. Philosophical Transactions of the Royal Society A 369: 957-975.

Vörösmarty, C., M. Meybeck, B. Fekete, K. Sharma, P. Green, and J.P.M. Syvitski. 2003. Anthropogenic sediment retention: major global-scale impact from the population of registered impoundments. Global Planetary Change 39: 169-190.

Vörösmarty, C.J., P.B. McIntyre, M.O. Gessner, D. Dudgeon, A. Prusevich, P.A. Green, S. Glidden, S.E. Bunn, C.A. Sullivan, C.A. Reidy, and P.M. Davies. 2010. Global threats to human water security and river biodiversity. Nature 467: 555-561.

Ward, J. V. (1989). The four-dimensional nature of lotic ecosystems. J. Nth. Am. Benthol. Soc. 8: 2-8.

Ward, J.V., and J.A. Stanford. 1995. Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. Regulated Rivers: Research and Management 11: 105-119.

Ward, D.P., N. Pettit, M.F. Adame, S.E. Bunn, M.M. Douglas, and S.A. Setterfield. 2016. Seasonal spatial dynamics of floodplain macrophyte and periphyton abundance in the Alligator Rivers Region (Kakadu) of northern Australia. Ecohydrology 9: 1675-1686.

Wohl, E. 2017. Connectivity in rivers. Progress in Physical Geography. 41: 345-362.