A Conceptual Review of Aquatic Ecosystem Function and Fish Dynamics in the Lake Eyre Basin, Central Australia

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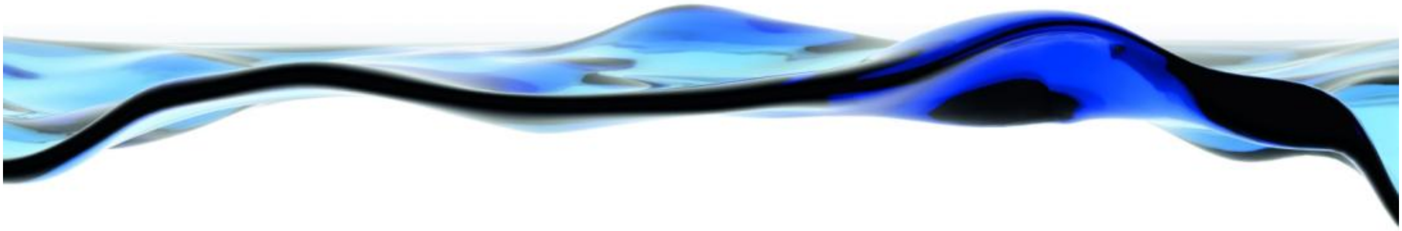

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Table of Contents

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Executive Summary

Conceptual models represent an important step in the process of implementing Strategic Adaptive Management of natural ecosystems and resources (McNeil and Wilson 2014). Conceptual models convey how we understand the system to work and can highlight key gaps in our knowledge that can be resolved by data collection and analysis to refine those models (Kingsford and Biggs 2012). A series of conceptual modelling products have been developed in Lake Eyre Basin (LEB) in arid central Australia to describe the relationship between the function of aquatic ecosystems and the influence of climate and hydrology that drive one of the world's most variable river ecosystems (Puckridge *et al*. 1998, 2000, Costelloe *et al*. 2004).

This report is the first phase of a project commissioned by the Goyder Institute for Water to develop methods to assess condition, identify vulnerabilities and forecast risks to the aquatic ecosystems of the Lake Eyre Basin. A range of outputs from several key research and management projects were reviewed to identify the sources of information and data that could contribute to the development of a framework of conceptual modelling that informs the assessment of environmental condition in the Lake Eyre Basin. This report presents existing models that capture the functional ecology of aquatic habitats in the Lake Eyre Basin and develops new models that address knowledge gaps and expand existing models and analyses to be relevant to Basin-scale management.

Over 30 models were reviewed, evaluated or developed in this report. These models have improved our conceptual understanding of three key themes:

- The role of climate and hydrology in driving ecosystem function in the LEB.
- The functional attributes of aquatic habitats that influence the dynamics of fish assemblages and populations across the spectrum of hydro-climatic variability.
- The ecological responses of fish assemblages to hydrological and habitat variables based on life history traits of Lake Eyre Basin Species.

A key finding from this project is that observing and understanding the full range of variability in the LEB climate, habitat and ecological responses is vital to developing methods for assessing environmental condition in the Basin. It is recommended that specific models from each of the above themes be further developed, populated and validated through the analysis of existing Lake Eyre Basin Rivers Assessment (LEBRA) monitoring data and other available monitoring datasets. These models will inform the development condition assessment methods. Limitations to the further development of these models were identified. Spatial coverage of hydrological data and long-term ecological monitoring data are two key limitations to the further development of models identified in this report.

Introduction

The Lake Eyre Basin (LEB) is the largest river basin in Australia draining a catchment area of 1.14 million km^2 (Kotwicki and Allen 1998). The Basin is in the arid center of the world's driest inhabited continent and mean annual rainfall and runoff is the lowest of any major river basin in the world (Kotwicki and Allen 1998). Periodically, however, monsoonal conditions associated with the La Niña phase of the El Niño-Southern Oscillation (ENSO) phenomenon results in large and widespread flooding (Allen 1985, Kotwiki and Isdale 1991). This flooding results in broad scale inundation of wetland habitats, driving some of the largest and most persistent wetlands in the country with slow moving floodwaters spreading across a low gradient catchment with extremely high floodplain to catchment area ratio (Roshier *et al.* 2001).

Driven by climatic extremes of heat, aridity and deluge, rivers and wetlands of the endorheic basin possess one of the most variable hydrological regimes on the planet (Puckridge *et al*. 1998, 2000). Despite this variability and climatic harshness, or more realistically because of it, the Basin is home to one of the most naturally intact arid aquatic ecosystems in the world, with very little water resource development, urbanisation or other anthropogenic influences typically associated with the broad scale decline in most of the world's major river basins (Morton *et al.* 1995, Walker *et al.* 1997).

Rapidly developing resource extraction industries, including oil and gas, increasing tourism and political drive to promote the future development of irrigated agriculture in Queensland, has increased public concern about the protection of the Basin's water resources and aquatic ecosystems (Walker *et al.* 1997). This concern led to the formation of the Lake Eyre Basin Ministerial Forum under the Lake Eyre Basin Intergovernmental Agreement (LEBMF 2000) and collective effort on behalf of the State and Commonwealth jurisdictions to protect and guide sustainable management of the Basin's resources. The Agreement provides for the sustainable management of the water and related natural resources associated with cross-border river systems in the Lake Eyre Basin to avoid downstream impacts on associated environmental, economic and social values. The Agreement incorporates a number of guiding principles that recognise the significance of the Lake Eyre Basin for ecological, pastoral, cultural and tourism reasons, and the need to make decisions which will foster ecologically sustainable development using a precautionary approach. A Strategic Adaptive Management Framework (Kingsford and Biggs 2012) was recommended by the Scientific and Community Advisory Groups (LEBMF 2012) as an approach to integrate management and science within a participatory and adaptive context that informs future management decisions.

The Lake Eyre Basin Rivers Assessment (LEBRA) is central to the Ministerial Forum and aims to monitor and assess the environmental condition of the Basin's waterways (LEBMF 2012). This assessment complements a range of other government programs aimed at assessing natural resource management (NRM) issues and industry impacts. These programs converge upon the need to capture, assess and improve our understanding of how Lake Eyre Basin ecosystems function within the context of extreme climatic and hydrological variability and how this relates to the vulnerability of biota and ecosystems to human pressures.

To assist in developing our understanding of LEB ecosystems and facilitate the assessment of environmental condition through LEBRA, the Goyder Institute for Water funded a research program entitled "Development of integrated indices to assess condition, identify vulnerabilities and forecast risks to the aquatic ecosystems of the Lake Eyre Basin". This program had six tasks:

1. Identification of condition, damaging processes and key predictive indicators.
2. Collation and analysis of ecological monitoring/condition datasets.
3. Development of indicators of condition for the Lake Eyre Basin at multiple scales.
4. Nutrient sources.
5. Population and connectivity metrics of aquatic biota.
6. Cultural indicators of water resource and aquatic health and sub-regions.

This report relates to the first task in this program. A critical step in understanding the dynamics of highly variable ecosystems such as the Lake Eyre Basin wetlands is to develop a conceptual understanding of the key processes driving ecosystem function, and the responses of biota and ecosystem components to those factors. It is also important to identify the scales at which drivers and responses operate in the landscape context, so that theoretical and conceptual frameworks can be applied to real world situations, sites and data.

The current report aims to develop a framework of conceptual models that captures the nature of climatic and hydrological factors driving aquatic ecosystem processes in the Lake Eyre Basin's rivers, as well as identifying the broad scale ecological patterns and processes that can be linked to those drivers. The report builds on published research conducted through various universities and research institutions, as well as government programs and reports produced for State and Commonwealth Departments. The conceptual models presented are intended to provide a framework for more detailed modelling of ecological processes and the identification of indicators and thresholds that can be utilised to guide the Strategic Adaptive Management of the Lake Eyre Basin's waterways, biota and aquatic ecosystems.

This report aims to develop detailed conceptual models that validate and critique broader conceptual framework models such as the hydro-climatic model and summarise a wide range of influences, processes and responses at the core of ecosystem function. Conceptual models will represent the various ecological processes that operate to influence the dynamics of fish assemblages and refuge habitat function in the Lake Eyre Basin from which specific ecological indicators and thresholds can be determined. A requirement of the conceptual models is that monitoring and assessment data can be applied to validate, develop and improve ecological models and elucidate indicator and threshold values that can contribute to optimising investment in monitoring, research and management of aquatic ecosystem assets in the LEB.

This report utilises available literature including published scientific papers, government and consultants reports to develop a suite of models that summarise aspects of fish ecology and aquatic refuge function in the Lake Eyre Basin. The suite of models is intended to:

- Showcase published models that conceptualise fish refuge ecology in the Lake Eyre Basin.

- Develop new models that address knowledge gaps based on relevant data and literature.
- Where possible, extend the scope of existing models to a whole of basin scale.
- Where possible, develop hypotheses that can test key models against monitoring data.

A range of conceptual models will be developed and presented in the current report, however, detailed assessment or analysis of all models presented are beyond the scope of the current project. This report will set up a framework of models and ideas that can be utilised to undertake further analyses and assessments of ecological data, particularly for the purpose of assessing basin-scale environmental condition using fish monitoring data. It is anticipated that a subset of these models will be targeted for further scientific analysis under the next stage of the Goyder LEB project. The suitability of models for this purpose will depend on the quality and utility of available data sets.

Since the range of models and ideas presented in this report are largely conceptual, they require further development and technical supporting evidence before they can be directly applied to informing condition assessments through well-defined indicators and thresholds. There are limitations to the further development of models based on the quality of data used to develop ideas and models, restricted spatial or temporal applicability of models, and lack of suitability for validation or analysis using the current suite of available monitoring data.

Materials and Methods

Conceptual Modeling

A number of conceptual models have been developed in the past to convey the variability in aquatic habitat availability, connectedness and changes in ecological processes that accompany these changes in the Lake Eyre Basin. These models have aimed to summarise and communicate the habitats, components and processes that are important to aquatic ecosystems and biota. A brief tabulation of various conceptual modeling products was summarised in Imgraben and McNeil (2013a, 2013b) and are represented below in Table 1.

Pictorial models are popular for their capacity to communicate complex ecological processes simply in a picture that "says a thousand words" in a form that can be easily interpretable to a wide range of audiences. A number of projects have produced detailed pictorial models that present the components and processes associated with aquatic habitats, changes to habitats expected under varying climatic and hydrological scenarios, and interconnectedness of habitats at reach and catchment scales under varying hydro-climatic scales, and pathways and processes involved with impacts and threats to aquatic ecosystems (Costelloe *et al.* 2004, McKenzie-Smith *et al.* 2004, Sheldon *et al.* 2005, Scholz and Fee 2008, Imgraben and McNeil 2013b, Qld DEHP 2013a, 2013b). These kinds of pictorial conceptual models represent the broad scale general trends, threats and risks observed for the Basin‘s rivers.

Ourreport, however, is concerned not with the general dissemination of information to the broader community but rather the development of specific conceptual models that can be used to create hypotheses, identify ecosystem indicators and use them to develop thresholds of potential concern for ecosystem components and processes. This requirement limits the type of conceptual models that can be utilised to specifically focused models that present quantifiable patterns that can be tested with monitoring data.

The intent of this report is to identify and develop suitable conceptual models that represent the collective understanding of climatically driven hydro-ecological processes and patterns produced from research and monitoring programs. Previously published analytical outputs and models will be assessed for their ability to describe key aspects of hydro-ecological function in the LEB. Where possible these models will be developed or new models created to provide a broad platform for:

A. Informing on key aspects of ecological processes in LEB ecosystems.
B. Identifying indicators of environmental condition.

Commensurate with the LEBRA monitoring, the scope of the current modelling is confined to fish, basic water quality (salinity, temperature, oxygen, turbidity and pH) and hydrology. This approach will enable us to develop methods for assessing condition in the LEB that are consistent with the current scope of the LEBRA monitoring program.

Table 1. Summary of existing conceptual models relevant to the Lake Eyre Basin (updated from Imgraben and McNeil 2013a).

Reference	Scale	LEBRM Types	Description
Costelloe *et al.* (2004)	Local landscape-scale (~1 km)	Connected basin systems Watercourse Waterhole Floodplain	Hydrologically driven ecological state models that represent eight stages of river function: • Extreme drought • Local rainfall event • Prior to flood Season • Large regional flood • Receding flow • Disconnection • Regional flows • local flows Each stage is represented by visual models of inundation and connectivity at the waterhole-floodplain scale and a cross sectional river channel model identifying water level and habitat inundation patterns.
McKenzie-Smith *et al.* (2004) (cf. Sheldon *et al.* 2005)	Regional and habitat-scale (LEB-specific)	Connected systems: Watercourse Waterhole Floodplain Floodout	Animated Adobe® Flash® models (CD ROM format) describing hydrologic and geomorphic processes at different geographic levels within the LEB catchment. Also describe temporal variation. The models describe processes in headwater, channel, waterhole and terminal wetlands, and in different hydrologic phases.
Sheldon *et al.* (2005)	Regional and habitat-scale (LEB-specific)	Connected systems: Watercourse Waterhole Floodplain Floodout	Pictorial and tabular models displaying spatial and temporal variation in hydrology, geomorphology and biological components for: • Headwaters • River channel and waterholes • Terminal wetlands
Scholz and Fee (2008)	Aquatic ecosystem type (not LEB specific)	Connected basin systems lakes swamps	Adobe® Illustrator® models titled: • Inland salt lakes • Arid zone lakes • Terminal depression lakes • Inland arid zone swamps The models identify the broad drivers, components and processes relevant to each type.
McNeil *et al.* (2011a)	Neales catchment	Connected systems: Watercourse Waterhole Floodplain Floodout	Diagrammatic conceptual models for fish ecology in the LEB, presenting interrelated models with an overarching model that combines them. The models cover such factors as: • Climate • Hydrology • Connectivity • Refuges and refugia
QLD DEHP (2013a)	Freshwater biogeographic province	Watercourse	Pictorial models at a landscape scale for the Lake Eyre and Bulloo province, one for each of: • General overview • Climate • Geology and topography • Hydrology • Water quality • Habitat
QLD DEHP (2013b)	Aquatic ecosystem type (not LEB- specific)	Connected basin systems lakes swamps Isolated basin systems Lakes swamps	Adobe® Illustrator® models representing hydrology, geomorphology, fauna and flora of the following arid and semi-arid types: • Floodplain lakes • Non-floodplain lakes • Saline lakes • Tree swamps • Lignum swamps • Grass, sedge, herb swamps • Saline swamps

The conceptual framework is built around the hydro-climatic model developed initially from a scientific assessment of the critical aquatic refuges in the Neales River catchment in the west of the Basin (McNeil *et al*. 2011a), which in turn built upon previous monitoring under the LEBRA fish trajectory pilot monitoring program (McNeil *et al.* 2008) and an extension of this monitoring conducted under funding from the South Australian Arid Lands Natural Resource Management Board (SAALNRMB). The hydro-climatic model was initially developed to extend the knowledge of LEB rivers to incorporate patterns from the arid interior of the Basin targeting the Neales, Macumba, and lower Diamantina/Warburton and Cooper catchments. Its purpose was to expand on the more advanced scientific understanding developed in the less arid sections of the mid and upper Cooper and Diamantina catchments upon which a LEBRA Fish Trajectory Model was formulated to develop and pilot a fish monitoring program for LEBRA that can inform on the condition of the Basin using fish-based metrics (Humphries *et al.* 2007).

The Hydro-Climatic model has since been used to inform the Strategic Adaptive Management of LEB rivers in response to potential impacts of resource development (McNeil and Wilson 2015) due to the need to account for inconsistent temporal scenarios resulting from hydro-climatic variability. The model incorporates three key components of Lake Eyre Basin hydro-ecology:

- Hydro-climatic phase following seasonal (1 y) and supra-seasonal (~10 y) cycles.
- Aquatic refuge classification focused on seasonal and supra-season refuge function.
- Key hydro-ecological components and processes focused on the ecology of fish and relevant aspects of hydrology and water quality.

The hydro-climatic model was developed to deal with the broad range of habitats present in the arid interior where river flows are far less common and more variable in nature than the eastern catchments (Puckridge *et al*. 1998, Roshier *et al.* 2001). These included extremely ephemeral river systems with no permanent refugia, saline river reaches, spring wetlands of the Great Artesian Basin (GAB), anthropogenic habitats such as bore drains and dams, an abundance of ephemeral terminal lake systems, salt lakes, and large refuge waterholes that are often the last downstream refugia and/or are isolated from broader networks unlike refuge waterholes farther upstream (Sheldon *et al.* 2010). All of these habitats are connected at some time with the Basin's river network, and therefore warrant our attention as components of the Basin's ecology.

This report intends to delve into the detail behind the hydro-climatic model (McNeil *et al.* 2011a) and reveal the conceptual understanding of the processes that drive it. The framework of conceptual models produced will provide an entry point to the development of hypotheses and the identification of indicators and thresholds that are critical to maintaining biodiversity, ecosystem resilience and ecological functions. Where possible, conceptual models will be developed through the application of scientific data from past and current monitoring and assessment programs to test key hypotheses and where possible identify and develop data based models that can represent the highly variable dynamics of the natural ecosystem. Analysis will subsequently inform highly targeted threshold values (Thresholds of Potential Concern – Kingsford and Biggs 2012) that represent irreversible or unacceptable ecological tipping points that threaten the long-term condition of the Basin.

In this report the scope of hydrological and aquatic habitat types is confined to these riverine systems and connected habitats but excludes isolated endorheic catchments, dunal swales, and most springs, unless they are regularly inundated or connected to river channels. This maintains consistency with recent classification of the Basin’s waterways that emphasise the nature of connectivity for ecology and management of the LEB (Scholz and Fee 2008, Imgraben and McNeil 2013).

Results

Hydro-Climatic Model

With the rainfall largely driven by monsoonal activity in the summer (Roshier *et al.* 2001) and large flood events driven by the El Niña phase of the ENSO phenomenon (Kotwiki and Isdale 1991) driving one of the most variable river systems on Earth (Puckridge *et al*.1998), it is not surprising that ecologists have focused firmly on hydro-climatic drivers to conceptualise and explain the dynamics of aquatic ecosystems in the Basin. Almost all models developed for the Lake Eyre Basin have their genesis in the variability in rainfall and river flows and the changes to habitats, aquatic ecosystems and biota that are driven by these cycles. The models generally incorporate the concepts of *boom* and *bust* periods, representing booms with increases in inundated habitat area and resources, and hydrological connectivity driving the expansion of species assemblages and abundances during high rainfall periods. Subsequent fragmentation and isolation of habitats and breakdown of fish assemblage structures, lowering of abundance and development of disease during dry *bust* periods follow.

Recent publications have attempted to summarise the developing knowledge of aquatic ecology in the Basin and present simplified conceptual models that summarise the climatic and hydrological drivers of arid aquatic ecosystem processes. Sheldon *et al*. (2010) present a series of models that describe general patterns of habitat connection and disconnection, response models to describe dispersal strategies of aquatic organisms, hypothesised assemblage shifts over periods of connection and dis-connection, as well as for prolonged disconnection as encountered in the Basin during drought periods (Sheldon *et al.* 2010). Arthington and Balcombe (2011) present a fish focused approach highlighting the importance of the periods of increasing and decreasing connectivity that intersperse the traditional boom (flooding) and bust (no flow) phases. This contribution highlights that hydrological cycles do not always move predictably between the wet and dry extremes, but can transition between lower levels of increasing and decreasing waterbody connectivity without a strong boom or bust signal. Both of these papers summarise a large body of work conducted in the Queensland sections of the Basin and present a detailed discussion of the patterns that underpin these conceptual models.

The four phase model presented by Arthington and Balcombe (2011) moves toward the hydro-climatic structure presented by McNeil *et al.* (2011a). The hydro-climatic model attempts to integrate the phases of hydro-climatic states with patterns of habitat and refuge inundation and connectivity, as well as the aspects of fish life history and ecology that are synchronous with these variations in hydrology and habitat character (McNeil *et al.* 2011a). Developed to account for the extremely arid and variable western and central reaches and catchments of the Basin, this hydro-climatic model also presents four phases of climate driven hydrology, describing the importance of the phases interspersing *boom* and *bust* for driving resilience and resistance processes for freshwater fish. The hydro-climatic phases are structured in a *bust* - *resilience* – *boom* – *resistance* sequence [alternatively described as bust-build-boom-collapse; McNeil and Wilson (2015)] and predict the cyclical importance of various types of refuge habitats throughout these phases (McNeil *et al*. 2011a).

This report focuses on the development of an overarching hydro-climatic model that integrates the various published aspects of fish ecology, as well as the geographical variability in connectedness and regularity of flow across the Basin's diverse catchments and reaches. The overarching model will incorporate a four phase hydro-climatic model and attempt to describe the changes that these phases impose upon various types of refuge habitats and the responses of inhabitant fish communities. The four phase hydro-climatic model includes:

***Dry/Bust* phase:** Describing periods of drought (or seasonal drying) for which hydrological conditions are dominated by the absence of significant rainfall or flow and fish populations retract into isolated refuge habitats.

***Resilience* phase:** Describing periods of improved rainfall and flow following drought. Hydrological conditions include localised rainfall and flow, low flows and in-channel flows. Whilst the *Resilience* phase is important ecologically, it is acknowledged that hydro-climatic variability is such that dry seasons could be broken immediately by large floods on some occasions.

***Wet/Boom* phase:** Characterised by high rainfall periods driven by monsoonal rain. *Wet*/*Boom* phase conditions include widespread hydrological connectivity with flooding and very high flows reaching far into the downstream extents of rivers and filling terminal wetlands and lakes. Fish populations expand across inundated areas.

***Resistance* phase:** Whilst resistance relates specifically to biotic tolerance of environmental conditions, the *Resistance* phase is one of broad scale catchment drying resulting in decreasing connectivity and isolation of habitats, as well as declining environmental conditions within remaining habitats. Hydrological conditions shift from flooding to medium-low flows with potentially rapid shifts to in-channel, localised and very low or zero flows.

The utility of the over-arching model will be the development of component models that describe a conceptual understanding of key ecological processes and patterns that can be expected when investigating ecological data from the Basin. The model will assist with the application of existing datasets to test conceptual models and hypotheses and develop indicator rules and threshold definitions within the hydro-climatic context of the LEB. Whilst the details of various model components, including definitions of hydro-climatic phases and refuge types are presented throughout the following sections, it is prudent to provide a representation of the hydro-climatic model at this point to set up the over-arching framework through which these definitions are presented (Figure 1, 2).

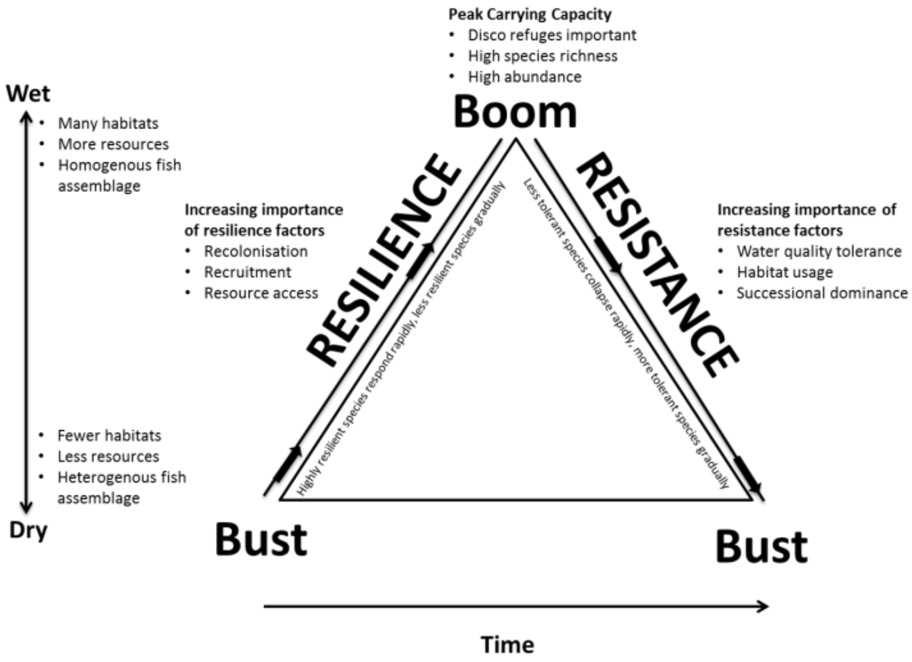


Figure 1. Conceptual understanding of fish community resilience and resistance traits through boom-bust hydro-climatic cycle. This model can be applied over annual, decadal and potentially 20-30 year time scales.

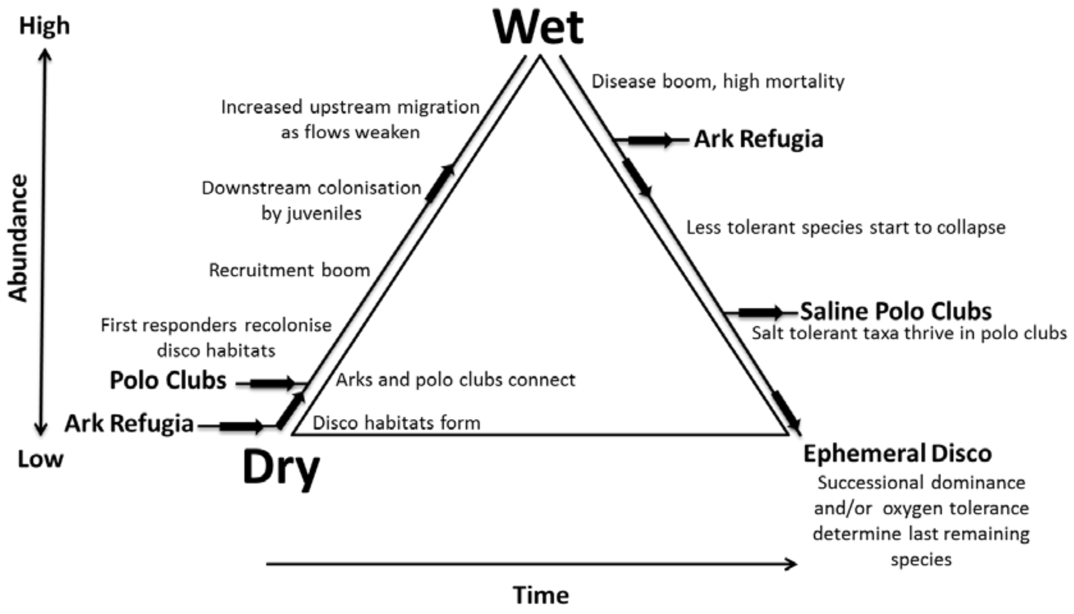


Figure 2. Conceptual understanding of ecological drivers influencing changes in fish abundance and the role of refugia during wet-dry cycles. This model can be applied over annual, decadal and potentially 20-30 year time scales. See Table 2 for refugia type terminology .

Functional Habitat Types - Refuges

Surviving the impacts of extreme climate in the semi-arid and arid regions of the LEB requires a strong dependence upon the presence of aquatic refuges through time (Davis *et al*. 2013a). Refuge habitats are those that can convey resistance and resilience to biotic communities from the impacts of bio-physical disturbance (Sedell *et al*. 1990). Whilst refuge habitats may also convey protection to biota from impacts of flow, water chemistry and biotic interactions (e.g. predation) (Magoulik and Kobza 2003, Lake 2008), we focus primarily on refuges from climatic and specifically drought related impacts such as desiccation, habitat loss and water quality declines (temperature, hypoxia, salinisation) that occur during seasonal dry periods in LEB (Arthington *et al.* 2010, McNeil *et al.* 2011a).

The term refuge and refugia will therefore be used here to refer to the protective role of habitats for biota against impacts of climatic drying and drought. However, there is a distinction made in the literature between habitats that serve as ecological refuges for biota, and those that act as evolutionary refugia (Davis *et al.* 2013a, 2013b).

Davis *et al.* (2013a) present a conceptual model outlining factors that influence ecological refuges and evolutionary refugia (Figure 3); however, it is acknowledged that these definitions are dependent on the traits of biota, and the habitat conditions associated with refuge habitats. Groundwater fed habitats are more likely to serve as evolutionary refugia, whilst surface water systems, driven by rainfall and runoff, are likely to provide shorter term ecological refuge, however, some habitats may serve as both. Permanent riverine waterholes, particularly those with groundwater connections, breach the conceptual distinction presented. The influence of species dispersal traits is central to the functionality of the habitat.

Conceptual models developed for this project and subsequent analysis of assemblage structure, habitat function and permanence may illuminate the role of Lake Eyre Basin refuges for fish. Given the uncertainty around distinctions and overlap between ecological refuges and evolutionary refugia all habitats described in the current report will refer to functional refuges (consistent with Robson *et al.* 2008), acknowledging that the conceptual models represent the role of evolutionary refugia amongst these, particularly where dealing with absolute permanent waterbodies.

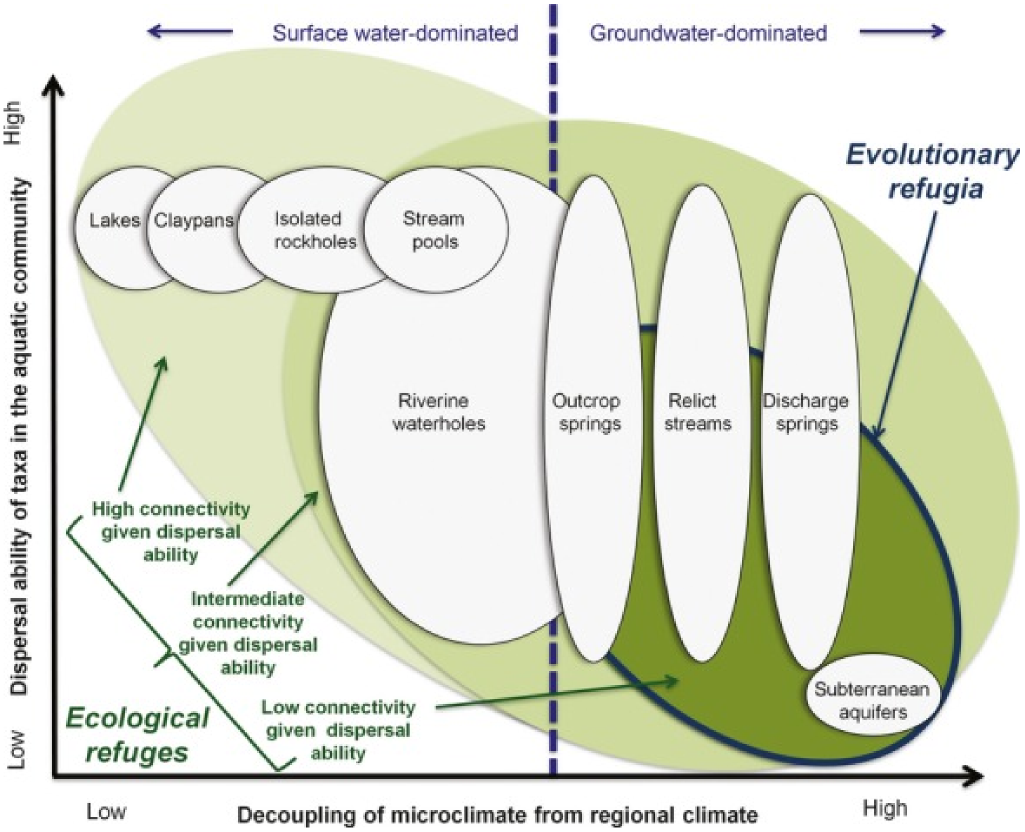


Figure 3. Conceptualisation of the major differences between evolutionary refugia (aquatic habitats supporting populations with low dispersal ability but high climatic decoupling) and a range of ecological refuges (aquatic habitats supporting populations with varying dispersal abilities and exposure to ambient climatic processes). Aquatic habitats with the greatest degree of decoupling of microclimate from regional climate are the most likely to act as evolutionary refugia. Those with the least decoupling function as ecological refuges for only the most mobile of aquatic taxa. Some habitats potentially act as both an evolutionary refugia and an ecological refuge, depending on the dispersal traits of the taxa they support, their geographical proximity and hydrological connectivity. Figure reproduced from Davis *et al.* (2013a).

Our conceptual understanding of the ecology and management of aquatic drought refuges has advanced significantly following the Millennium drought (Crook *et al.* 2010) that impacted most of Australia between 1997 and 2010 (see Lake 2003, Bond *et al*. 2008, Lake 2008, Sheldon *et al.* 2010, McNeil *et al.* 2013a, b). Sheldon *et al.* 2010 postulated that refuge waterholes provided the only refugia for most aquatic biota (including fish) in the LEB. However, Fensham *et al. (*2011), and McNeil *et al. (*2011a) presented refuge classifications that demonstrated the role of spring fed and anthropogenic refuges as important for the diversity of fish in the LEB.

Of particular relevance to the broader conceptualisation and management of aquatic refuges was a classification system developed by Robson *et al*. (2008) for a range of aquatic organisms. These classifications were applied to freshwater fish of the Murray-Darling Basin (McNeil *et al*. 2013b) and Neales River in the LEB (McNeil *et al.* 2011a). A brief summary of classifications and examples is provided below in Table 2.

Table 2. Icthyocentric refuge classification for aquatic habitats in the Lake Eyre Basin. Adapted from Robson *et al.* 2008 and McNeil *et al.* (2011)

Habitat (Asset) Class	Refuge Type (from Robson *et al*. 2008)	LEB Habitats (from McNeil *et al.* 2011a, Davis *et al.* 2013a)	Examples
Non perennial rivers and streams (including waterholes)	Ark	Permanent or near permanent waterholes	Cullyamurra WH Algebuckina WH Pandie-Pandie WH Andrewilla WH, Yammakirra WH
	Polo Club: Saline	Saline waterholes (35ppt-120ppt)	Peake WH, Baltacoodna WH, Ultoomurra WH, Tardetakerrina WH, Lower Neales Waterholes (snakehead etc.). Note: Hypersaline waterhole above 120ppt provide refugia for halophilic algae and other taxa but not fish.
	Polo Club: Spring	Connected groundwater fed wetlands	North Freeling Spring, EFN 027
	Disco:	Large non-permanent waterholes important for population building following extreme drought when they dry completely.	Hookies WH, Stuarts WH, Angle-Pole WH, Stony X-ing, Cuttapirra WH
	Casino	Based on local connectivity and rainfall	
	Anthropogenic	Dams and bore drain wetlands	New Freeling Spring, Mungerannie Bore, Big Blythe Bore, Eaglehawk Dam, Oodnadatta Town Water Supply Dam.
	Stepping Stones	Ephemeral tributaries and creeks	Lora Creek, Arkaringa Creek, Ockendon Creek, Strzlecki,
Seasonal/ephemeral wetlands	Disco		Goyder Lagoon, Lake Hope, Coongie Lakes, Eringa, Carpomoongana
Swamps and floodplain wetlands	Disco	Ephemeral swamps and billabongs on floodplains connected through overbank flows	Embarka Swamp,
Salt lakes	Polo Club: saline		Lake Eyre, Lake Blanche, Lake Callabonna, Lake Gregory

The current report assesses the applicability of these definitions for defining and conceptualising aquatic refuges for LEB fishes and explores how refuge types function and interact within the highly variable climatic context of the LEBs waterways. The types of habitats that can provide refuge for freshwater biota in arid regions includes non-perennial streams and rivers, floodplain systems and salt Lakes (Robson *et al*. 2008). Further classification for arid zone aquatic habitats (Davis *et al*. 2013a, b) identified that permanent, low connectivity riverine waterholes and discharge springs are likely to be important evolutionary refugia for fish. This reflects the previous application of the Robson *et al*. (2008) classification to LEB fishes in the Neales River (McNeil *et al.* 2011a), where several types of riverine waterhole and groundwater fed waterholes were identified, each of which was hypothesised to function in varying roles through time and space to support the resistance and resilience requirements of LEB fishes and maintain the ecological processes crucial for surviving the extreme climatic disturbance present in the LEB.

Ark Refuges

Ark refuges (Robson *et al.* 2008) are the classical type of refuge that conveys broad-scale (e.g. catchment, basin) refuge to populations and assemblages over evolutionary timescales (Davis *et al.* 2013a). These serve as the source populations for the biodiversity of the ecosystem (Sedell *et al.* 1990) and must support the survival of at least two members of each species for populations to persist through periods of disturbance without re-introduction from outside sources. This definition requires that not only do ark refuges persist through drought disturbance but that conditions remain adequate to support the survival of individuals in a condition and abundance that enables building of post-disturbance resilience. The provision of refuge must incorporate adequate quality of water, aquatic habitat and protection from biotic impacts such as predation that can cause deleterious impacts on species in confined systems (Rosenberger and Chapman 1999, Magoulic and Kobza 2003, McNeil and Closs 2007).

Whilst the limitations of species to persist within refuges are intimately linked to their tolerance of refuge conditions, the concept of ark refuges suggests that these are habitats that demonstrate conditions acceptable to the persistence of the broader fish assemblage. Therefore, whilst some refuge types (e.g. saline polo clubs) are restricted in the conveyance of refuge to tolerant species, arks are generally high quality habitats suitable for the survival of all species (Robson et al 2008). These ark refuges provide source populations for the Basin's aquatic biota (in particular aquatic obligates such as fish) on an evolutionary time scale (Sedell *et al.* 1990, Davis *et al*. 2013a).

Across the Lake Eyre Basin the function of ark refuges for fish is predominantly served by deep permanent or near-permanent waterholes (Arthington *et al.* 2005, 2010, Balcombe *et al.* 2005, 2007, Sheldon *et al.* 2010). The persistence of ark refugia are heavily dependent on the regularity of flow and the extent of cease to flow periods. In the Neales River, potential evaporation rates of 2.1-2.4 m per year, an ark refuge has to be >4 m deep to survive a single wet season without flows (Costelloe and Russell 2014). The deepest and most permanent waterhole in that system, Algebuckina, underwent extreme drying and water quality decline after 24 months without flow in late 2013, which may have challenged its function as a refuge for large bodied fish (Mathwin *et al*. 2015).

Indeed fish kills of large golden perch were observed during spring 2013 with subsequent surveys in 2014 failing to detect any surviving golden perch following the resumption of flows and replenishment of the waterhole (unpub. data). Anecdotal evidence suggests that large bodied species, particularly golden perch (*Macquaria ambigua* sp.) may have been depleted at Algebuckina in the past, followed either by restocking of these species for recreational purposes from eastern LEB catchments (Travis Gotch (DEWNR), Andrew Clarke and Rodney Fullerton, Allendale Station pers. comm.), or by migration across Lake Eyre. Either scenario is supported by genetic evidence that suggests golden perch in the Neales are indistinct from lower Warburton/Diamantina stocks (Faulks *et al.* 2010). In addition, all fish surveys prior to ARIDFLO in 2001 (Costelloe *et al.* 2004) failed to identify a range of large bodied and freshwater species including golden perch, Hyrtl's tandan (*Neosilurus hyrtlii*), silver tandan (*Porochilus argenteus*, Barcoo grunter (*Scortum barcoo*) and Welch's grunter (*Bidyanus welchi*) (Unmack 1995, Wager and Unmack 2000), all of which could theoretically have been translocated from the Warburton

Diamantina. Relatively benign conditions at Algebuckina may have subsequently supported golden perch, whilst the tandan species have never been caught since and Barcoo and Welch's grunter caught only at Algebuckina in very low numbers since 2003. Anthropogenic translocation is another potential source of confusion for waterhole monitoring programs, as these programs generally assume that monitored populations arrived at the sites naturally, particularly for species common to the LEB or similar to LEB species (e.g. Murray-Darling golden perch *Macquaria ambigua* and Silver perch *Bidyanus bidyanus*).

Spring fed waterholes and wetlands have also been described as potentially serving as ark refuges (McNeil *et al.* 2011a), however, these shallower habitats are not suitable for protecting larger bodied species such as golden perch and grunter and are therefore acting more like polo club refuges (see below) than arks due to the size selective nature of refuge provision. As a result, riverine system management has become focused primarily on the role of larger more permanent waterholes for the protection of fish assemblages at the catchment or basin scale (McNeil and Cockayne 2010, LEBMF 2012). The role of these large waterholes as ark refuges is becoming better understood through a number of research and monitoring projects. In the mid-sections of the Diamantina and Cooper catchments, where annual river flows are relatively reliable (Hamilton *et al.* 2005) large refuge waterholes are a common feature of the landscape (Silcock 2009, Fensham *et al*. 2011). In these regions, large waterholes provide broad networks of refuges that become interconnected during periods of high rainfall and river flow and isolated during dry periods.

Mapping and classification of permanence has been undertaken for waterholes (including springs) in the Cooper and Diamantina catchments (Silcock 2009) based upon spatial analysis, mapping, local knowledge and historic records. The accompanying spatial layer in Fensham *et al.* (2011) remains the most comprehensive mapping of potential refuge waterholes in the LEB. However, the classification presented was likely to have overestimated the permanence of some waterholes, especially for arid, highly ephemeral catchments during extreme drought conditions (Kerezsy *et al.* 2013). In addition, the report identifies that even permanent waterholes may have 'dubious refuge value' due to collapses in water quality and other drought impacts during dry periods (Silcock 2009). Work being undertaken as part of the *Bioregional Assessments for Coal Seam Gas and Large Coal Mining* under the Commonwealth Office of Water Science, is currently undertaking additional mapping and modelling of waterholes and other aquatic ecosystem 'assets' for focus regions within the outer regions of the LEB where the Pedirka, Arckaringa and Galilee coal bearing sedimentary basins are accessible (DEWNR unpublished data).

An emerging issue with the current data on waterhole refuge use is that of anthropogenic refuges, which are poorly studied and understood (Robson *et al.* 2008) and groundwater fed refuges which are rarely assessed as part of waterhole surveys. Where bore drain wetlands, constructed dams or spring refuges have connection to waterholes and river channels, localised rainfall and flow events could potentially result in the movement of small-bodied fish species from these polo club refuges into riverine waterholes. Patterns from the Macumba (SARDI unpublished data) suggest that local anthropogenic refuges may be contributing to the persistence of some species in the upper Macumba catchment, challenging the long held view that no fish refuges exist in the catchment (Sternberg *et al*. 2014). It is possible that small anthropogenic or spring fed refuges in the upper Mulligan River and saline polo club refuges in the mid Mulligan (Kerezsy *et al.* 2013) could serve as a local source of smaller bodied species (particularly glass fish and hardyhead which are otherwise conceived to be slow recolonisers); a pattern that most likely cannot be picked up through waterhole monitoring but only through comprehensive spatial assessment. Similarly, Bore Drain wetlands on the floodplain of the Peake Creek (McNeil *et al.* 2011a) provide a permanent source refuge for small-bodied species, predominantly the exotic gambusia (*Gambusia holbrooki*) to survive and recolonise broader catchment habitats (McNeil *et al*. 2012).

Polo Club: Selective species refuges

Saline Polo Club:

In the Lake Eyre Basin, saline waterholes have been identified as polo club refuges where salinity exceeds ~35 ppt (sea-water) reaching over 120 ppt where the tolerance limits of fish species restrict inhabitation (McNeil *et al.* 2011a). Saline polo clubs have been recorded in the Peak Creek and lower Neales, Warburton Creek and lower Cooper Creek, and generally represent arid areas where saline groundwater inputs maintain pool depth following the evaporation of surface waters after flow cessation. Species that utilise saline polo clubs are Lake Eyre hardyhead (*Craterocephalus eyresii*) and desert goby (*Chlamydogobius eremius*). Very low numbers of spangled perch (*Leiopotherapon unicolor*) and bony herring (*Nematalosa erebi*) have also been recorded from saline polo clubs (McNeil *et al.* 2008, 2011a, McNeil and Schmarr 2009). Saline polo clubs enable inhabitants to undergo huge population booms not achievable in less harsh refuges due to competition and predation pressures.

Saline polo clubs form due to the seepage of saline groundwater into pools, ideally with enough inflow to maintain the pool habitat through seasonal dry periods. However, these habitats also become fresh during rainfall driven flow events and therefore do not function as polo clubs at this time – instead they serve as disco refuges (see below) for freshwater species to utilise, potentially feeding upon the polo club members already abundant therein. At the extreme end of drought disturbance, as is the normal state for some of the extremely arid interior reaches of the Basin (e.g. lower Neales) the saline phase of these habitats is so extensive that extremely hypersaline conditions develop and are indeed the normal state of aquatic habitats in these reaches (McNeil *et al.* 2011a). Although local fishes have some of the highest salinity tolerance of all freshwater fish in the world (Glover 1973, Glover and Sim 1978a, b), these habitats develop such a high level of salinity that they are predominantly fishless for most of the time.

Spring Polo Club:

A second type of polo club refuge is the perennial, shallow and occasionally warm habitat associated with discharge springs. Isolated GAB springs are a critical refuge type for desert gobies where they will be sole inhabitants precluding any introductions. Where GAB springs are located in river channels or subject to inundation during floods, other species may be present.

The presence of gambusia in many spring habitats across the Lake Eyre Basin has impaired the refuge value of these springs. It is likely these gambusia were translocated directly into springs although entry from adjacent river systems is highly likely if connecting flows possess low velocity and persist for an extended period as gambusia are not rapid colonizers (McNeil and Costelloe 2011). Two spring pools (North Freeling Spring and EFN027) are known to exist within the Peake Creek channel and these springs are both deeper (subject to riverine geomorphic processes) and higher in fish diversity (McNeil *et al*. 2012). Being relatively shallow, these connected springs are not likely to support large bodied species such as golden perch, Barcoo grunter or Welch's grunter.

As the most perennial of all habitats in the Neales catchment, it is likely that these connected springs form the only truly permanent refuges in the system.

The possible anthropogenic introduction of several fish species to Algebuckina outlined above may indicate that the persistence of large bodied species in the catchment is due only to translocation, and that the true assemblage is limited to species that can persist in spring fed polo club refuges. Alternatively, intermittent loss of these species may be temporarily replenished if recolonisation from the Warburton groove across Lake Eyre is possible (see Murphy *et al.* 2014). Both theories suggest that the Neales is naturally driven by spring polo club refugia, as opposed to riverine arks, which would drive the assemblage patterns in the catchment closer to those such as the Finke, where spring fed reaches have shaped the fish fauna over long periods of disconnection from other catchments (Cockayne *et al*. 2012, 2013, Sternberg *et al.* 2014). These patterns highlight the need to develop catchment scale refuge models for conceptualising the catchment scale role of the various refuge types in driving the ecology of each catchment or reach.

A number of disconnected (isolated from broader riverine systems) spring refuges are also important refugia for Lake Eyre Basin fishes. Dalhousie springs form a complex of hot water springs that are isolated from riverine habitats due to loss of connectivity through the lower Finke and Macumba Rivers. Endemic species include Glover's hardyhead (*Craterocephalus gloveri*), Dalhousie mogurnda (*Mogurnda thermophila*), Dalhousie hardyhead (*Craterocephalus dalhousiensis*), Dalhousie catfish (*Neosilurus gloveri*) and Dalhousie goby (*Chlamydogobius gloveri*). The springs are also refuges for more widespread spangled perch, but no other species common to the LEB. Gambusia has been introduced to a large number of springs and eradicates desert goby wherever it has been introduced (McNeil *et al.* 2012). The same incursion has occurred across a number of the springs at Edgbaston where the endemic Edgbaston goby (*Chlamydogobius squamigenus*), Edgebaston hardyhead (*Craterocephalus* sp.) and red finned blue eye (*Scaturiginichthys vermeileipinnis*) have been severely impacted wherever gambusia have spread (Wager and Unmack 2000, Kerezsy 2009, Kerezsy and Fensham 2013). Elizabeth Springs near the Georgina/Diamantina in the far west of Queensland also has an endemic goby (*Chlamydogobius micropterus*) (Fensham *et al.* 2011).

Non GAB springs in the Lake Frome catchment support an isolated population of purple spotted gudgeon; the Flinders mogurnda (*Mogurnda clivicola*), which persist only in a single spring fed reach of Balcanoona creek and a translocated population is present in a spring fed reach in the nearby Nepoiue creek (Pierce *et al*. 2001, McNeil *et al.* 2011b). The Frome Creek catchment feeding Lake Eyre from the south has a number of spring fed pools that contain spangled perch, most notably Mudlapinna Spring (McNeil *et al.* 2011b) and Arkoona Creek (SARDI unpublished data). Springs in the upper MacDonnell ranges provide permanent habitats where spangled perch persist (Davis *et al*. 2013a, Sternberg *et al*. 2014). For these isolated springs, the issue of potential hydrological connectivity is central to the role that these spring refuges play in the broader ecology of Lake Eyre Basin fishes in the long term.

Disco Refuges

Disco waterholes describe the vast majority of the non-permanent aquatic habitats across the Lake Eyre Basin and are the principal aquatic habitat expression of the boom and bust cycle across the landscape. The LEB disco classification was built upon that of Robson *et al.* (2008) to describe non-permanent waterholes that, during wetter times persist through seasonal dry spells to provide refuge for inhabitants (McNeil *et al*. 2011a). In the longer term, however, disco refuges are unable to maintain this role and deteriorate and desiccate during extreme or extended periods of zero flow (i.e. drought). During wetter periods this category makes up a substantial proportion of waterholes, lakes and wetlands in the LEB and provides a substantial habitat in which fish and other aquatic biota can spawn, feed and grow, during wetter periods. Disco refuges are important for building resilient and robust populations and for mixing of genetic material from recently connected refuges across catchments.

Having a reasonable period of persistence, disco waterholes present relatively benign environmental conditions for much of their existence, to which all arid species are well-adapted (Glover and Sim 1978a, 1978b). Removed from the yoke of environmental harshness during the *Resilience* and *Wet* Phases, biotic interactions and processes are likely to become the dominant mechanisms controlling assemblage and abundances of fish in waterholes (Jackson *et al.* 2001) at least whilst environmental disturbance mechanisms remain low.

Within a few hydrological seasons, the climatic cycle may become increasingly drier, leading to reduced flow replenishment, increased evaporation and water loss until disco refuges are eventually lost across the landscape. This can frequently occur within a single hydrological season for example in the Neales, waterholes that are relatively shallow (<1.5 m) will dry annually under average cease to flow periods (Costelloe and Russell 2014). Where ground water inputs are sufficient to prevent desiccation, disco waterholes are likely to becoming increasingly saline and their assemblages will shift according to salinity tolerance gradients, resulting in a developing polo club structure (McNeil *et al*. 2011a). The polo club assemblage may then persist until the resumption of flow when conditions (e.g. salinity) improve and colonizing species can return to the site, although many may dry completely in extreme drought (Mathwin *et al*. 2015).

Anthropogenic Refuges

The role of anthropogenic refuges is poorly described in the literature (Robson *et al.* 2008, Markwell and Fellows 2008) but potentially significant given the ongoing development of dams and water storages to support pastoralism. McNeil *et al*. (2011a) describe a number of constructed stock dams on the Neales River catchment that were observed to serve as disco type refuges for a range of fish species consistent with other disco refuges in the region. These authors also describe the role of uncontrolled bore wetlands as permanent refuges for fish species. McNeil *et al.* (2012) further describe the role of bore wetland refuges as key refuges for introduced gambusia which was found to numerically dominate the assemblage of bore drain wetland, in all probability using these stable refuges to launch repeated colonisation forays into the broader river system during periods of connectivity. These refuges for exotic pests, especially gambusia, maintain a constant threat to the ecological stability and biota of the Basin (Wager and Unmack 2000, Kerezsy 2009). Although it appears to have been eradicated (Thwaites *et al*. 2013), the population of common carp (*Cyprinus carpio*) in Leigh Creek also persisted solely within the anthropogenic refuge of the Leigh Creek retention dam. Clearly there is potential for anthropogenic refuges to threaten as well as enhance the viability of Lake Eyre Basin fish assemblages and ecosystems.

It is hypothesised that alien species dominated bore drains may provide a high threat to future stability and integrity of riverine ecosystems through the provision of these stable, permanent habitats. This provides a platform for the gambusia to take advantage of any opportunity to dominate a weakened or destabilised fish assemblage, should any impact cause significant disturbance to the broader riverine population. Such a disturbance could eventually lead to the domination of LEB fish ecosystems by gambusia, currently prevented by the intact hydrology and natural assemblage of the Basin's fish fauna (McNeil and Costelloe 2011). Recently located permanent bore drains in the Macumba River catchment may also be serving as refuges for some species (Sternberg *et al.* 2014). The historical understanding for the catchment is that no permanent refuges exist in the connected riverine ecosystem, despite the presence of several deep, but leaky, waterholes. Historical perception is that fish fauna is dependent entirely on colonisation from the Diamantina/Warburton when both the Macumba tributary and the Warburton channel are flowing (Wager and Unmack 2000).

Stepping Stone Refuges

Stepping stone refuges are of use to fish as an intermittent or ephemeral refuge and refer specifically to the dispersal of biota (Robson *et al.* 2008). In the Lake Eyre Basin stepping stone refuges exist where there are tributary or river flows that connect extant refuge habitats. In the Neales River, stepping stone refuges provide colonisation for fish (especially rapid colonisers such as spangled perch, rainbowfish and bony herring) across a range of refuges (including ephemeral creeks, springs, dams and river sections) during localised flow events. They have also been described during the *Wet* Phase to support the colonisation of slower colonisers, such as desert goby and barred grunter) throughout the catchment during extended periods of connective river flows (McNeil *et al.* 2011a).

Casino Refuges

Casino type refuges are considered to be those that have by chance been spared the impacts of disturbance that falls upon surrounding habitats (Robson *et al.* 2008). In the Lake Eyre Basin, isolated weather systems are responsible for extremely isolated events of heavy rainfall that can cause individual tributaries or river reaches to flow in isolation from the broader catchment. These events can fill refuges, and improve the persistence of otherwise isolated water bodies. In the Neales River, localised rainfall events have been shown to fill networks of disco refuges, but being insufficient to connect ark refuge habitats, waterholes remained fishless until more substantial catchment flows occurred (McNeil *et al.* 2008). These circumstances could, however, provide connectivity across refuge habitats, and can therefore provide opportunities for fish to move into and out of refuge habitats, either supporting colonisation or enabling retreat to more permanent refuges. Casino refuges are therefore applicable to waterbodies across the Basin and could provide opportunities for fish depending on specific idiosyncrasies of the volumetric, spatial and temporal aspects of each individual event.

Refuge Transitions and the Influence of the Hydro-Climatic Environment

The classification of habitats presented above is a useful tool in understanding and modelling the function of aquatic ecosystems in the LEB. This understanding is critical to effectively inform gradients of environmental condition and in understanding the difference between naturally driven variability and human induced changes to ecological function. This in turn is essential for predicting the consequences that any impact on the ecological system may have for the human values that drive our need for protecting environmental condition (MacDonald and McNeil 2012, McNeil and Wilson 2014).

A key aspect of the Basin's ecology is that it is driven by extreme climatic and subsequently hydrological variability, driving boom-bust ecosystem dynamics. With this in mind it is essential to consider that refuge definitions and classifications are not static, but are subject to changes driven by the climatic and hydrological variability of the environment. For ark refuges, the concept is one of stability or tolerable conditions through time. The arks preserve the biota of the region through *Dry* and *Wet* phases alike, although some variation in biotic metrics is very likely, (e.g. fluctuations in abundance and even assemblage structure through *Resilience* and *Wet* phases as species dynamics are influenced by emigration of colonisers, increases in habitat availability and food web structure etc.). Similarly, polo club springs are characterised by their stability through time but are defined by their shallow habitat and reduced pelagic and open water habitat which selects for smaller bodied species.

For other refuge types, be they waterholes, lakes, wetlands or dams, the manner in which they provide refuge is wholly specific to the hydro-climatic conditions at the time, and the traits of the biota that enable them to move into new habitats during the *Resilience* phase and tolerate conditions in *Resistance* phase. Therefore, the conceptual models for disco and saline polo clubs are more transient, dynamic models that reflect the influence of species tolerances and recolonisation behaviors depending on the current hydro-climatic phase. Additionally, these are in turn dependent upon the spatial location of refugia as hydrological and refuge dynamics are likely to vary across catchments and reaches, highlighting the interplay between hydrology, spatial location and the refuge dynamics for native fish. Functional refuge zones may exist across the Basin, within which refuge and fish population dynamics may respond in predicable ways to climatic and hydrological regimes.

The conceptual assemblage model for a saline polo club waterhole for example, will constitute a limited assemblage where the most tolerant species are numerically dominant. However, through hydrological connectivity in the *Resilience* phase, rapid colonisers that quickly move into the former polo club and are able to tolerate the recently freshened conditions can utilise the waterhole for resilience building and potentially even utilise the resources provided by the abundant polo club species as prey. For the *Resilience* phase, the polo club waterhole is effectively a disco waterhole, with rapid colonisers becoming dominant and expressing recruitment and population growth as the wet season progresses.

However, unlike ark refuges, conditions in polo club waterholes eventually return to their *Dry* phase condition into the *Resistance* phase and with salinity gradually increasing to toxic levels, less resistant species will become chronically and eventually fatally impacted. Once waterholes become disconnected and opportunity for escape has passed, intolerant species will be lost and the assemblage structure and abundance patterns will again favour highly abundant tolerant species.

Spatial Catchment Refuge Models

The complex nature and distribution of various refuge and connected habitats across the Lake Eyre Basin necessitates further consideration be given to the spatial distribution of various refuge types at scales appropriate to their ecological function. The specific scale of importance to the Lake Eyre Basin Rivers assessment is that of the reach, catchment or basin scale (LEBSAP 2008, 2009a, 2009b). Individual sites (such as a single refuge habitat) are worthy of consideration, primarily when they have a significance beyond the local scale (e.g. at the reach or catchment or whole of basin).

The function of refuge waterholes is therefore of exceptional significance, when they are assessed in the context of the reach, catchment and basin scale role that they play in maintaining viable fish populations and in supporting the resistance and resilience of fish at the population scale. It is for this reason that LEBRA monitoring (and a range of other ecological projects in the Lake Eyre Basin) has to date been focused on key refuge habitats and networks and their function in delivering broader scale services that support ecosystem processes.

To advance our understanding of how refuge habitats work at these scales, a range of spatial models have been developed to conceptualise the basin-wide (Figure 4), catchment and reach (Figure 5) specific distribution and function of refuges and networks of refuges and to explore the functional roles of these habitats and networks across varying levels of connectivity and isolation driven by the hydro-climatic variability inherent in the hydro-climatic model. We therefore present a series of spatial models that capture the nature of refuges within various catchments (Figure 5) and reaches within the Basin, to provide a basin scale model of spatial refuge function. These models are simple enough to enable easy conceptualization of the hydrological and biological processes that link these habitats together into functional ecological units.

These models can subsequently be used to test assumptions and hypotheses about the role of refuges at relevant spatial scales, and will be informed by a range of data including aspects of hydrological connectivity and persistence, not currently available in the project databases. These models can therefore provide a significant point of linkage to the spatial analyses of hydrology and habitat availability being developed within Task 3 of the current Goyder LEB project. As such, these spatial models provide a mechanism for communicating and driving hydro-ecological outputs from that task and in guiding collaborative analysis of hypotheses and the identification of indicators and thresholds resulting from collaboration across Tasks 2 and 3.

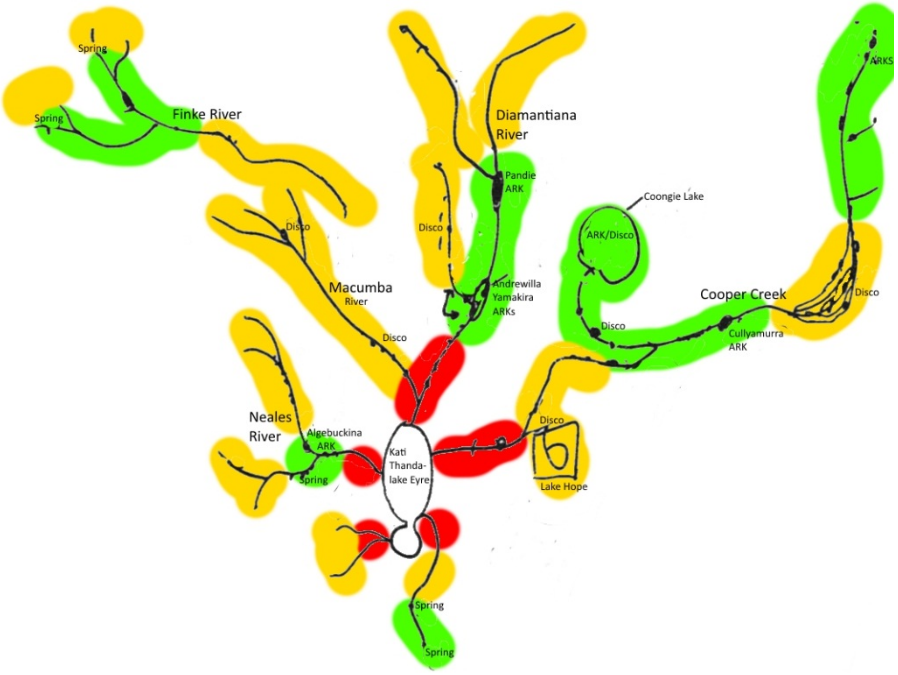


Figure 4. Mud-map example of a conceptual Spatial Refuge Model for the Lake Eyre Basin summarising refuge distribution and function across catchments and reaches.

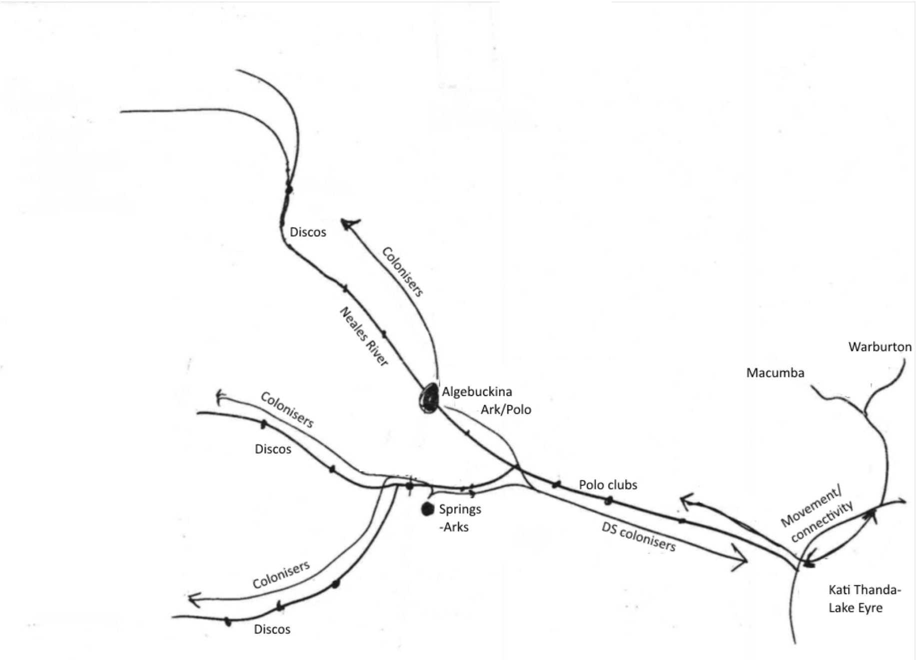


Figure 5. Mud-map example of a spatial refuge model for major catchments of the Lake Eyre Basin summarising the distribution and function of refuges at the catchment scale.

Seasonal and supra seasonal drought disturbance

Beyond flooding and connectivity, dry season and drought disturbance is the principal mechanism through which climate and hydrology influence the biota of the arid Lake Eyre Basin. In particular, it is the key mechanism driving the critical importance of refuges to the survival of Lake Eyre Basin species. The Hydro-Climatic Model sets out seasonal and supra-season cycles of alternating drought and inundation. Of central importance to biota is the impact of seasonal *Pulses* of disturbance on an annual scale, and supra-seasonal *Presses* of disturbance that ramp in intensity and impact during supra-seasonal drying (Lake 2003, 2008). Both types of drought disturbance impose impacts upon aquatic biota and importantly, both influence the distribution and function of aquatic refuge habitats, albeit in two different ways.

The importance of aquatic refuges is driven by their role in protecting biota from one wet season to the next, enabling species to resist the seasonal impacts of drought. This largely describes the role of disco refuges during the *Wet* and *Resilience* phases as large numbers of waterbodies support a range of fish species through to the following flow seasons. However, during the ramping disturbance of supra-seasonal drought, the level of drought disturbance increases in intensity whereby disco refuges become dry and thus, the role of ark and polo club refuges become critical in supporting biota through to wetter climatic periods. The varying role of seasonal and supra-season drought disturbance in influencing the function of refuge habitats and in turn, of impacting inhabitant biota is conceptualised in Figure 6 below.

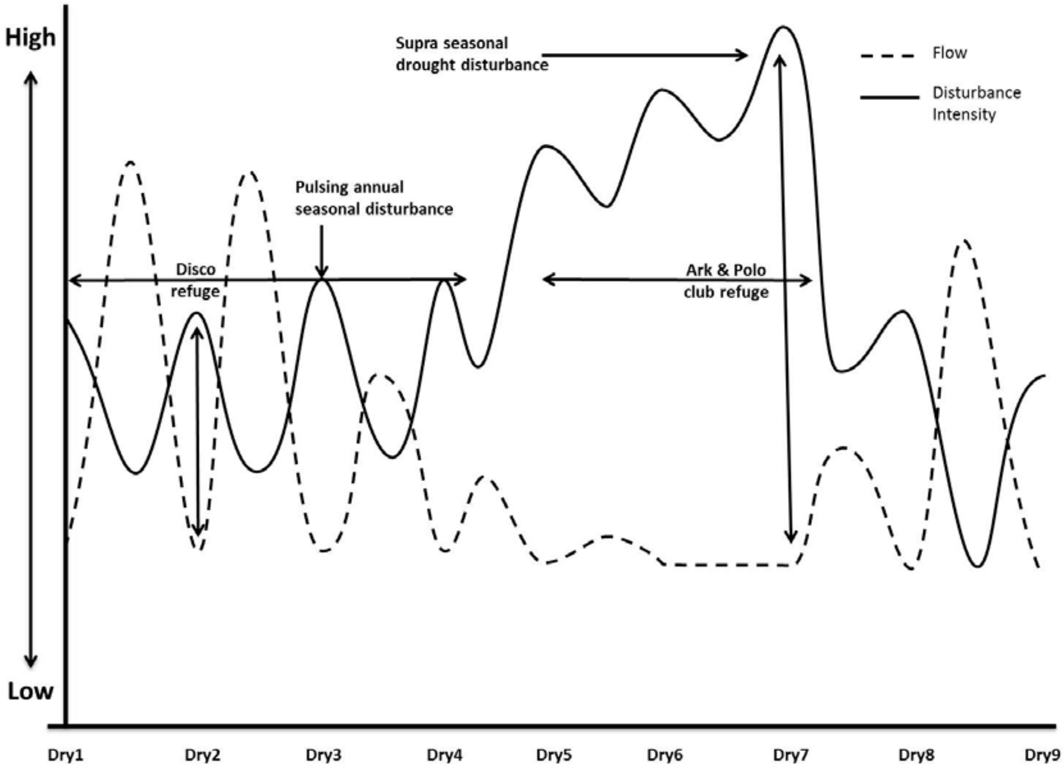


Figure 6. The role of drought disturbance in impacting aquatic refuges and biota during seasonal dry pulses and ramping perturbation associated with extended, supra-seasonal drought.

The relationship between flow level, the depth of a refuge habitat and the rate at which water evaporates from the waterhole is central to the persistence of waterbodies during periods of no flow during the *Resistance* and *Dry* phases of the hydro-climatic cycle (cf. Hamilton *et al*. 2005). Whilst more detailed hydrological persistence models are available (Costelloe *et al*. 2003, Costelloe 2008, Costelloe 2011, Hamilton *et al*. 2005) we have presented two conceptual diagrams to describe the relationship between river flow levels and the water level response of ark and disco refuge habitat (Figure 7). We have also developed a simplified conceptual diagram outlining how the relationship between habitat depth, evaporation rate and the time between inflows determines whether or not a habitat can remain permanent (ark refuge) or will dry completely (disco refuge) during extended drought periods (Figure 8).

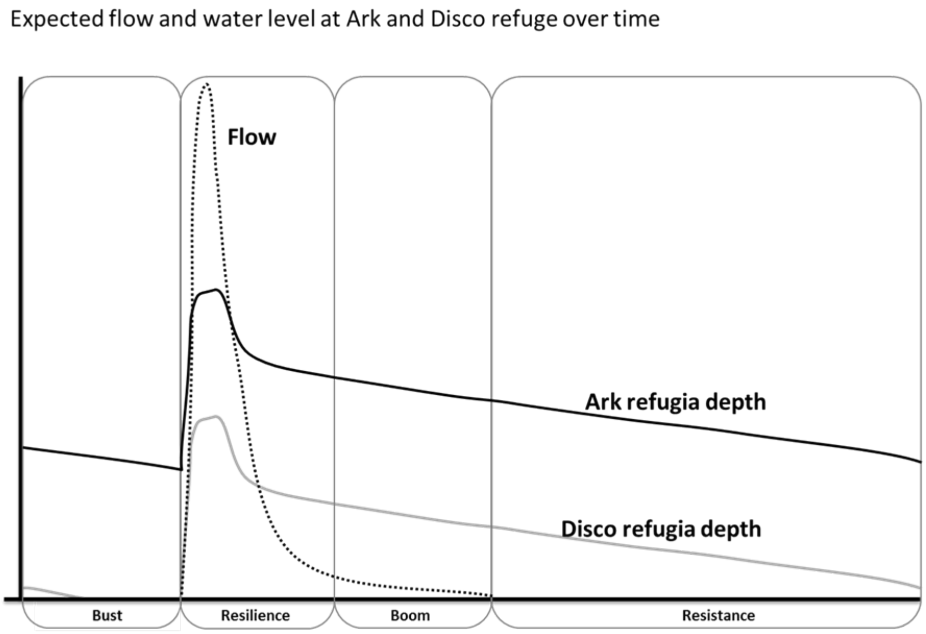


Figure 7. Conceptualised flow and water level responses for riverine refuges (ark and disco) across hydro-climatic phases.

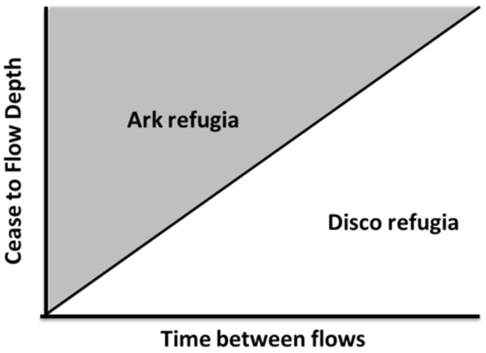


Figure 8. Conceptual model outlining the relationship between evaporation rate, depth of habitat and persistence indicating the likelihood of a habitat functioning as an ark or disco refuge. Models based on the evaporation loss rate of 2.1m/year from Hamilton *et al.* (2005)

Hydrological Components

Imgraben and McNeil (2013a) presented three key components of Lake Eyre Basin hydrology (flow regime, periodicity and connectivity) that relate to hydro-ecology and the function of aquatic habitats. These components were based on cross-jurisdiction and multi-disciplinary workshops conducted in 2013 in Adelaide and Brisbane. Each of these components possesses a number of sub-components or is linked to key processes that drive their ecological function. To support the development of conceptual models in the current report, hydrological attributes (components, sub components and processes) used to develop conceptual models in the current report are presented in Table 3 below.

Table 3. Hydrological components, sub-components and processes consistent with the classification of Imgraben and McNeil (2013a)

Hydrological Component	Sub-Component	Indicative Process
Flow regime	Flow volume:	-Zero flow
		-Local Flow
		-In channel Flow
		-Overbank Flow
		-Flooding
	Flow Periodicity:	-Seasonality
		-Commence/cease to flow
Water Regime /Persistence	Drawdown	
	Cease to Flow	
	Groundwater influence	
Connectivity	Disconnected	
		Zero flow
	Longitudinal	Local (isolated flows connecting small subsets of habitats)
		In channel (connectivity of refuge waterholes and connection to disco waterholes)
	Lateral	Overbank (localised connectivity of floodplain, tributary, lake and wetland)
		Flooding (General connectivity)

Flow regime and water regime combine to account respectively for water levels during periods of flow and periods of habitat isolation, with 'cease to flow' being the switching metric between these two components. Connectivity, however, is indelibly linked to flow regime but is considered a significant component of catchment and basin hydrology in its own right. For the purposes of conceptual modelling, connectivity has been classified under the same categorization as flow regime and therefore, the listing above also indicates how each hydrological regime category links to components of connectivity. Furthermore, the concept of connectivity can be characterised using the habitat/refuge classification to add spatial and ecological context to each flow/connectivity class. Consistent with thinking from the ARIDFLO program (Costelloe *et al*. 2004) the flow regime has been separated into categories based on the relative magnitude of flows, consistent with the hydrological conditions encountered in the Lake Eyre Basin (Figure 9).

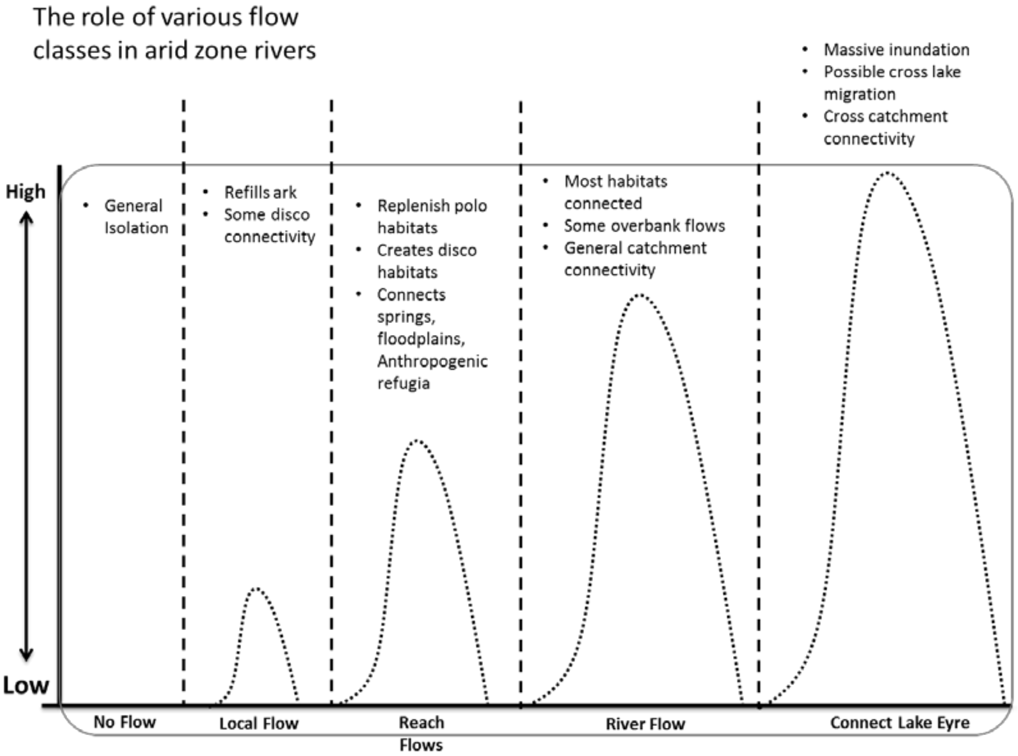


Figure 9 Conceptual flow classes relevant to functional habitat and ecological components and processes of Lake Eyre Basin Rivers.

Although they are identified as separate components, water flow regime and water regime are directly linked as it is the combined effect of flow on habitat, depth, persistence and connectivity, all of which drive biotic and ecosystem responses to flow (Bunn and Arthington 2002). Within a habitat, water level is determined by flow until the cease to flow point is reached and subsequently water level is determined by evaporation coupled with any groundwater loss or gains. We present a conceptual cross section of a waterhole to demonstrate the various ecologically relevant flow stages that can be expected during changes in flow level and water level across the hydro-climate cycle (Figure 10).

The relationship between water level and ecological components and processes are central to the processes influencing the *Resistance* phase within increasingly isolated habitats, whilst the flow level, through its influence on connectivity, dispersal and inundation of habitats and resource production is the principal driver of the *Resilience* phase. The functional relationships between hydrology and habit variables presented in Figure 10 are further simplified in Figure 11 to provide basic relationships between measurable response variables to facilitate generation of explicit hypotheses and analyses.

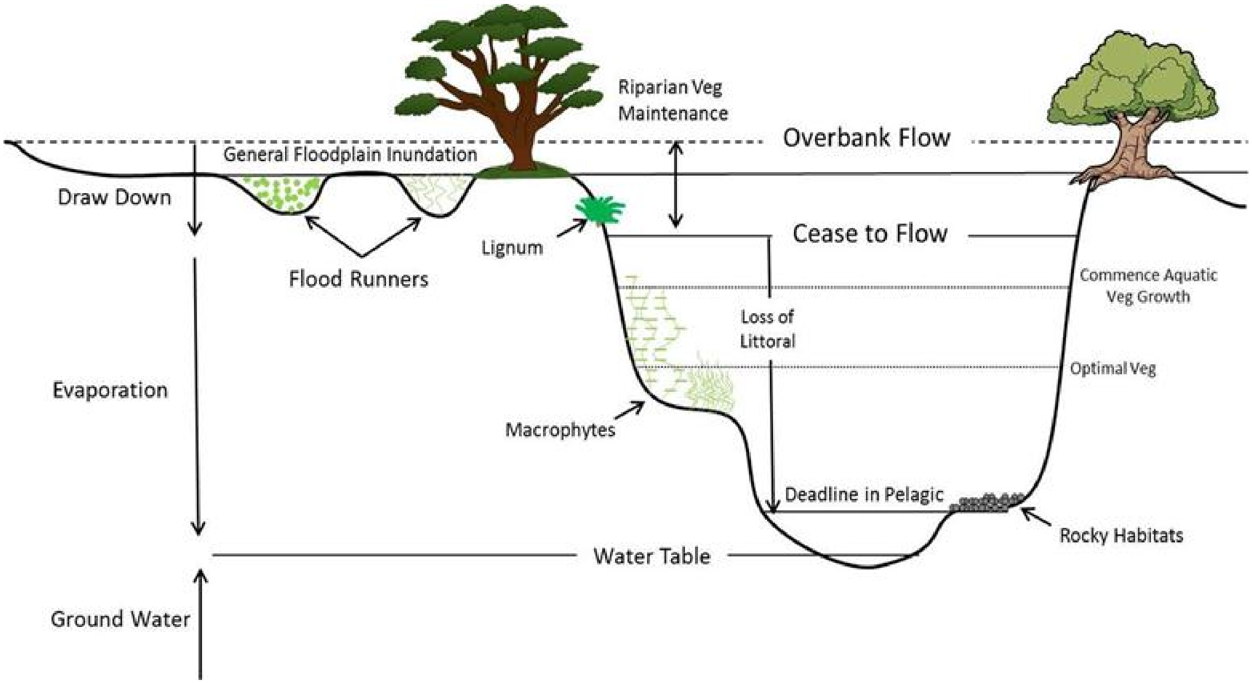


Figure 10. Modelled hydro-ecological water level stages encompassing flow volume bands and persistence underpinning ecologically relevant flow and water levels.

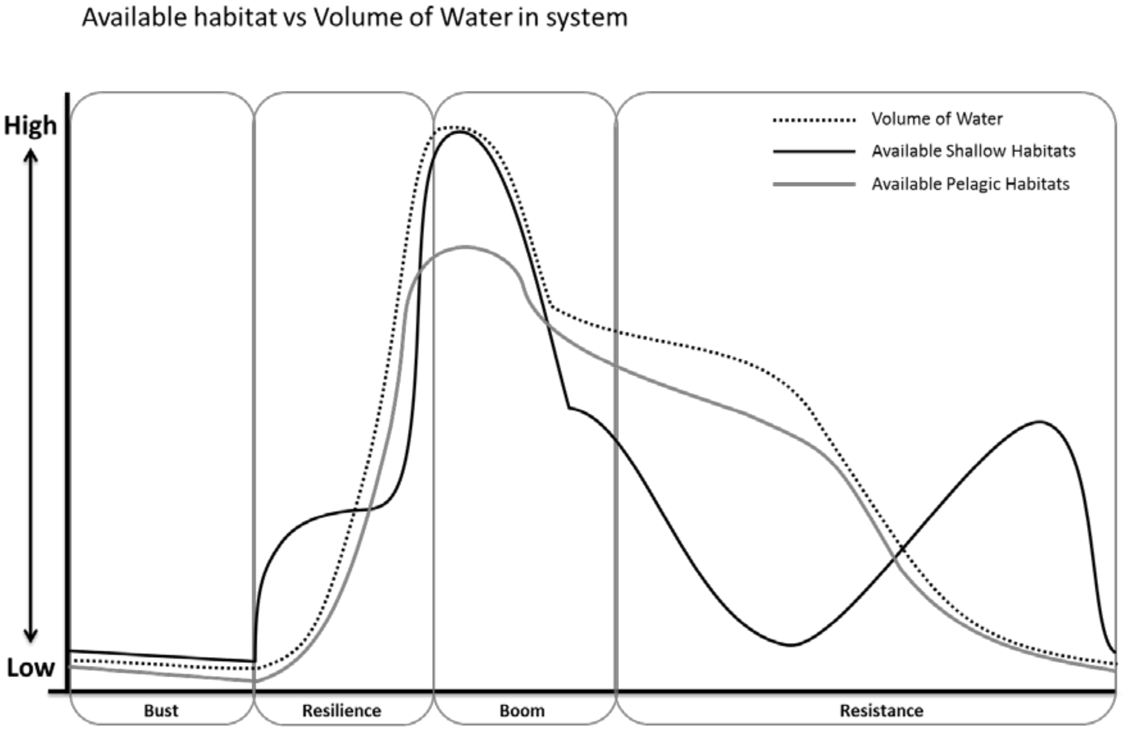


Figure 11. Influence of flow volume on the availability of littoral and pelagic habitat across the hydro-climatic cycle.

Biological traits of fishes

There is a reasonable amount of information published describing the ecological and biological traits of fishes in the Lake Eyre Basin. Since around half the fish fauna of the Basin is not endemic (Unmack 2001) information from the Murray-Darling Basin and from coastal catchments to the north and east of the Basin is also informative (McDowell 1996, Pusey *et al.* 2004). The collation of biological traits for fish of the Lake Eyre Basin will support the analysis of a wide range of conceptual models presented throughout the current report and will provide a point of reference for the interpretation of modelling outputs and the development of indicators and thresholds for environmental condition in the Lake Eyre Basin. Concepts of biotic resistance and resilience have become central to understanding the role of climate in structuring arid aquatic ecosystems (Sheldon *et al*. 2010, Leigh *et al*. 2010, Arthington and Balcombe 2011) as demonstrated by their inclusion in the phases of the hydro-climatic model. Accordingly the use of fish biological traits and knowledge in supporting conceptual model developments will also be approached through the concepts of climatic disturbance, resistance and resilience.

Fish Trait Matrix

The collation of traits from various fish species into a single matrix is a key step in organising the life history information for each species in a consistent and comparable manner that can be utilised for identifying suites or guilds of species that may be expected to respond to environmental and ecological drivers in a similar and predictable manner, thereby supporting a wide range of ecological analyses (Winemiller and Rose 1992, Winemiller 2005). Fish traits have been collated for Neales River fishes (Table 4, 5) to provide a summary of biological information relevant to assessment of resistance, resilience and the use of refuge habitats (McNeil *et al*. 2011a).

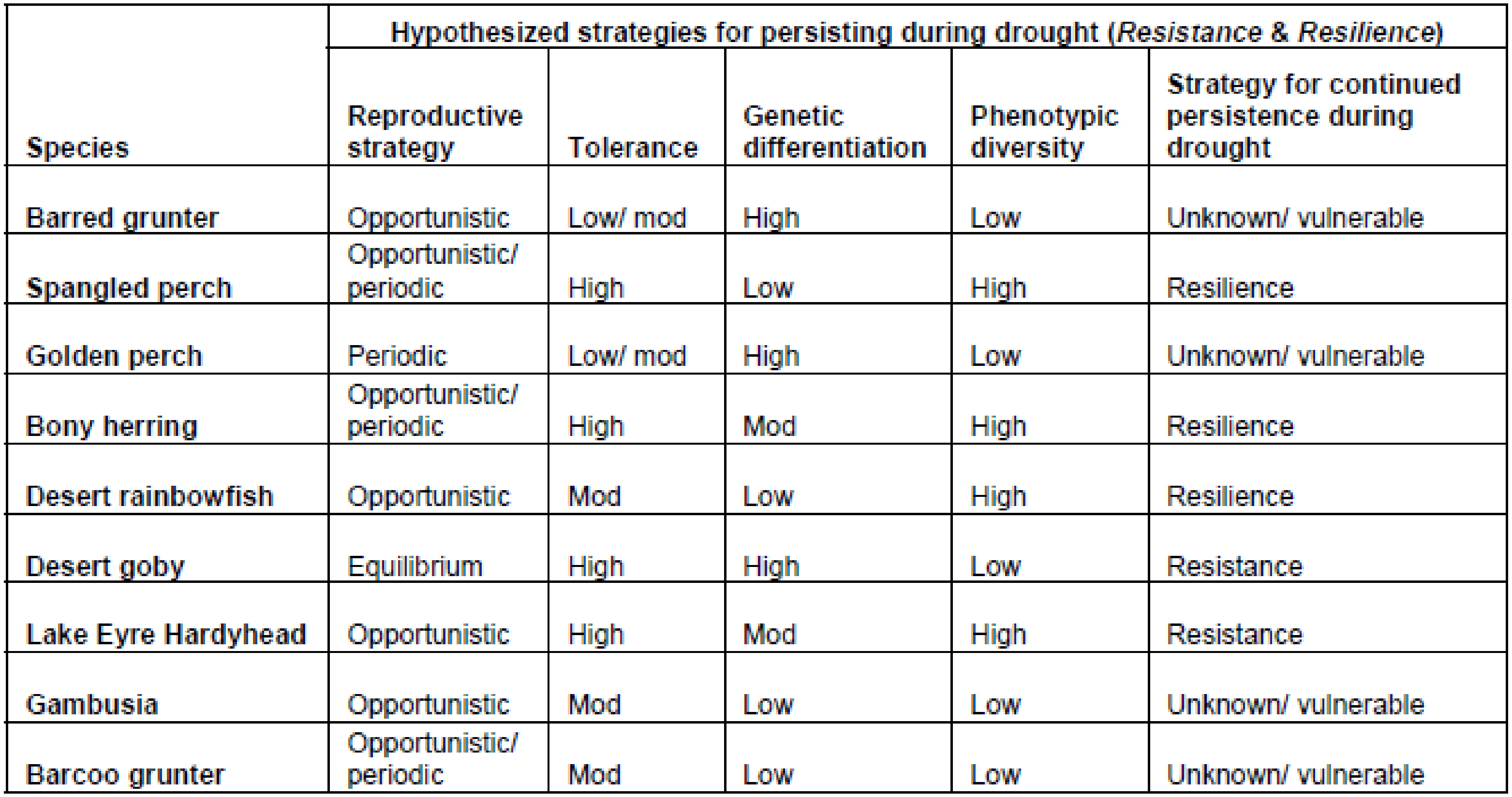
More comprehensive trait matrices have been developed to analyse the response of Murray-Darling Basin fishes to drought and develop hypotheses about the mechanisms for maintaining resilience and resistance capabilities under drought impacts (McNeil *et al.* 2013a). Similar collations of biological information have also been developed for fishes of northeastern Australia (Pusey *et al.* 2004) and much information can be gleaned from various field guides and reference texts such as Koehn and O'Connor (1990), McDowall (1996), Wager and Unmack (2000) and Allen *et al*. (2002); see also *life history strategies* in Arthington *et al*. (2010). In combination these reviews cover many of the fish species present in the Lake Eyre Basin Assemblage.

It is proposed that this conceptual understanding of fish traits be expanded to include all Lake Eyre Basin fishes, providing a collation of traits that can contribute to the analyses of hypotheses under the conceptual modeling framework provided. The provisions of trait based analyses will underpin a number of conceptual models presented here, and will further inform hypotheses and indicators that are produced from the planned analyses.

Table 4. Trait summary table for fishes of the Neales River (from McNeil *et al.* 2011)

	Species traits and ecological factors that relate to Climatic Resistance and Resilience										
Species	**Dispersal Ability**	**Distribution (Neales)**	**Distribution (LEB)**	**Distribution (Australia)**	**Reproductive Ecology**	**Etho-ecological reproductive guild**	**Fecundity**	**Longevity**	**Juvenile Mortality**	**Growth to maturity**	**Local abundance in drought conditions**
Barred grunter	LOW	Common	Uncommon/ patchy	Widespread	Non-adhesive eggs (0.6-.85 mm)	Non-guarder, Lithophil	40,000-77,000	MOD (3-5y)	Unknown	RAPID (<1 y)	MOD
Spangled perch	HIGH	Common	Common	Widespread	Sinking non-adhesive eggs (0.60-0.85mm). Facultative flow trigger.	Non-guarder, Lithophil	100,000+	MOD	Unknown	RAPID	MOD
Golden perch	MOD	Uncommon/ patchy	Common	Widespread	Semi-buoyant eggs (3.9mm) Flow trigger	Non-guarder, Pelagophil	500000+	HIGH (5y+)	Unknown	Likely SLOW (2+ y)	LOW
Bony herring	HIGH	Common	Common	Widespread	Buoyant eggs (1mm). Independent of flow. Spring and summer spawning.	Non-guarder, Pelagophil	30,000-800,000	MOD	Unknown	MOD (1 y)	MOD
Desert rainbowfish	MOD	Common	Common	Widespread	Adhesive eggs (0.8-0.95mm).	Non-guarder, Phytophil	20-100	LOW (1-3y)	Unknown	RAPID	LOW
Desert goby	LOW	Common	Moderate	Indigenous	Eggs 3mm. Nov-march spawning under rocks.	Guarder, Substrate Chooser, Lithophil	50-300.	LOW	Unknown	RAPID	HIGH
Lake Eyre hardyhead	MOD	Common	Uncommon/ patchy	Indigenous	Unknown, likely few adhesive eggs and protracted spawning.	Non-guarder, Phytophil	50-800 (~220 mean)*	LOW	Unknown	RAPID*	HIGH
Gambusia	LOW	Common	Uncommon/ patchy	Widespread	Live young. Protracted spawning.	Internal Bearers, Ovoviparity	<375	LOW	Unknown	RAPID	LOW
Barcoo grunter	HIGH	Uncommon/ patchy	Moderate	Indigenous	Buoyant, non-adhesive. Likely flow spawners.	Non-guarder, Pelagophil	100,000	MOD.	Unknown	Unknown	LOW
Source:	(McNeil and Schmarr 2009)	Current Survey + (Allen *et al.* 2002, McNeil *et al.* 2008, Balcombe and Kerszy 2008, McNeil and Schmarr 2009)		(Allen *et al.* 2002)	(Wager and Unmack 2000)	(Winemiller and Rose 1992, Wager and Unmack 2000, Pusey *et al.* 2004)	(Wager and Unmack 2000, Allen *et al.* 2002, Pusey *et al.* 2004)	(Wager and Unmack 2000, Pusey *et al.* 2004)		(Allen *et al.* 2002, Pusey *et al.* 2004)	(McNeil *et al.* 2008)

Table 5. Trait based strategies for resilience and resistance to seasonal and supra-seasonal drought disturbances for Neales River Fishes (McNeil *et al.* 2011)



	Hypothesized strategies for persisting during drought (*Resistance* & *Resilience*)				
Species	**Reproductive strategy**	**Tolerance**	**Genetic differentiation**	**Phenotypic diversity**	**Strategy for continued persistence during drought**
Barred grunter	Opportunistic	Low/ mod	High	Low	Unknown/ vulnerable
Spangled perch	Opportunistic/ periodic	High	Low	High	Resilience
Golden perch	Periodic	Low/ mod	High	Low	Unknown/ vulnerable
Bony herring	Opportunistic/ periodic	High	Mod	High	Resilience
Desert rainbowfish	Opportunistic	Mod	Low	High	Resilience
Desert goby	Equilibrium	High	High	Low	Resistance
Lake Eyre Hardyhead	Opportunistic	High	Mod	High	Resistance
Gambusia	Opportunistic	Mod	Low	Low	Unknown/ vulnerable
Barcoo grunter	Opportunistic/ periodic	Mod	Low	Low	Unknown/ vulnerable

Resistance and Resilience

A key aspect of persisting within climatically harsh arid environments relates to the ability for biota to deal with the impacts that the extremes of drought and flood disturbances may present. The central impact of drought on freshwater habitats relates to the increasing scarcity of freshwater in the landscape and the fragmentation and desiccation of a wide range of aquatic habitats. Essentially, this represents a limitation in the primary water resource essential for the survival of freshwater-dependent biota and freshwater ecosystem processes (Humphries and Baldwin 2003, Lake 2003). Most organisms possess a range of physiological and behavioural mechanisms and/or life history stages that allow resistance to impacts (i.e. the ability to persist) and resilience (i.e. the ability to recover from impacts) such as desiccation, water quality impacts such as salinity and hypoxia and/or habitat contraction (Lake 2003, McNeil and Closs 2007, McNeil *et al.* 2013c, Kerr *et al.* 2013). These concepts of biotic resistance and resilience are central to understanding the impacts of drought on aquatic biota and underpin the overall resilience of ecosystems to drought disturbance.

A number of recent studies in the Murray-Darling Basin explored the role of biotic resistance and resilience in relation to the climatic impacts of extreme drought associated with the ten-year millennium drought that impacted heavily on aquatic ecosystems in that region (Bond *et al.* 2008, Lake 2008, Crook *et al.* 2010, McNeil *et al.* 2013a, 2013b). These investigations revealed that whilst most species had vary resistance and resilience traits, a key factor associated with endangered or threatened fish species was that these species were less resilient than other species, and in particular had poor recolonisation potential associated with increasingly patchy distribution contracting into small areas of their former range (McNeil *et al.* 2013b). Conversely, the fish species distributions in the Coorong were largely driven by resistance potential across extreme gradients in salinity (McNeil *et al.* 2013c).

In the Murray-Darling Basin the increased impact of drought on less resilient species is likely to be associated with the enormous number of barriers that prevented recolonisation from refuges following extreme drought periods. In the Lake Eyre Basin, however, resistance and resilience mechanisms of fish are likely to be far less impacted by the relativley low level of human disturbances such as barriers and it is therefore more likely that resistance and resilience traits of species evolved in response to climatic and hydrological variability to which species are accustomed, will underpin population persistence. The opportunity to build knowledge of these species under natural environmental controls in the Lake Eyre Basin may in turn assist with the management and protection of these species in the Murray-Darling.

One aspect of the analysis of biological traits should therefore include the assessment of resistance and resilience traits in relation to the hydro-climatic model. Indeed, the rising and falling limb of the hydro climatic model are named for the varying dependence on resilience and resistance traits in determining fish ecology during the periods preceding and following *Dry* and *Wet* climatic phases. How do species traits relating to resilience and resistance influence fish dynamics across time and space?

Resistance Mechanisms

The principal impacts of climatic drying on aquatic habitats in the Lake Eyre Basin are the loss of surface water and habitat and declining water quality within drying refuges. Loss of habitat and habitat heterogeneity is critically important in shaping late dry season fish assemblages in the mid-Cooper (Arthington *et al*. 2010) with various aspects of physical habitat linked the loss of several species from drying waterholes.

The role of salinity is critical within particular areas where saline groundwater inputs drive increasingly saline waterbodies. Spatially, salinity impacts are likely to be highest in the mid Peak and Neales catchments, the lower Neales, Lower Macumba and Warburton (including Kallakoopah), the Mulligan, Eyre Creek and parts of the Georgina and in the lower Cooper downstream of Cuttapirrie Corner during periods of no flow (Costelloe *et al*. 2003, Costelloe 2011, McNeil *et al.* 2008, 2011a, Kerezsy 2010, Schmarr *et al.* 2013, Kerezsy *et al*. 2013). In the mid Cooper, however, Arthington and Balcombe (2011) found that variation in salinity was not related to the persistence of fishes during waterhole drying. The distribution of these saline waterholes can be conceptualised using a catchment-scale spatial refuge model.

Water Quality Tolerance and Fish Distribution

Water quality tolerance thresholds describe the levels of mortality expected from various levels of environmentally lethal variables and drive the relationship between species persistence across gradients of environmental water quality parameters. Some of the earliest surveys of fish fauna in the Lake Eyre Basin placed a strong emphasis on the collection of water quality data and their influence on the tolerance and distribution of species (Llewellyn 1973, Glover 1973, Ruello 1976, Glover and Sim 1978a, b). Wager and Unmack (2000) summarised available knowledge of the tolerance of Lake Eyre Basin fishes to water quality parameters.

Salinity

Glover (1978a) summarised field observations and rudimentary tolerance thresholds for Lake Eyre and Dalhousie hardyhead, spangled perch, carp gudgeon (*Hypseleotris* spp.), Australian smelt (*Retropinna semoni*), silver perch (most likely a misidentification of Welch's grunter), gambusia and purple spotted gudgeon (most likely *Mogurnda thermophyla*). McNeil *et al.* (2011a) conducted field laboratory experiments on selected species to determine survival thresholds (lethal concentrations) for salinity from spangled perch, desert rainbowfish (*Melanotaenia splendida tatei*), barred grunter (*Amniataba percoides*) and desert goby, however, these data were never correlated to the distribution of species in relation to water quality parameters in the field. Tolerances of estuarine fish species determined using identical laboratory methodologies were, however, correlated extremely closely to the temporal and spatial variation in fish distribution across a dynamic salinity gradient of fresh to hypersaline in the Coorong over annual seasonal cycles (McNeil *et al*. 2013c). Therefore, the field laboratory salinity tolerances observed by McNeil *et al.* (2011a) can be applied to tolerances in the field with some caution.

Current knowledge (McNeil *et al.* 2008, 2011, McNeil and Schmarr 2009, Cockayne *et al*. 2012, 2013, Sternberg *et al.* 2014) has been used to develop a conceptual salinity distribution model for all riverine fishes in the Lake Eyre Basin (Figure 12) with relative abundances and distribution presented in relation to field salinity conditions. More detailed search of the literature and data analysis as well as the identification of published thresholds will enable these species specific hypotheses to be tested, accurate salinity thresholds to be identified and the relationship between laboratory tolerance and field distributions assessed (e.g. McNeil *et al*. 2013c).

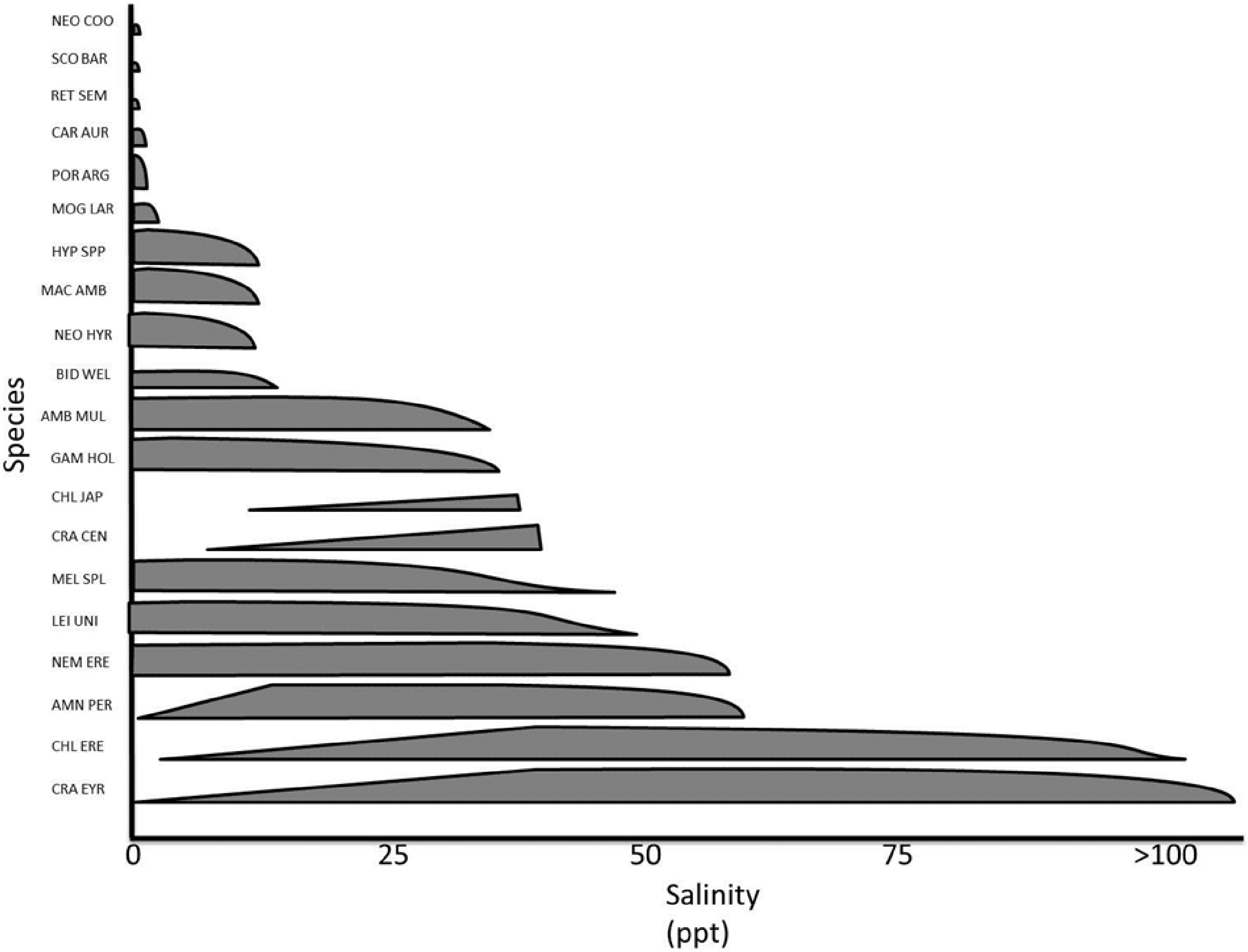


Figure 12. Conceptual model for the distribution and indicative abundance of LEB fish species across the tolerable salinity gradient of waterbodies from McNeil et al. 2008, 2011, McNeil and Schmarr 2009, Cockayne *et al*. 2012, 2013, Sternberg *et al.* 2014. NEO COO = *Neosiluroides cooperensis*, SCO BAR = *Scortum barcoo*, RET SEM = *Retropinna semoni*, CAR AUR = *Carassius auratus*, POR ARG = *Porochilus argenteus*, MOG LAR = *Mogurnda larapintae*, HYP SPP = *Hypseleotris* spp., MAC AMB = *Macquaria ambigua*, NEO HYR = *Neosilurus hyrtli*, BID WEL = *Bidyanus welchi*, AMB MUL = *Ambassis mulleri*, GAM HOL = *Gambusia holbrooki*, CHL JAP = *Chlamydogobius japalpa*, CRA CEN = *Craterocephalus centralis*, MEL SPL = *Melanotaenia splendida*, LEI UNI = *Leiopotherapon*

unicolor, **NEM ERE =** ***Nematalosa erebi***, **AMN PER =** ***Amniataba percoides***, **CHL ERE =** ***Chlamydogobius eremius***, **CRA EYR =** ***Craterocephalus eyresii*****.**

In addition to the species specific relationships between salinity and field distribution, the total abundance of fish and the maximum number of species expected can also be predicted across the range of salinity encountered in the Lake Eyre Basin. The following conceptual model (Figure 13) indicates a linear decline in the maximum species richness expected as salinity increases, but that abundance is predicted to peak under moderate salinity conditions (as encountered in Disco refuges following recession of flows, with a second peak at the extreme end of the gradient where Polo Club species are expected to become highly abundant as they capitalise on the absence of competition and the presence of saline food web resources (e.g. fairy shrimp). Fresher conditions are predicted in Ark refuges where maximum species richness is predicted to be highest.

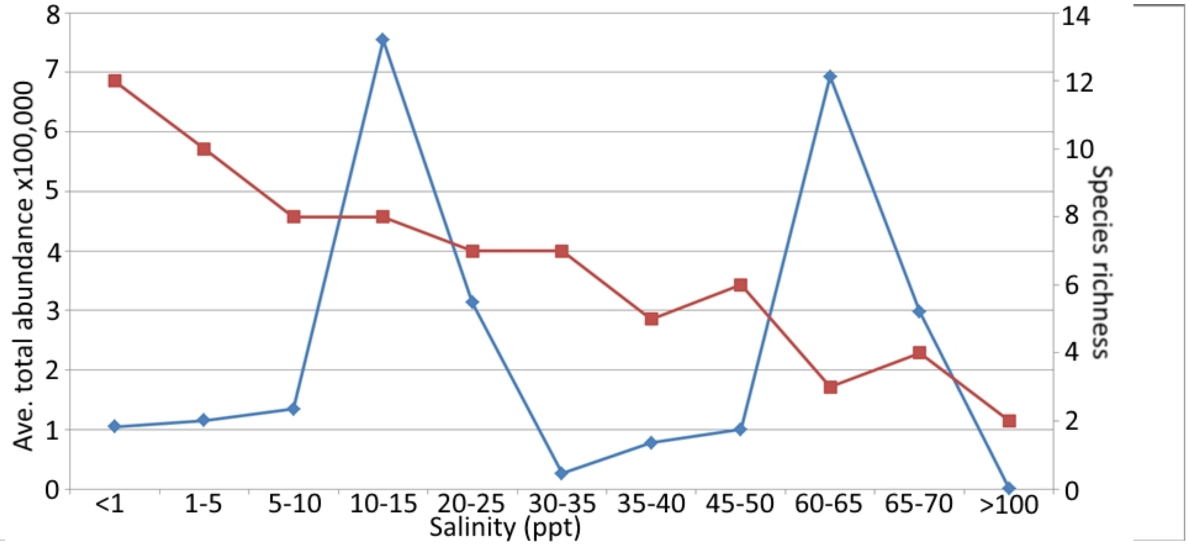


Figure 13 Conceptual model describing the predicted relationship between salinity on the x axis (ppt), average total abundance (blue) and species richness (red) on the y-axis, likely to be highly catchment or reach specific.

The interaction of harsh salinity levels and environmental stability is likely to play a significant role in the evolution of biota from the Lake Eyre Basin (Williams 1985) and this should be reflected in the traits that fish possess. Although based on invertebrate biota, Williams proposes a conceptual model outlining the relationship between salinity disturbance, environmental predictability and the evolution of *K*-, and *r*-selected traits (*sensu* Grime 1979), each of which represented a particular evolutionary life history strategy (Figure 14). K-selected species are equilibrium species and dominate under stable environmental conditions where they have a competitive advantage. They have low fecundity and higher parental investment, are long lived and have stable population sizes. R-selected species are opportunistic that dominate under fluctuating environmental conditions relying on rapid dispersal and have high growth rates, high fecundity, little parental care, and fluctuating population sizes.

A further classification of A-selected species has been presented for saline impacted waterbodies in arid central Australia (Williams 1985). These adversity species are likely to be advantaged by predictable extremes in environmental impact, and therefore may be of extreme relevance to fish species that are most abundant in saline polo club refuges in the Lake Eyre Basin (e.g. desert goby and Lake Eyre hardyhead (Costelloe *et al*. 2004, McNeil *et al* 2008). Consideration of this model following the assembly of trait matrices is likely to be useful in supporting a range of conceptual models presented here, particularly those that deal with environmental and water quality responses of biota.

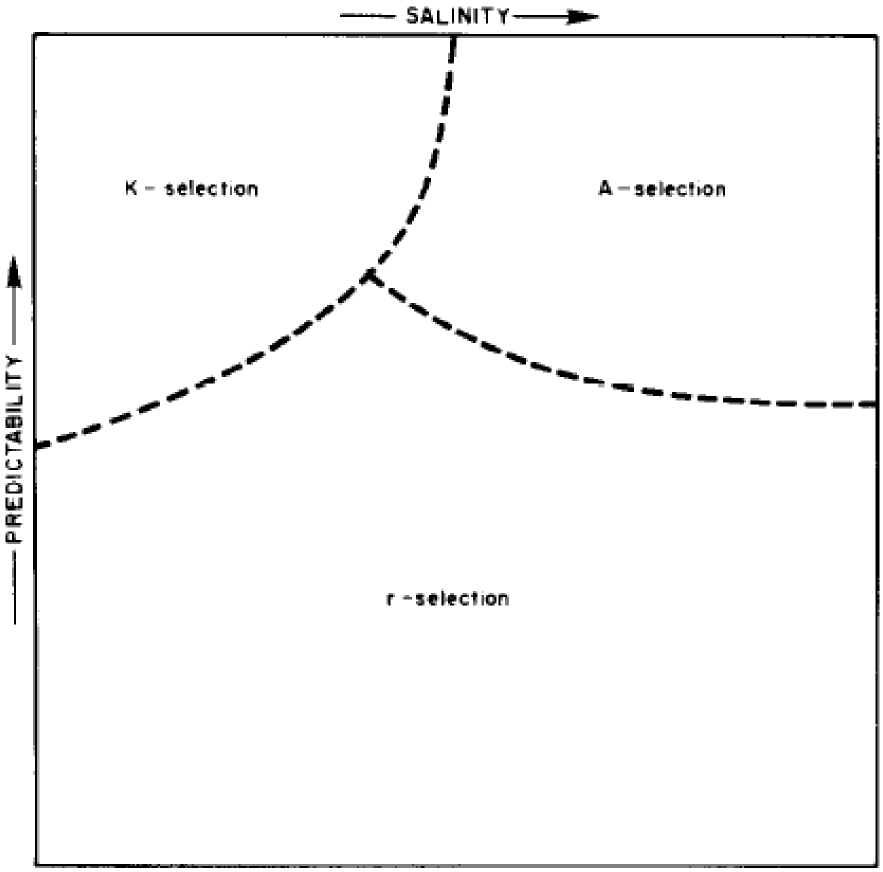


Figure 14. Conceptual model from Williams (1985) describing the relationship that environmental predictability and salinity are likely to have on the biological trait characteristics of inhabitant fauna.

Dissolved Oxygen

There is little data available to describe the role of dissolved oxygen or hypoxia in influencing the ecology of fish or freshwater ecosystems in the Lake Eyre Basin. Ruello (1976) suggested that hypoxia relating to algal blooms could be responsible for large fish kills in Lake Eyre, although no evidence was provided to support this and salinity was extremely high in the lake. Glover (1978) provides a range of observations on the hypoxia tolerance based on field distributions and rudimentary tolerance testing on Dalhousie and Lake Eyre hardyhead, spangled perch, silver perch (Welch’s grunter), Australian smelt, carp gudgeon, desert goby and Dalhousie mogurnda. McNeil *et al.* (2011a) provided field based experimentally derived hypoxia tolerance data for desert goby, spangled perch and desert rainbowfish. Some data can be inferred from studies from neighbouring catchments on the same or very similar species to those found in the Lake Eyre Basin. For example hypoxia tolerance estimates, at warm water temperatures have been experimentally derived for spangled perch (Gehrke and Fielder 1988), western carp gudgeon, Australian smelt, gambusia and goldfish (*Carassius auratus*) (McNeil 2004, McNeil and Closs 2007) collected from the neighboring Murray-Darling Basin. Similarly, Murray-Darling Basin species that are closely related to Lake Eyre Basin species of golden perch (Gehrke 1991), rainbowfish (*Melanotaenia fluviatilis*), and southern purple spotted gudgeon *(Mogurnda adspersa*) (Dwyer *et al.* 2014) have also been assessed for hypoxia tolerance.

Water Temperature

Water temperature is high and variable across waterbodies of the Lake Eyre Basin and is especially high in warm springs of Dalhousie (Glover 1978a, Kodric-Brown and Brown 1993) where fish inhabit springs that are frequently between 36ºC and 46ºC (Wager and Unmack 2000). Water temperatures ranging between 13ºC and 36ºC are common across a range of GAB and non-GAB springs across the Lake Eyre Basin (McNeil *et al.* 2011b, McNeil *et al*. 2012). This range of temperatures is more consistent with that of waterholes across the Lake Eyre Basin which reflects ambient temperature conditions ranging from ~14ºC during winter to ~33ºC but more commonly in the high 20ºC's in mid-summer (McNeil *et al.* 2008, 2011a, McNeil and Schmarr 2009, Cockayne *et al.* 2012, 2013, Sternberg *et al.* 2014).

Water Quality and Refuges Under the Hydro-climatic Model.

Overall, water quality is predicted to vary across hydro-climatic phases and will differ among refuge habitat types (Figure 15). Whilst water quality in ark refuges is predicted to remain relatively high across phases, disco and polo club habitats are predicted to decrease in water quality following the cessation of flows over the *Resilience* phase (although some water quality impacts such as blackwater events can be expected to accompany flow (Kerr *et al.* 2013, McCarthy *et al.* 2014). Declining water quality through time is predicted, but not uniform for refuge types.

A key predicted difference between disco and polo club refuges during the *Resistance* phases will be the drivers of water quality collapse during the *Resistance* phase, with disco refuges drying more rapidly and suffering increases in water temperature and hypoxia prior to complete desiccation (Figure 15). For saline polo clubs, water level is rarely lost completely as water is maintained through saline groundwater inputs, leading to depth or salinity driven disturbance. For spring polo clubs, a similar pattern occurs with pool depth as the key driver of disturbance rather than water quality.

The impacts of extreme environmental harshness associated with these water quality declines though the *Dry* phase can present selective pressure on the inhabitant biota and variability in species tolerances can be conceptualised to drive the fish species likely to be present during across hydro-climatic phases. For example, in polo clubs, the abundance during the *Dry* phase is expected to be dominated by resistant species that possess relatively high tolerance for environmental impacts, whilst resilient species, with stronger traits for dispersal and population building will become increasingly dominant at these sites during the *Resilience* and *Wet* phases (Figure 16).

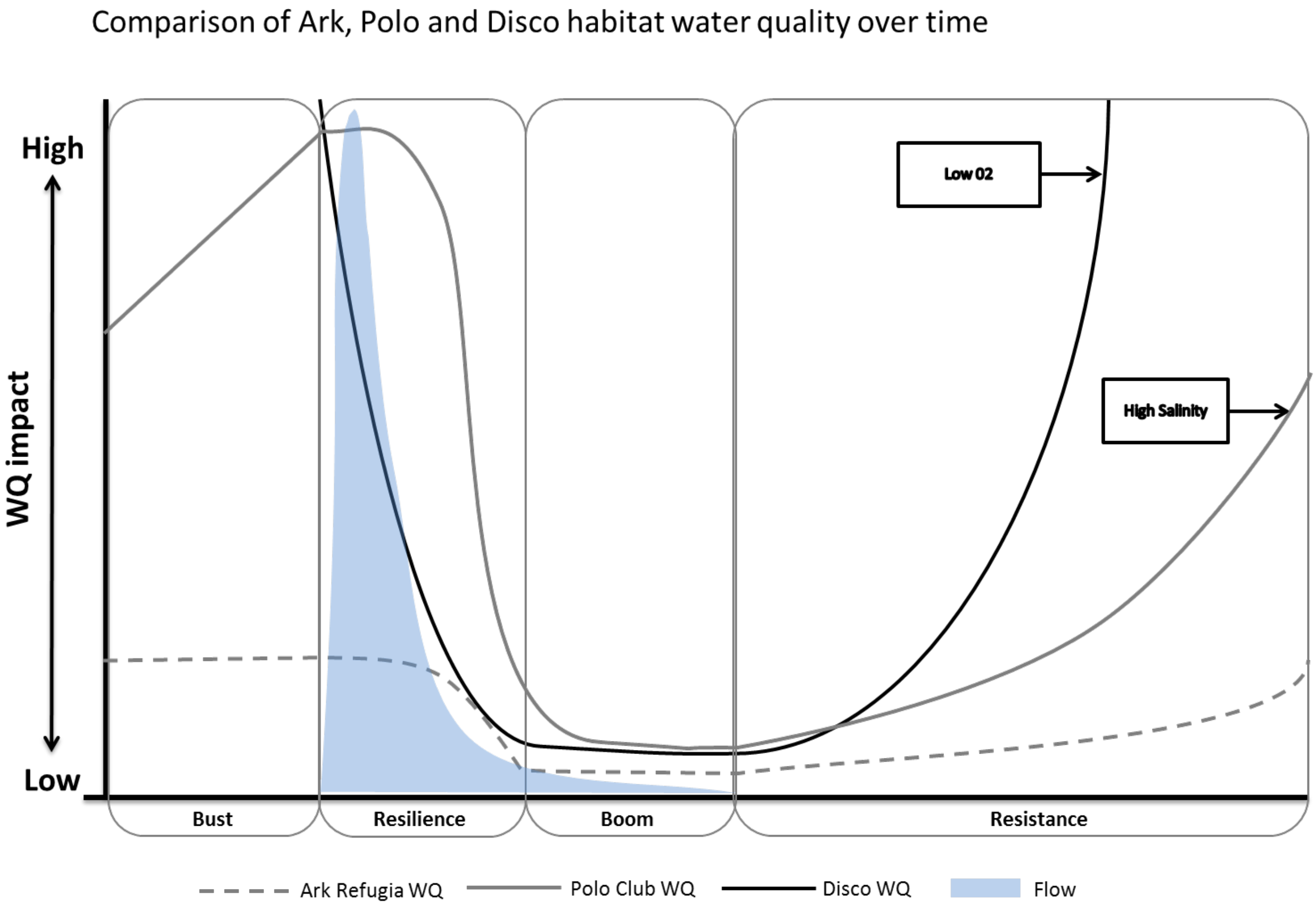


Figure 15. Conceptual model predicting variation in the water quality across refuge habitat types.

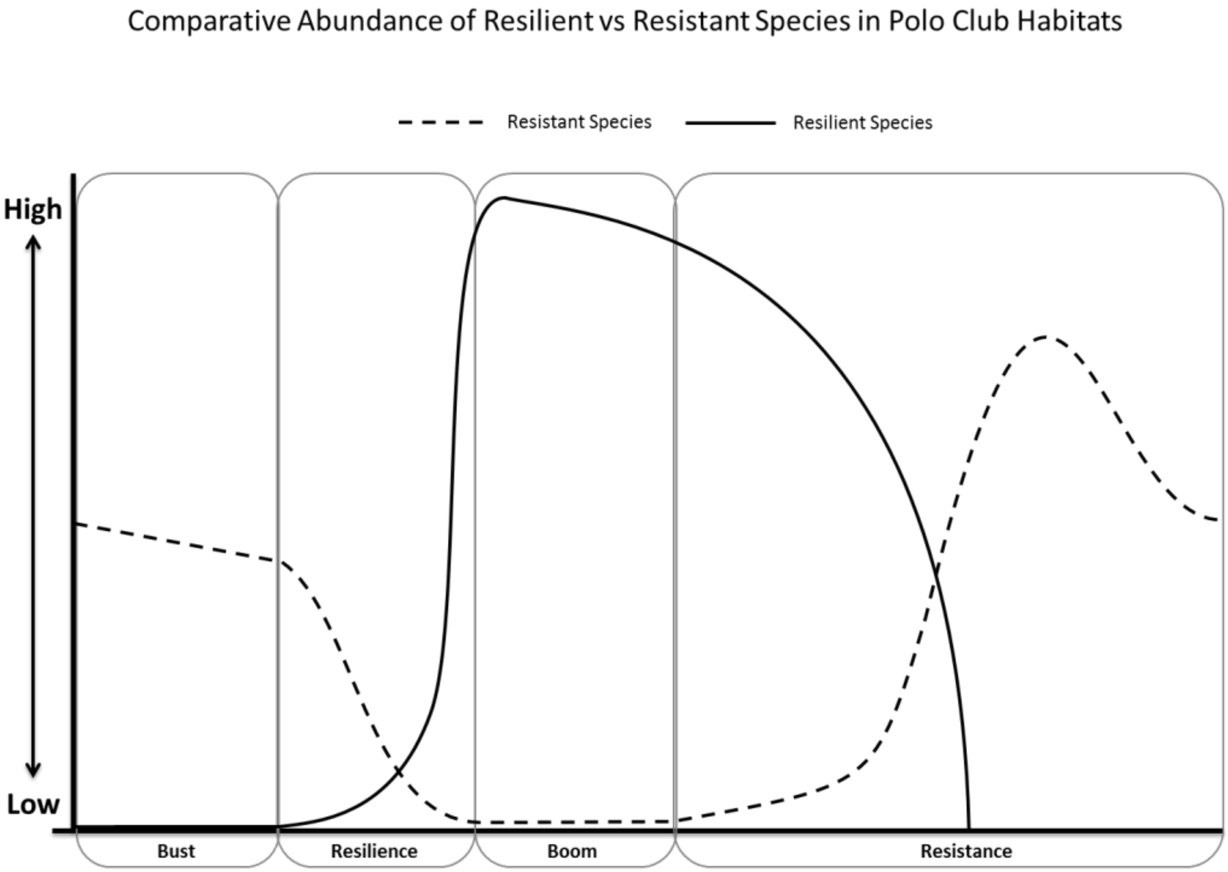


Figure 16. As water quality impacts increase in saline polo club habitats during the *Resistance* and *Dry* phases, habitats are predicted to be dominated by resistant species; conversely, resilient species are able to move in and dominate during the *Resilience* and *Wet* phases.

Resistance and the Loss of Species

Arthington *et al.* (2010) published a model of species turnover (Figure 17) from the Cooper catchment that focused primarily on the loss of species from waterholes with declining environmental conditions following a large flood year and entering into a period of supra-seasonal drying leading into a severe drought two years hence (Costelloe *et al.* 2004). This analysis therefore provides an effective model of species loss during the *Resistance Phase* (both seasonally and at a supra-season scale) and provides insight into the drivers of fish declines associated with large ark or disco waterholes during this phase.

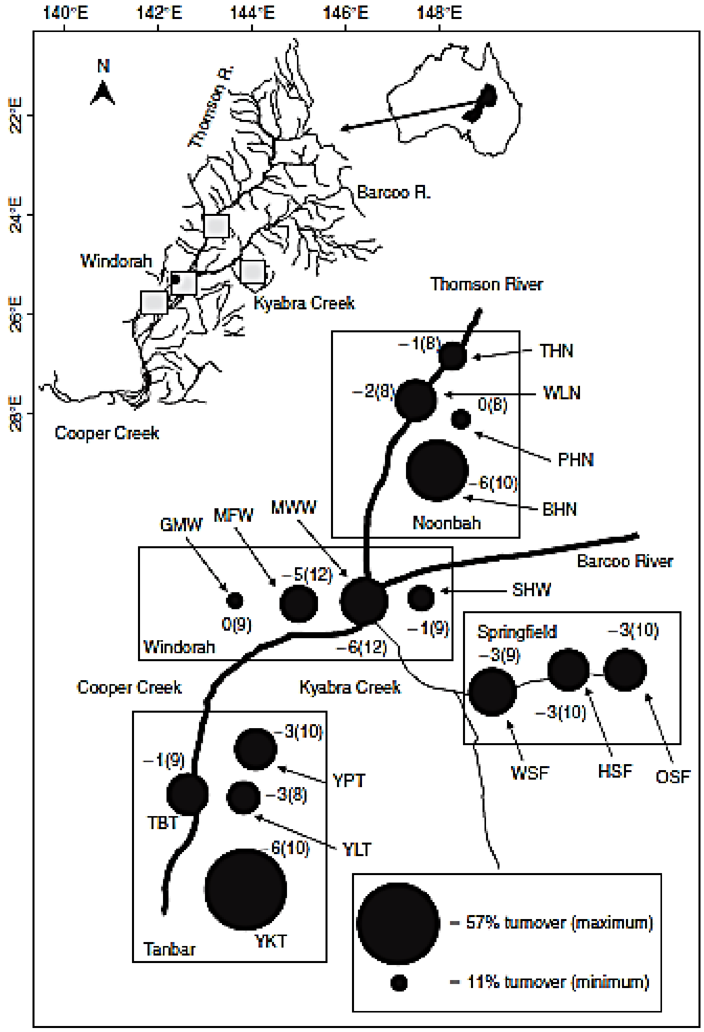


Figure 17. Analytical outputs showing the loss and gain of species during waterhole drying after cessation of floods in the mid-Cooper Creek. Figure reproduced from Arthington *et al.* (2010). Site codes: Noonbah reach: THN, Top; WLN, Waterloo; BHN, Bottom; PHN, Pelican; Springfield reach: WSF, Warrannee; HSF, Homestead; OSF, One-Mile; Windorah reach: MWW, Murken; SHW, Shed; GMW, Glenmurken; MFW, Mayfield; Tanbar reach: YKT, Yorakah; YLT, Yalungah; YPT, Yappi; TBT, Tanbar.

The loss of species in this example was attributed to a combination of water quality parameters and geomorphic variables, including decreases in water temperature, however there were no direct links made between individual species losses and intolerance of extreme water quality impacts (Arthington *et al.* 2010). Balcombe and Arthington (2009) noted Barcoo grunter, silver tandan and spangled perch with increasing pH in drying waterholes of the Cooper.

As a conceptual basis for setting hypotheses about the broad-scale gains and losses in species composition (assemblage change) for catchments and the Basin, the modelling of species turnover (Arthington *et al*. 2010) provides a sound approach for assessing the influence of hydro-climatic phase on fish assemblage structure at larger scales. Using the project database, this model can be expanded into a basin wide model and represented across phases, to represent both gains and losses at the catchment scale, and to investigate the drivers of these changes using environmental and trait data. This approach will enable the setting of expected appearances and disappearance of fish species from monitoring data as seasons and hydro-climatic cycles progress. However, drivers influencing these assemblage changes at such large spatial scales may be complex and difficult to generalise across reaches and catchments.

Resilience Mechanisms

Colonisation

Whilst it has long been acknowledged that dispersal ability and colonisation are key traits of biota in the Lake Eyre Basin (Williams 1985), fish as aquatic specialists do not have the inter-basin dispersal capabilities of many air or solid borne propagules. Instead the assemblage structure of fishes in the Lake Eyre Basin reflects the diminishing connectivity and dispersal opportunities afforded by the long-term drying to which the Basin has been subjected over past millennia (Unmack 2001, 2013) precluding transport by birds (*Pers.obs* McNeil) or via rains of fishes (Whitley 1970). The processes of recolonisation in freshwater fishes following disturbance is an ongoing area of interest to fish ecologists and managers, with large scale removal projects failing to detect variable recolonisation of reaches (Albenese *et al.* 2009) and some data is emerging from broad scale natural disasters such as bushfire (Lyon and O'Connor 2008). The extreme drying events observed in the central Lake Eyre Basin, however, provide catchment scale natural experiments where species are removed through drought perturbation and required to colonise from refuge habitats thousands of kilometers distant (McNeil *et al.* 2008, McNeil and Schmarr 2009, McNeil *et al.* 2011a, Kerezsy *et al.* 2013). Systematic colonisation of a previously dry reach following drought (McNeil *et al.* 2011a) provides a starting point for conceptualizing the likely relative colonisation strategies of fish species (Figure 18).

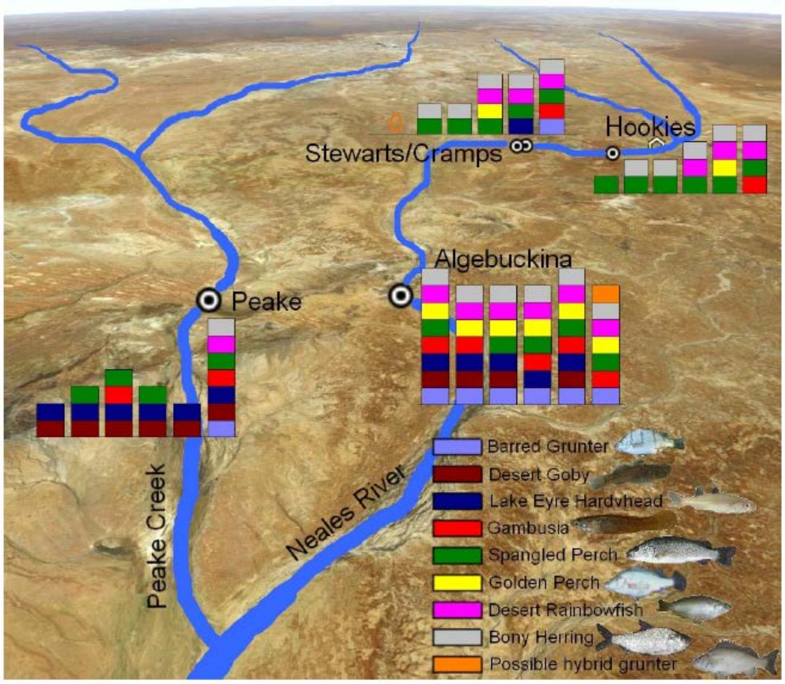


Figure 18. Conceptual model for variable upstream colonisation following drought. Results of a three year bi-annual survey of fish in the Neales River demonstrating the successive recolonisation of previously dry habitats via upstream migration from Algebuckina waterhole following resumption of flow. Figure reproduced from McNeil *et al*. (2011a).

Many aspects of colonisation have been discussed above in the context of the hydro-climatic model and the roles of the various refuge habitats in supporting ecological processes for fish. However, a brief recap of our conceptual understanding of colonisation processes and in particular, the understanding of comparative colonisation potential across species is warranted. Colonisation is a process central to the maintenance of population scale persistence and is intrinsically linked to the role of hydrological and habitat connectivity in driving ecological function and maintaining viable fish populations (McNeil *et al.* 2013b).

A number of species, in particular spangled perch and bony herring have been identified as extremely rapid colonisers and are predicted to be able to move into previously dry habitats within very short periods of in-channel and even localised flow (McNeil *et al*. 2008, Kerezsy *et al*. 2013). Colonisation movements of these species occur over inundated paddocks and into dams far from river channels, fuelling speculation of rains of fishes (Whitley 1970, Unmack 2001) and of aestivation and drought resistant eggs in native fish (Wager and Unmack 2000). In contrast, a number of species have been identified as very slow colonisers, with desert goby (McNeil and Schmarr 2009) the slowest to move. Intermediate colonisers include desert rainbowfish and golden perch at the rapid end, and barred grunter, *Mogurnda* spp., introduced goldfish and gambusia, at the slower end (McNeil *et al*. 2011a).

For some species, contradictory views have been presented, for example glassfish (*Ambassis mulleri*) have been described as both rapid (Kerezsy *et al.* 2013) and slow (Sheldon *et al.* 2010, Huey *et al.* 2011a, 2011b) colonisers. ARIDFLO found that they were intermediate colonizers, of the Coongie Lakes system following multiple seasons of large flooding (Costelloe *et al*. 2004). A conceptual prediction of relative colonisation speed is represented in the draft trait summaries provide earlier in Table 6 and 7 and an updated and comprehensive collation of trait data for all Lake Eyre Basin species is required to effectively analyse and predict the relative colonisation potential across species. Trait analysis will also be utilised to test for the presence of clades, or guilds of species that share similar movement strategies such as the *networkers* or *permanent refugial* groups predicted in Sheldon *et al.* (2010) (Figure 19). Trait analysis is likely to reveal further structure in the colonisation patterns of Lake Eyre Basin fishes.

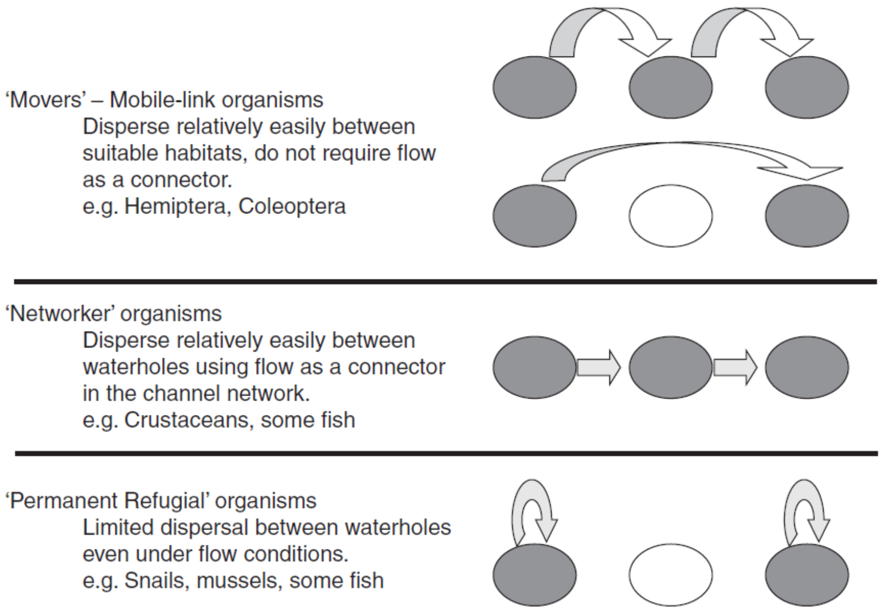


Fig. 2. Different dispersal strategies used by organisms in fragmented river landscapes. Waterholes denoted in grey contain water, whereas those in white are dry. Arrows depict movement of organisms within and among waterholes.

Figure 19. Sheldon *et al.* 2010 presented three dispersal classes for Lake Eyre Basin biota, two of which apply to fish species.

There have also been observations of different fish species dominating upstream and downstream colonisation events across the various catchment of the Lake Eyre Basin. Whilst the species summarised above largely relate to active upstream migration, species composition moving downstream into previously dry reaches on the head of floodwaters in the lower Cooper and Diamantina are very different to those predicted from upstream colonisation.

Species such as silver tandan and glassfish have been observed to dominate these downstream flood migrations in the Diamantina (McNeil *et al*. 2008, McNeil and Schmarr 2009) whilst resilient species such as spangled perch, bony herring and golden perch have been observed colonizing previously dry downstream reaches of the Cooper following drought (Schmarr *et al*. 2013). The long distance (200 km+) migration of a tagged golden perch in the lower Cooper following flows (Schmarr *et al*. 2013) validates the local scale patterns of the mid-Cooper floodplain (Balcombe *et al*. 2007) and genetic-based predictions (Musyl and Keenan 1992, Faulkes *et al*. 2010).

It is unknown how active and passive dispersal mechanisms are adopted nor to what degree stochastic and deterministic process influence catchment wide dispersal. No existing analyses or conceptualisation exist to differentiate between upstream and downstream colonising strategies of fishes from the Lake Eyre Basin. Trait collation and analysis coupled with analysis of data from newly inundated reaches where known refuges are located upstream or downstream should be undertaken to describe these processes and identify potential movement guilds for the first time.

An important aspect of the functioning of waterhole refuges is the connectivity between the river, waterholes and floodplain areas and the movement of fish into recently inundated floodplain habitats following high flows. During boom periods in the LEB, large areas of floodplain become inundated (Walker *et al*. 1995, 1997, Bunn *et al*. 2003) and become important habitats for fish to access food resources, grow rapidly and build resilient populations (Balcombe *et al*. 2005, 2007). Most species of fish move onto floodplains during inundation with multiple size classes suggesting spawning and recruitment in response to flows or flooding (Balcombe *et al*. 2005).

Spawning on a flood pulse facilitates the utilization of resources by juveniles as well as adults (Balcombe *et al*. 2007). However, few of the food sources consumed on floodplains are terrestrially sourced. Only spangled perch and desert rainbowfish have been found to consume terrestrially sourced food items as a small proportion of their diet (Balcombe *et al*. 2005, 2007, *in press*). Aquatic food resources derived from algal production during floodplain inundation dominate fish diets (Bunn *et al.* 2003, 2006a, 2006b) rather than allocthonous resources e.g. organic matter and sediment from a drainage basin (Balcombe *et al.* 2005). It is clear that floodplain inundation represents a significant increase in the habitat and resources available for fish species during the *Wet* phase. Additionally, floodplain connectivity is an important factor influencing fish assemblage of waterholes, throughout seasonal drying periods (Arthington *et al*. 2005).

Figure 20. Potential relationships between *β* and habitat availability. Solid line = inverse proportional, dotted line = negative linear.

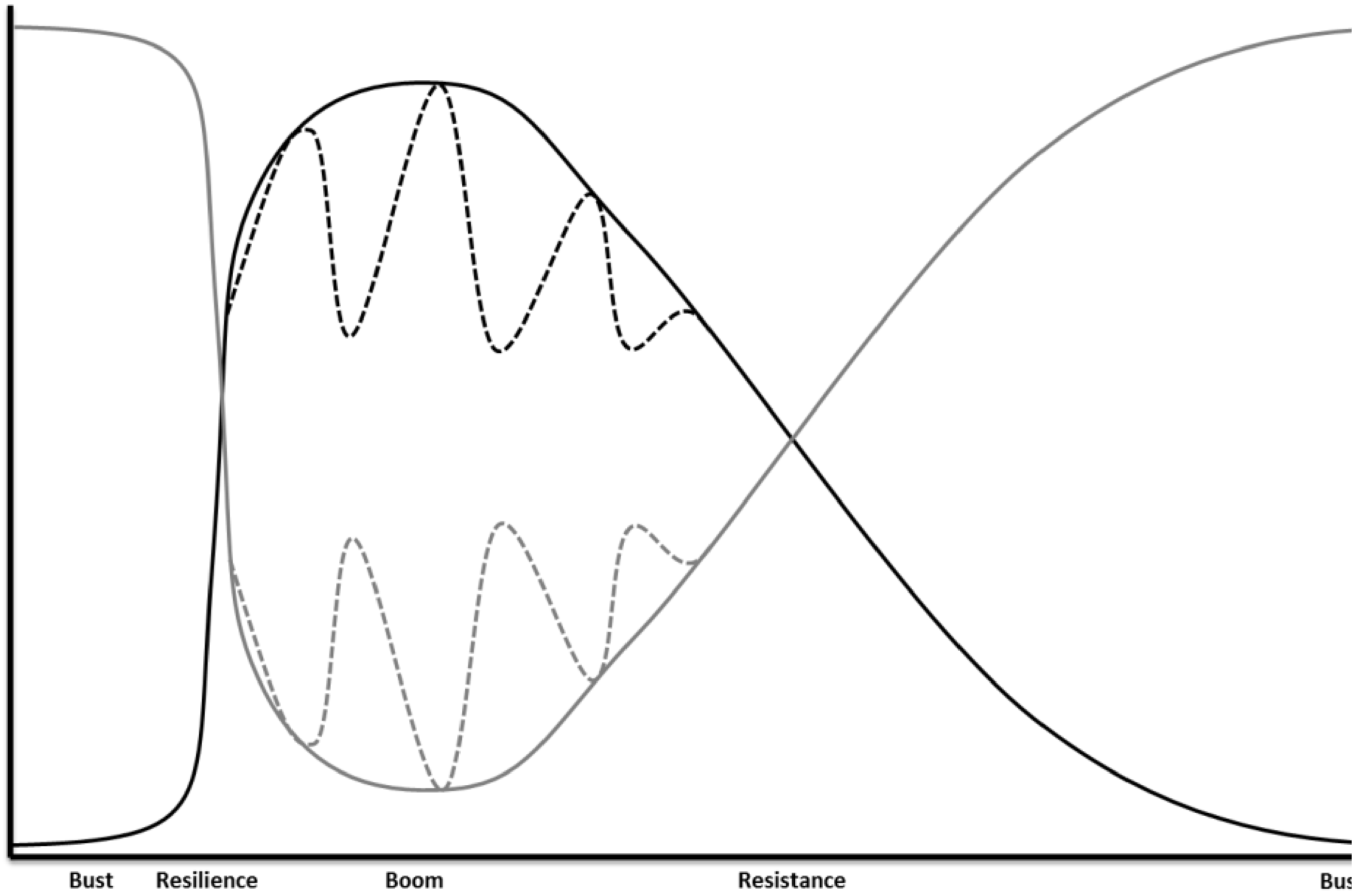


Figure 21. Expected relationship between *β* (grey line) and habitat availability (black line) over a complete hydro-climatic cycle. Dotted lines indicate period of supra-seasonal inundation through multiple wet seasons.

Box 1. Habitat availability vs β

There are two premises driving this conceptual model. First, that habitat heterogeneity drives high beta –diversity (β), and second, that drying of habitat drives increased habitat heterogeneity through diversifying WQ and structural conditions in remaining waterholes.

This leads to a basic hypothesis for this conceptual model that β has a negative relationship with habitat availability. Thus, the more habitat becomes available during and after flooding, the more fish assemblages in each habitat homogenise (i.e. all waterholes have the same species).

A similar relationship has been established between β and flow variability for fishes (Horwitz 1978), and β and habitat heterogeneity for macroinvertebrates (Astorga et al 2014). We expect that the nature of the relationship may be inverse proportional or negative linear (Figure 20).

We would expect that during long periods of disconnection under the *Dry* phase, the availability of habitats will decrease to a very low number with very large differences in WQ and structure between those habitats (Figure 21). This will in turn drive large differences in the fish assemblages between habitats (increase in β).

As floodwaters inundate the system the number of habitats increases dramatically, while the floodwaters will also enable species to disperse throughout the system which homogenises the assemblage at any given habitat (decrease in β).

Assemblages will eventually reach a point during the *Wet* phase where there will be a high degree of homogeneity. If the system receives multiple flows in subsequent seasons, we expect that the habitat availability and β will fluctuate accordingly (dotted lines in Figure 21).

When the system inevitably starts to dry (entering the *Resistance* phase), the number of habitats will begin to decrease and those remaining habitats will diverge from each other in WQ and structure. This divergence will drive differences in fish assemblage resulting in β returning to peak levels in the ensuing *Dry* phase.

Recruitment

The ability for fish to successfully spawn and recruit juvenile fishes into the adult reproductive population is a fundamental necessity for the viability of fish species. Of all of the ecological processes relating to the sustainability of fish, the regular occurrence of spawning and recruitment is most important. However, the steps involved in the regular occurrence of recruitment are complex and easily disturbed by anthropogenic modifications of hydrology and habitat.

The process of recruitment requires that appropriate cues in water temperature, flow and barometric pressure are sufficient to induce the development of reproductive tissues (ovarian and testicular development) which in turn depend upon the physical condition and health of individual fish having been sufficiently resourced to enable gonadal development in response to cues. The process subsequently requires that spawning cues bring male and female fish together and that access to spawning habitats (often requiring connectivity via channel flow or inundation) and the condition of spawning habitats (such as rocky interstices, hollow logs, macrophyte beds or riffles) is adequate. The work of Balcombe *et al.* (2005, 2006, 2007, 2014, Balcombe and Kerezsy 2009 and Kerezsy *et al*. 2011) has produced a baseline of knowledge around the recruitment and juvenile fish distributions for a range of Lake Eyre Basin species during periods of floodplain inundation, low flow and no flow in central and western Queensland. Kerezsy *et al*. (2011) identify a number of spawning strategies for Lake Eyre Basin fishes, describing most species as either continual or seasonal no-flow recruiters, whilst Hyrtl's tandan, Barcoo grunter and Welches grunter exhibit flow-dependent recruitment. Glassfish and spangled perch exhibit flexible recruitment strategies (Figure 22a).

Once spawning is successfully completed, conditions must develop to support the survival of larvae. Following yolk absorption, larvae must have access to adequate supplies of food resources (including phytoplankton and zooplankton) and subsequently avoid becoming a food item themselves before locating appropriately secure habitats and food resources to grow to adult size. This outline demonstrates the complexity of the interacting and cumulative factors that are required for successful recruitment. As such, recruitment reflects the hydrological and water quality condition of aquatic habitats for young fish as well as the availability of resources and habitats for adult survival, condition and larval and juvenile development.

Recruitment has also been a central component in a range of monitoring and assessment projects from sites across the Basin (Costelloe *et al.* 2004, McNeil *et al.* 2008, 2011, McNeil and Schmarr 2009, Schmarr *et al.* 2013, Cockayne *et al.* 2012, 2013, Sternberg *et al.* 2014, Mathwin *et al*. 2015). These classifications, presented in Figure 22b, differ somewhat from those of Kerezsy et al. (2011). An objective of analysis of these conceptual models should be undertaken to develop a single, basin wide or catchment specific model of flow-recruitment relations. The spatial location of spawning and recruitment habitats has not been assessed at the Basin scale and data analysis may reveal differences in the spawning and recruitment patterns for species across various catchments and river reaches.

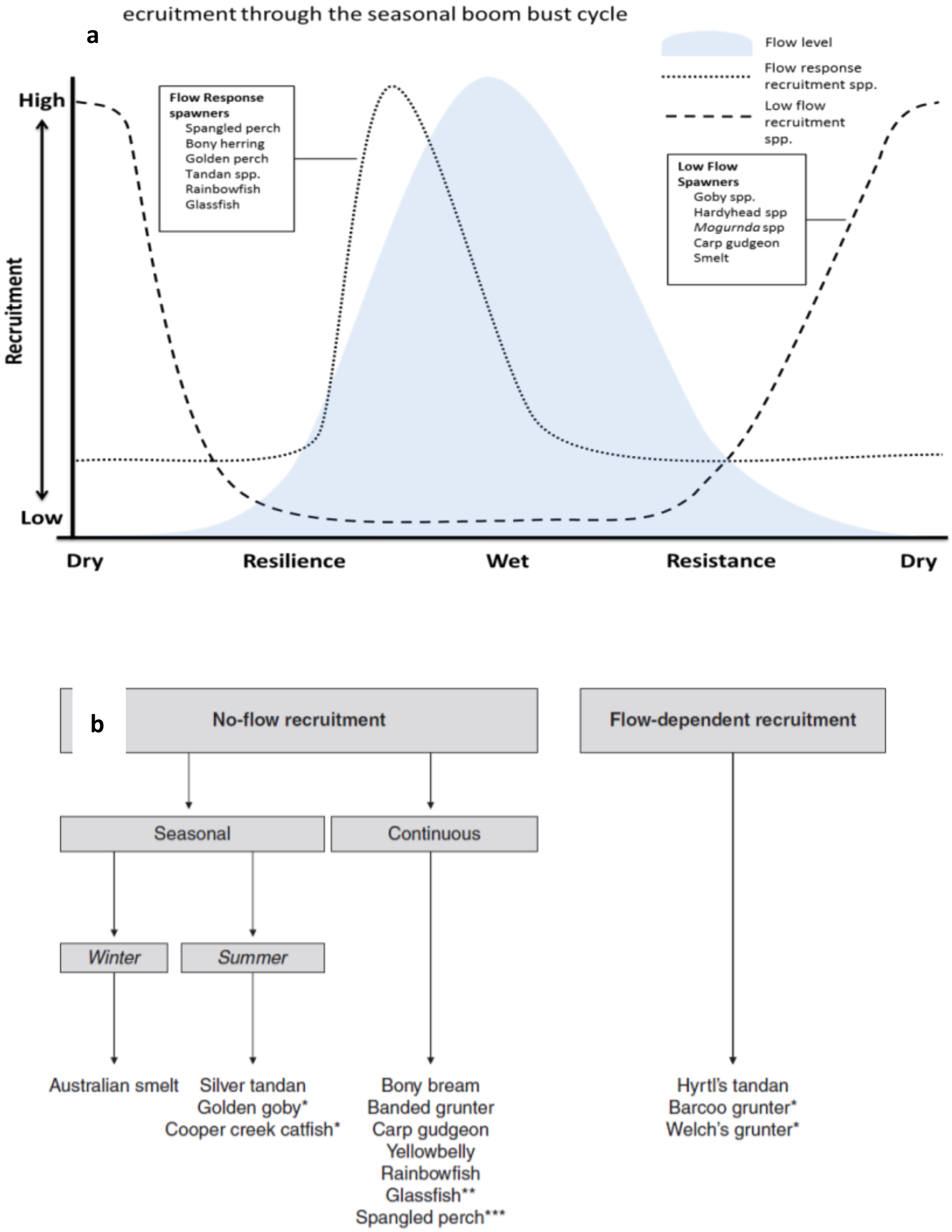


Figure 22 Conceptual models outlining predicted recruitment patterns in the LEB; a: across the hydro-climatic cycle for a selection of species hypothesised to be flow response or low flow spawners summarised from (McNeil *et al*. 2008, McNeil and Schmarr 2009, McNeil *et al*. 2011, Cockayne *et al*. 2012, 2013, Schmarr *et al*. 2013, Sternberg *et al*. 2014). b: Conceptual model of flow-based recruitment guilds from the Queensland LEB. * indicates <200 fish sampled, **indicates species demonstrating flow response and no flow recruitment, * indicates species recruiting under all conditions. Figure reproduced from Kerezsy *et al.* (2011).**

Assemblage Structure

Resistance and resilience mechanisms facilitate the dispersal and persistence of fishes based on their relative biological traits. These complex ecological interactions of environmental and biotic control eventually determine the distribution of species across the Basin. Assemblage structure, is therefore one of the primary lenses through which the cumulative influence of ecological processes can be viewed. Accordingly, assemblage structure is one of the most powerful indicators of ecological function and is the principal indicator for reporting on ecosystem condition and health (Jackson *et al.* 2001).

Ark Refuge Assemblages

Fish assemblages tend to become homogenous across waterholes during wet periods as fishes are able to move freely between refuge waterholes through networks of aquatic connectivity (Balcombe *et al*. 2007, McNeil and Schmarr 2009, Sheldon *et al.* 2010). However, this is not always so, with ARIDFLO data showing that during extended connectivity over three years, *Wet* phase assemblages in Coongie Lakes continued to be dynamic (Puckridge *et al*. 2010).

In general, the effective mixing of fish populations in the LEB tends to be strong within catchments but weak across catchments (Musyl and Keenan 1992, Huey *et al.* 2006, Hughes and Hillier 2006, Faulkes *et al.* 2010, Huey *et al.* 2011a, 2011b) suggesting that whilst fish can move freely across connected waterbodies during wet periods, significant barriers to regular dispersal exist between catchments, most likely due to the geomorphic, environmental and hydrological conditions in Lake Eyre that do not support free movement of fish from one catchment to the other (Unmack 2001). Furthermore, this pattern is not consistent across fish species with some species dispersing regularly across connected waterholes (e.g. Hyrtl's tandan, silver tandan, bony herring and Australian smelt) whilst others are more highly structured within catchments, with less dispersal between refuge waterholes during connectivity (e.g. desert goby, glassfish) (McNeil *et al.* 2008, Kerezsy *et al.* 2013, Huey *et al.* 2011a, 2014).

This cross waterhole colonisation is also played out at larger spatial scales in arid catchments of the LEB where networks of permanent refugia do not exist. In the Neales River, rapid colonisers (spangled perch, bony herring, desert rainbowfish) move out of ark refuges to recolonise previously dry catchment habitats immediately following post drought connectivity, whilst slower colonisers took more than one season (gambusia, LEB hardyhead, golden perch) up to several seasons (desert goby, barred grunter) of connectivity to recolonise from ark refuges (McNeil *et al.* 2008, McNeil and Schmarr 2009). This suggests that the catchment position of refuges is likely to be important as well as their persistence.

Consistent with this pattern, fish in the Macumba River recolonise from permanent refuges in the Diamantina/Warburton catchment at predictably variable rates with spangled perch, bony herring and desert rainbowfish present in the upper tributaries following post drought connectivity and intermediate colonisers (golden perch, glassfish, Hyrtl's tandan, silver tandan, Barcoo and Welch's grunter only able to move into the lower reaches of the catchment during the same period of flow (Cockayne *et al.* 2012, 2013). These patterns are supported by Kerezsy *et al*. (2013) showing that fish moving from the same region in the lower Diamantina/Warburton into the dry Eyre Creek/Mulligan river catchment following catchment-scale drying. In the Mulligan spangled perch, bony herring and desert rainbowfish moved into upper catchment waterholes joined by glassfish and silver tandan and, *Hyrtl's* tandan, golden perch, Barcoo and Welch's grunter, golden perch and golden goby (*Glossogobius aureus*) in the mid to lower reaches following connectivity.

Polo Club refuge Assemblages

Saline polo clubs are defined by their saline conditions during the *Resistance* and *Dry* phase of the hydro-climatic model, however, these same habitats will become fresh during rainfall driven flow events and therefore do not function as polo clubs necessarily during *Resilience* or *Wet* phases– instead they serve as disco habitats for freshwater species to utilise (potentially feeding on the Polo Club members). Therefore, during periods of freshwater flows, salinity should drop and saline tolerant species should decrease in abundance, and move to other areas. New species should appear during the *Resilience* Phase (moving to a disco assemblage and eventually ark during the *Wet* phase), but after the cessation of fresh inflows the Resistance phase should eliminate non tolerant biota in a predictable pattern dependent on physiological tolerance mechanisms. Booms in saline invertebrate biota often occur following the loss of intolerant fish and subsequent booms in hardyhead and goby should follow.

The successional pattern for polo club refuges has not been demonstrated to be linked to food-web interactions (e.g. fresh fish consuming members, invertebrates utilising dead fresh fish, members utilising invertebrates), nor has the systematic loss of species been linked to tolerance thresholds. The end points for saline polo clubs are desiccation (in which case desert goby will be the last taxa present) or hypersalinity (in which case Lake Eyre hardyhead (juveniles) will be the last species present. Hypersaline pools can no longer support fish but may make up large sections of remnant aquatic habitat during *Dry* phase. Saline polo clubs should demonstrate the full cycle of boom and bust as harsh environmental drivers govern during the dry period and biotic phases govern during the *Wet* phase.

Spring polo clubs are far more stable with the vast majority of GAB springs dominated by a single species, the desert goby. Other springs have been invaded by- or had gambusia introduced into them and although a period of co-existence was reported, eventually gambusia became the only species recorded in these springs (McNeil and Costelloe 2011, McNeil 2012, Kerezsy and Fensham 2013). A smaller number of springs occur low down in the floodplain or river channel and these habitats often possess a wide range of small bodied fishes and may be expected to have all small bodied species from the catchment present at some stage (McNeil *et al.* 2011a). The assemblage of spring polo clubs is limited not by water quality but rather by depth and available habitat, being shallow and having wetland areas largely controlled by vent flow outputs although some sites (e.g. North Freeling Spring) have larger wetlands maintained by fluvial influences due to their position in the river valley (Wakelin-King 2011).

Disco Refuge Assemblages

The assemblage structure of Disco refuges is driven primarily by recolonisation following drought. Conceptually, species will recolonise previously dry reaches based on their capacity for upstream or downstream dispersal. Following drought in the upper Neales River, a series of disco waterholes were systematically colonised by rapid, moderate and slow moving species over consecutive seasons of seasonal flow connectivity. Rapid colonisers, spangled perch, desert rainbowfish and bony herring rapidly recolonised all waterholes immediately after reconnection, producing multiple size classes and utilizing invertebrate resources that were abundant during the 'fishless' phase prior to refuge reconnection (McNeil *et al.* 2008).

As such, these waterholes are likely to provide similar resource access and resilience building benefits as do floodplain areas in larger rivers (Balcombe *et al*. 2005, 2007). However, slower colonisers (golden perch, barred grunter, hardyhead, gambusia) are forced to move into habitats with already established multi-age class populations of rapid colonizing species. Whilst this could be a disadvantage in regard to interspecies competition for resources, the situation may provide a significant benefit to slower colonisers in the form of prey resources. In the case of the pest gambusia, having well established multi-generational assemblages established before they can colonise will add to the resistance potential of habitats to invasion and domination by this pest species (Moyle and Light 1996, Costelloe *et al*. 2010). As all species except bony herring are carnivorous, a move into a disco waterhole already teeming with larval and juveniles of the rapid colonists could result in access to a resilience building food resource from which their own population can be built.

During the *Resistance* phase, assemblage structure in disco waterholes should be structured via the relative tolerances or resistance strategies possessed by fish species. Trait analysis can be undertaken to build a model of expected assemblage responses to key drought impacts such as desiccation and changes in temperature, dissolved oxygen, and salinity. Conceptually, desert gobies are hypothesised to be most tolerant to desiccation (McNeil *et al.* 2011a) and spangled perch are also believed to be able to persist for some time in wet mud (Davis *et al.* 2013a); large bodied pelagic species such as bony herring, golden perch and grunters are likely to be least resistant. Hypoxia and high water temperature are also likely to play significant roles in structuring disco fish assemblages during drying (McNeil and Closs 2007) although little data exists for LEB species. Tolerance information can however be modelled using the water quality conditions from which fish have been recorded (Arthington *et al*. 2010, McNeil *et al*. 2013c).

As no LEB fishes have desiccation resistant life stages (Wager and Unmack 2000) total desiccation leads to the loss of all fish species. Local rainfall events have been observed to fill networks of disco refuges, but without connection to permanent source refugia, these waterholes will remain fishless becoming dominated by macroinvertebrates such as yabbies (*Cherax* spp.) and shrimp (*Macrobrachium* spp., *Paratiya* spp., *Caradina* spp.) (McNeil *et al.* 2008).

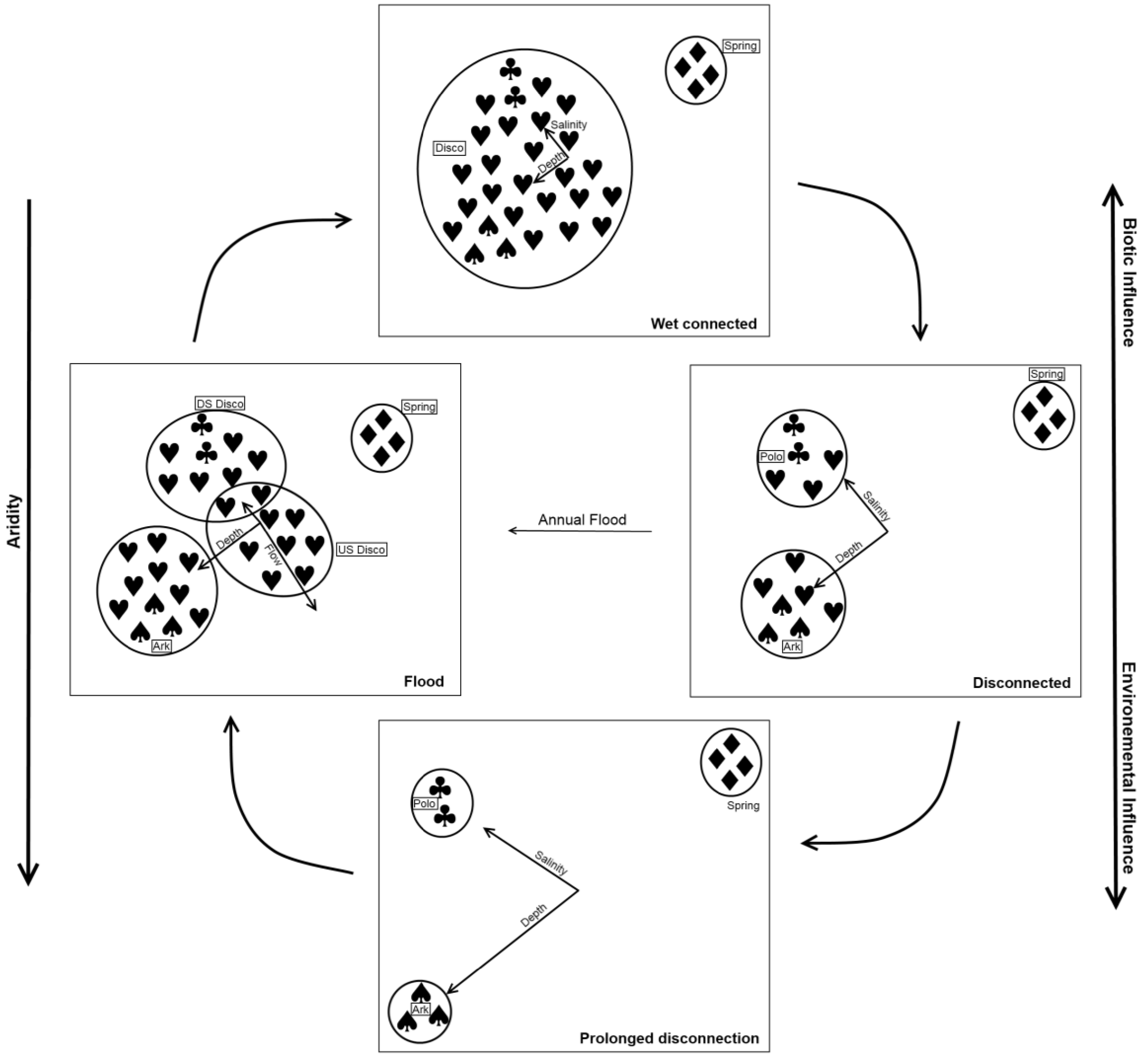


Figure 23. Conceptual model showing hypothesised assemblage changes across refuge types associated with phases of the hydro-climatic model. Based on the hypothetical assemblage model of Sheldon *et al.* (2010)

Box 2. Refuge assemblage dynamics conceptual model

This conceptual model (Figure 23) presents a series of hypothetical NMS plots with the predicted response of fish assemblages to a cycle of climate and hydrological conditions. The model can be tested by entering the fish and water quality data that we now have for the whole of the LEB at various phases in the hydro-climatic cycle. The basis for the model comes from Sheldon *et al.* (2010).

Springs should remain stable through the entire cycle. Some springs may connect to the river occasionally but are often unsuitable for other species to colonise.

After a prolonged period of disconnection, we would expect only a few waterholes to remain. These would be divided into two types of waterholes. Ark waterholes would have all of the species expected for the catchment and are primarily influenced by depth which is a function of longevity. Polo club waterholes would contain only species highly resistant to salinity, but they are also partly influenced by depth (i.e. they must last long enough to be maintained by the next flow).

At the commencement of a flood, a large number of waterholes become viable again. Ark waterholes will retain the species that exist there although at much lower densities than pre-flood. Newly created waterholes upstream and downstream will become disco habitats for species to colonise and utilise for spawning and recruitment. Disco habitats downstream of arks will be colonised mostly by fish with weaker rheotaxis. Disco habitats upstream of arks will be colonised by strong swimmers.

After prolonged period of connectivity, most habitats should have homogeneous fish assemblages. Differences between assemblages should relate to species dominance as a result of site-specific habitat influences.

As the system becomes disconnected, the increasing influence of environmental variables will drive changes in fish assemblages towards ark refugia assemblages, polo club assemblages or waterholes will dry completely. In the event that flows occur annually or more frequently, the cycle misses the prolonged period of disconnection and passes back through the flood and connected phases.

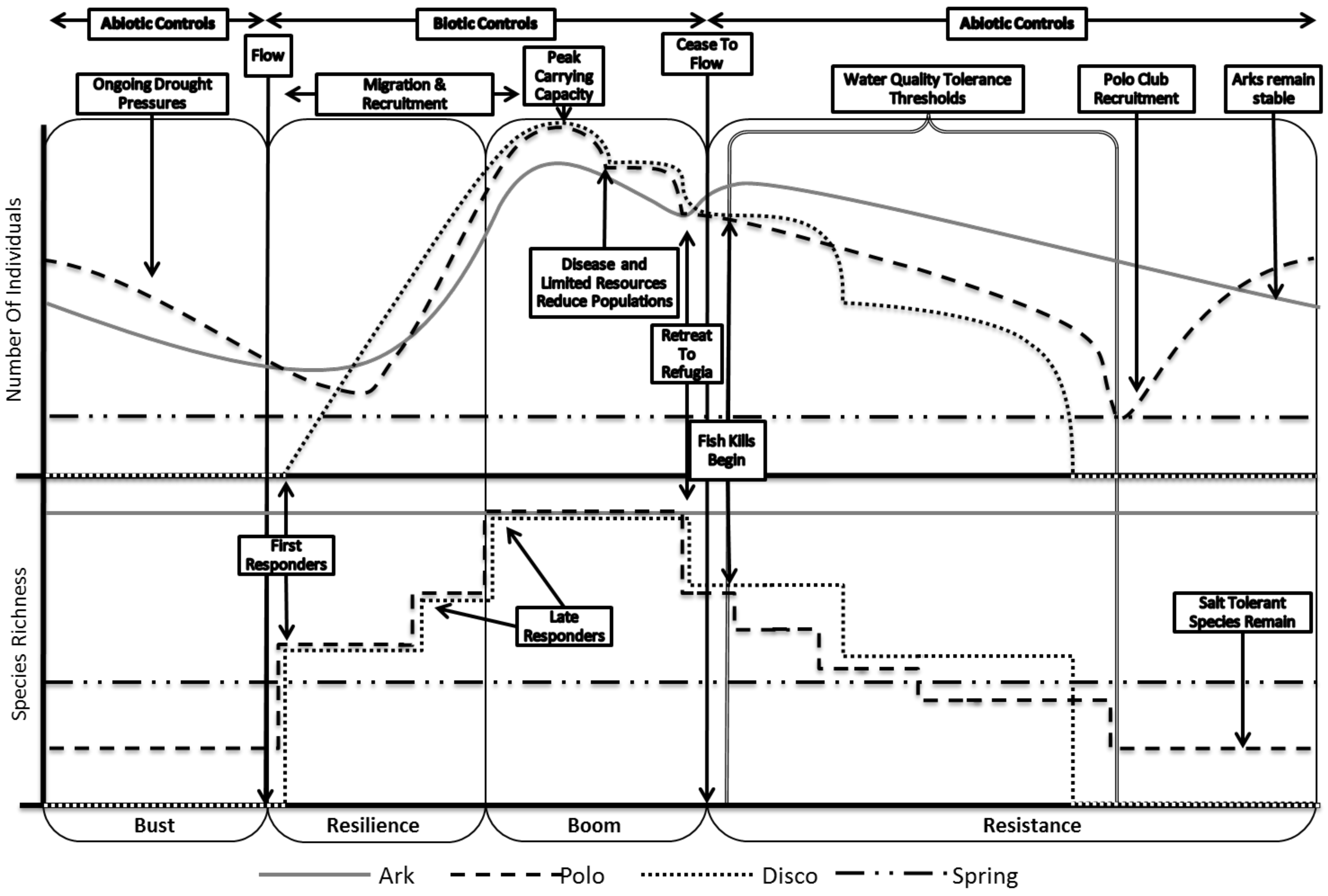


Figure 24. Conceptual model of successional changes in fish community abundance (top) and composition (bottom) within various habitat types over a boom-bust cycle

Box 3. Successional changes in fish communities

The conceptual model of fish community responses to the hydro-climatic regime (Figure 24) integrates several key components from conceptual models established in this report. The model shows the temporal response by the entire fish community within the catchment to the boom-bust hydro-climatic regime. The model incorporates biotic and abiotic factors to predict a net effect on the fish community. The model is informed by trait based responses to the hydro- climatic regime (Figure 27 and 28).

Ark habitats are predicted to support all species expected in the catchment throughout the hydro-climatic regime. Abundance is predicted to increase greatly through migration and recruitment during the resilience and boom phase, then gradually decrease under increasing drought pressure during the resistance and bust phase. This type of habitat is predicted to sustain species diversity and viable populations throughout the regime.

Polo club habitats are predicted to maintain a few species (gobies and hardyhead) that are highly resistant to decreasing water quality (salinity) during the resistance and bust phases, but will play a similar role to disco habitats during resilience and boom phases. At the onset of flow, these habitats rapidly become freshwater habitats and accumulate species based on the resilience traits of the species arriving from ark refugia upstream or downstream.

Near the end of the boom period, all species in the catchment are likely to be in these habitats, but diversity and abundance of most species are predicted to decline from this point on through retreat to deeper refugia and then declining water quality. As water quality changes over the Resistance phase, salinity resistant species are predicted to become dominant and increase abundance until water quality begins to approach critical thresholds for these species.

Disco habitats are by definition ephemeral habitats in this model. Under bust conditions, they will be completely dry and only become habitats at the onset of flow. As with polo clubs, these habitats rapidly become fresh at the onset of flow, and accumulate species (systematically based on the resilience traits of the species) arriving from ark refugia upstream or downstream.

Disco habitats are predicted to provide conditions for extremely high recruitment. Near the end of the boom period, all species in the catchment are likely to be in these habitats, but diversity and abundance of most species are predicted to decline from this point on through retreat to deeper refugia, then declining water quality and ultimately complete drying.

As predicted in previous models, GAB springs are expected to be stable throughout the hydro-climatic regime unless they are located within the floodplain or river channel.

Abundance

As with the drivers of fish assemblage structure, resistance and resilience mechanisms facilitate fish abundance in arid rivers based on their relative biological traits, with increased role of biotic controls determining the magnitude of fish abundance. High abundance is the result of successful spawning and recruitment, followed by high juvenile survival and then high adult survival and growth. Larval, juvenile and adult survival are dependent upon adequate food resources being available for each life history stage at the right time as well as avoiding predation by fish and other predators. Food availability is a direct result of the productivity in the system which is a complex outcome of nutrient input, climate, hydrology and stream morphology.

Ultimately, productivity is a limiting factor for the abundance of species across the Basin. Abundance is therefore another robust indicator for reporting on ecosystem condition and health. Primary productivity is controlled in part by the amount of nutrients brought into the system from sources upstream and from the floodplain (Figure 25), which in turn places a limit on the maximum carrying capacity of the system. This is then reflected in patterns of abundance.

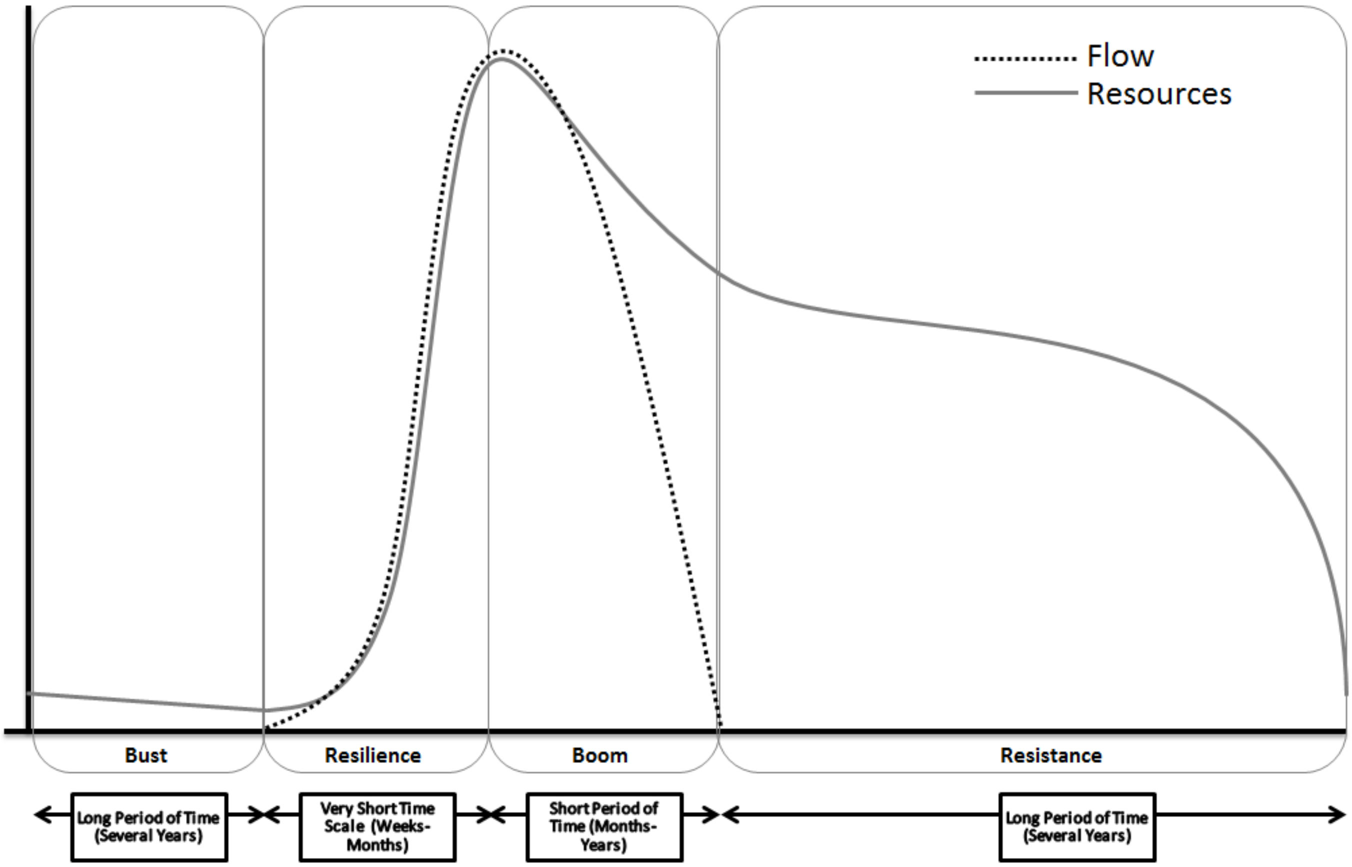


Figure 25. Conceptualised relationship between flow and resource productivity across hydro-climatic cycles.

The relationship between flow, carrying capacity and abundance is conceptualised in Figure 26. During the *Dry* phase, carrying capacity is low and corresponds with low abundance. The onset of flow in the *Resilience* phase introduces large amounts nutrients to the system (Balcombe *et al.* 2007), which increases the theoretical carrying capacity to a peak during the *Wet* phase. There is a delay between the input of nutrients and the utilization of primary productivity to reflect increases in fish abundance. ARDIFLO identified a ramping up of total abundance with successive flood pulses during an extended *Wet* phase in the Coongie Lakes (Costelloe *et al.* 2004, Puckridge *et al.* 2010) suggesting that large scale, supra-seasonal *Wet* phases may be important for building abundance driven resilience over and above what can be achieved during seasonal or smaller scale wet periods. The importance of algal derived primary productivity in supporting Cooper creek waterhole assemblages has been well established (Bunn *et al.* 2003, 2006a, Burford *et al. 2008*, Fellows *et al.* 2009)

At this point, fish abundance booms and may overstep the carrying capacity of the system leading to a rapid decline in abundance due to mortality from starvation and predation. From the end of the *Wet* phase, nutrients will gradually be entrained into the system with the carrying capacity declining accordingly, followed by fish abundance. Eventually the system will reach the stable state encountered during the *Dry* phase.

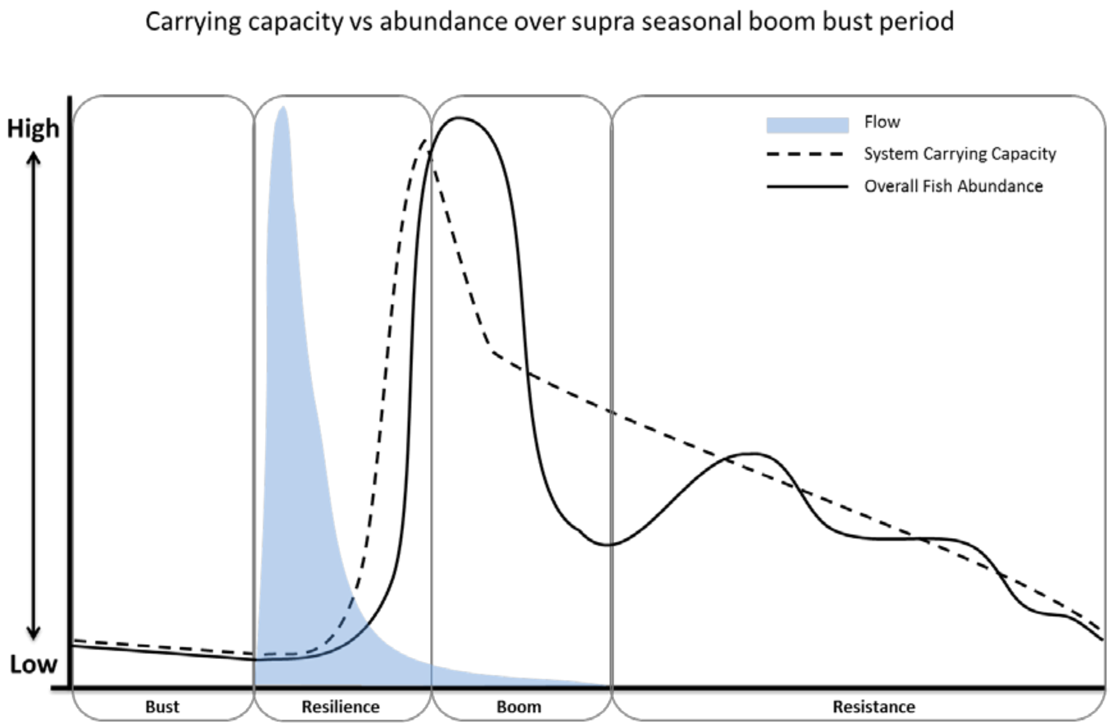


Figure 26 Conceptual relationships between carrying capacity and abundance of fish across supra-seasonal hydro-climatic cycles.

Ark refuge abundance

Due to the deep, stable and permanent characteristics of ark refugia, changes in abundance are less volatile than in polo club and disco refugia (see Figure 24). Increases in productivity drive increases in abundance, but the decreased reliance on an extensive floodplain in these refugia limits the productivity associated with high surface area shallow habitats. During the boom period, ark habitats have a fairly homogenous and stable fish assemblage and abundance. In the ensuing *Resistance* and *Dry* phases, abundance declines slowly with decreasing water levels. Abundance of some species will fluctuate with the onset and cease to flow with fish migrating out and then retreating to ark refugia.

Polo club refuge abundance

Fish species' resistance traits will determine the presence and abundance in polo club refugia during the *Dry* and *Resistance* phases (Figure 27). In highly saline conditions during the *Dry* phase, only hardyhead and gobies will survive, with both species maintaining high abundance. At the onset of flow, the abundance of resistant species will decline dramatically due to displacement, while resilient species will take over and become highly abundant (Figure 24, 27). During the *Boom* period, resilient species abundances will reflect those in disco habitats as the water quality conditions will be similar (Figure 24, 27). From cease to flow, polo club refugia will gradually increase salinity to the extent that resilient species abundances decline as they reach salinity thresholds (Figure 27).

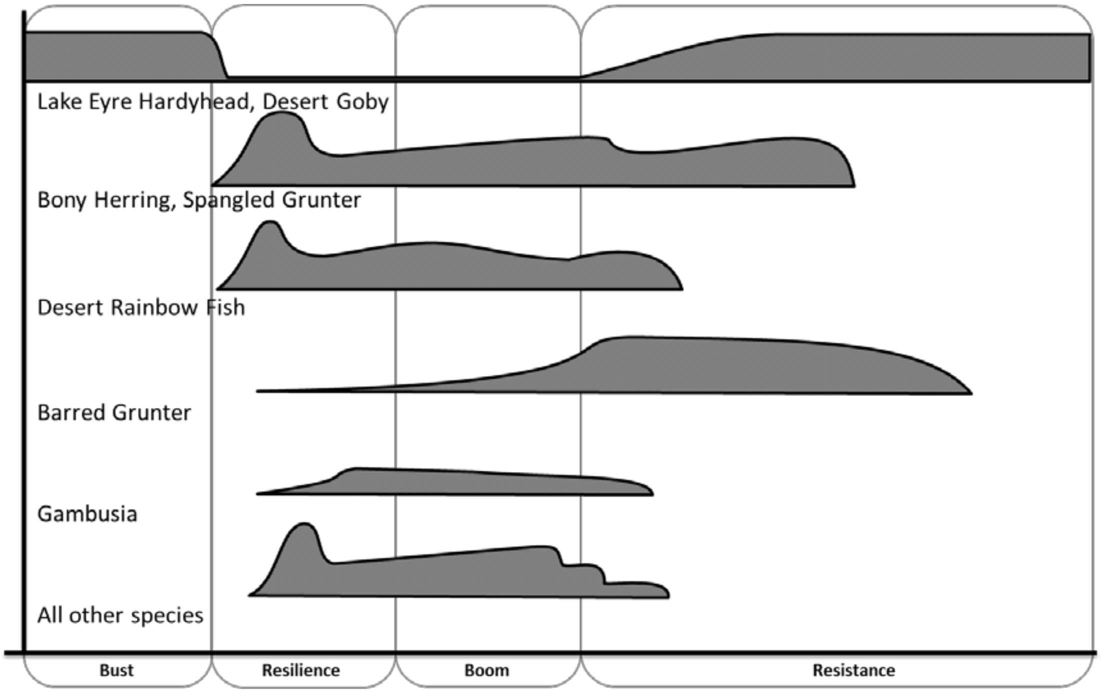


Figure 27. Conceptual model of trait based abundance responses to the hydro-climatic regime within saline Polo Club habitats, using a modified Gantt chart format.

Disco refuge abundance

By definition, disco habitats completely dry during the *Bust* phase. At the onset of flow, resilient species move into the freshly inundated Disco habitat and utilise these high productivity waters by rapidly spawning and recruiting resulting in a dramatic increase in abundance (Figure 24 and 28). After the initial explosion in abundance, disease and resource limits can cause a decline in abundance. Some species will retreat to deeper refugia causing further decreases in abundance. At cease to flow abundance will begin to decline with resource availability (Figure 24). In deeper Disco refugia, most species will continue to spawn and recruit seasonally until water quality declines past tolerance thresholds or the refuge dries completely (Figure 28).

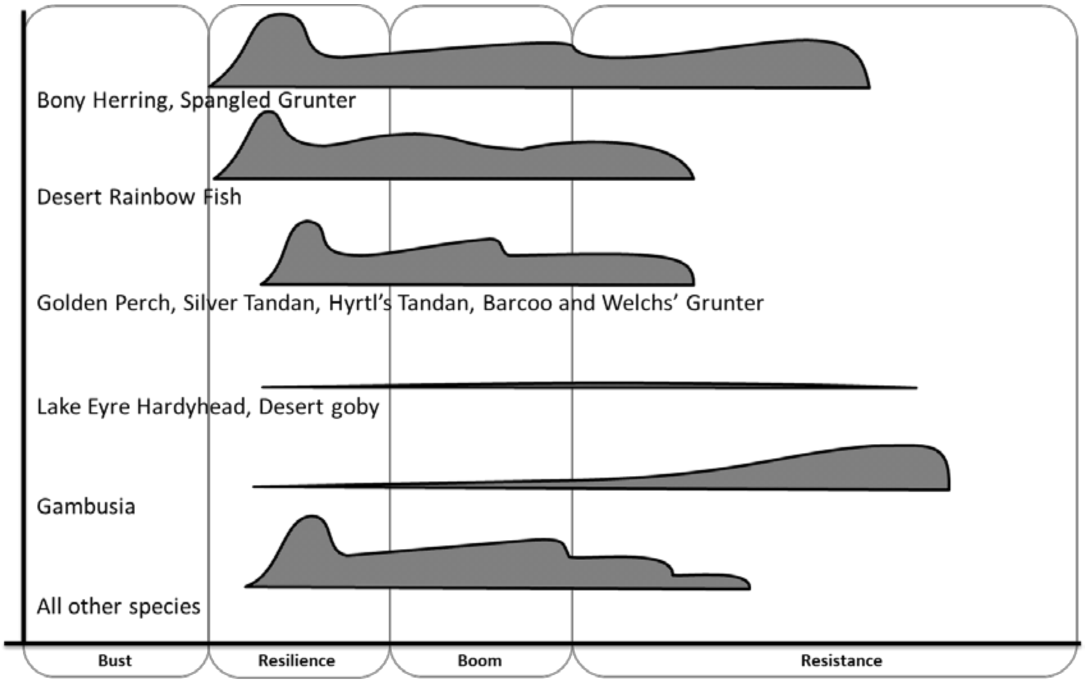


Figure 28. Conceptual model of trait based abundance responses to the hydro-climatic regime within ephemeral disco habitats, using a modified Gantt chart format.

Whilst the interactions between various biological factors and responses with various components of hydrology have been incorporated across a range of these conceptual models, it may be pertinent at this point to recap some of the key ecological responses that are predicted under each of the flow bands presented in earlier (Figure 9) these interactions are likely to be of high value in generating specific testable hypotheses. A summary table is presented below (Table 6).

Table 6. Modelled responses of biological components based on the various types of flow events for refuge types ranging from no flow to full connectivity with Lake Eyre.

Likely outcomes based on various types of flow events into Refugia (α= alpha diversity β= beta diversity)

	No Flow	Local	Reach	River	Connect LE
Disco/Polo Connect	No	No	Yes	Yes	Yes
Water Quality	↓	↓↑	↑	↑	↑
Colonisation	None	None	Partial	Full	Full
Recruit	Low	Medium	High	High	High
Diversity	α↓ β↑	α→ β↑	α→ β↓	α→ β↓	α↑ β↓

Exotic Fishes

Two exotic species, gambusia (*Gambusia holbrooki*) and goldfish (*Carrassius auratus*) are widely distributed in the Lake Eyre Basin, whilst the common carp have been recorded in the Leigh Creek retention dam (Pierce *et al.* 2001). Wager and Unmack (2000) state that the dam was poisoned and the carp population destroyed and the species was not detected during a recent search effort to locate extant populations in the catchment (Thwaites *et al.* 2013). Both gambusia and goldfish are patchily distributed across their range in the Lake Eyre Basin with gambusia dominating stable shallow spring habitats whilst goldfish are distributed predominantly in the mid reaches of the Cooper from Coongie Lakes to Windorah (Cockayne *et al.* 2012, 2013). Whilst goldfish numbers and distribution appear to expand and contract with flooding, gambusia tend to be extremely abundant in GAB springs and bore drains and some wetland habitats (McNeil *et al.* 2011a, 2012).

Despite long standing presence across the Basin, neither of these pest species has risen to the dominance that they enjoy over native fish in the Murray-Darling Basin under highly modified habitat and flow conditions. It is suggested that the naturally variable flow regime, coupled with the robust natural status of the native fish assemblage, precludes both species from successfully dominating Lake Eyre systems unless conditions are stable and shallow as in GAB springs, bore drains or shallow wetland habitats. Modification to the hydrology, habitat and biotic structure are likely, however, to enable increased invasion success for both species which may come to dominate under modified circumstances based on patterns from neighboring catchments (Costelloe *et al.* 2010, McNeil and Costelloe 2011).

The conceptual model for these species focuses on the expected abundances and distribution of the species along a gradient of hydrological stability-disturbance. The model shows stable hydrological conditions leading to high abundance of gambusia and moderate to low abundances of goldfish, whilst high flow disturbance leads to lower gambusia and higher goldfish abundances – linked with increased distributions of both species (Figure 29). The model proposes that the abundance and distribution are both reset through the hydro-climatic cycle so that booms in abundance and/or distribution of these species is subsequently reset, precluding domination of broader Basin habitats. It should be noted that the findings of Costelloe *et al.* (2010) and Cockayne *et al*. (2012, 2013) are contradictory and that goldfish abundance may respond to floods by increasing or decreasing abundance relative to native fish. Contradictory results may be underpinned by varying spatial controls across catchments or reaches where climatic, hydrological and ecological patterns lead to different responses in the exotic fish data. Spatial refuge models outlined in Figures 4 and 5 are likely to be extremely informative to this point, especially if exotic species can be linked to regionally-contained hydro-ecological patterns.

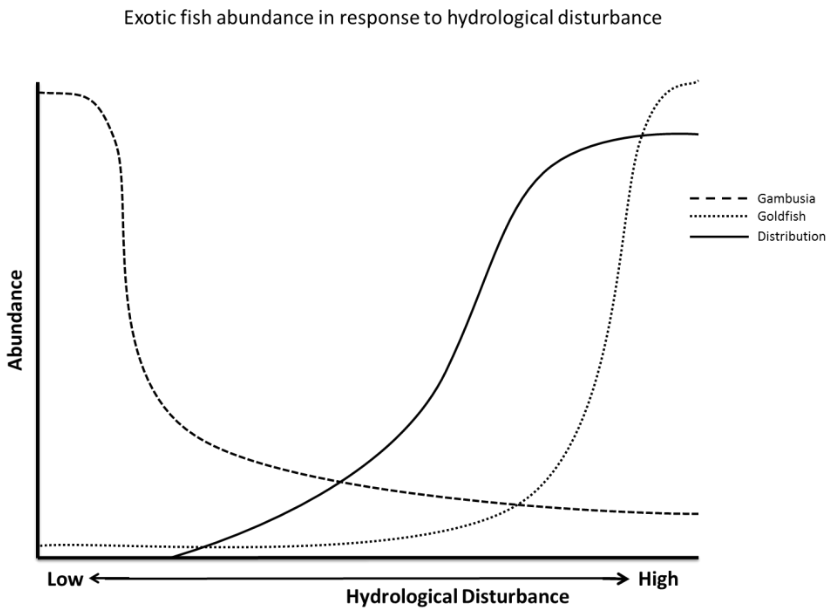


Figure 29. Conceptualised response of gambusia and goldfish abundance and distribution to a flow stability/disturbance gradient in the Lake Eyre Basin.

Disease

The prevalence of disease in fish of the Lake Eyre Basin has been highlighted since the ARIDFLO surveys detected large red ulcerations on a range of predominantly large bodied species in golden perch, Barcoo grunter, Welch's grunter, spangled perch, silver tandan, Hyrtl's tandan and bony herring. Disease was recorded at high levels in both the Diamantina and to a lesser degree in the Coongie Lakes region of the Cooper and some disease reported from the Neales (Costelloe *et al*. 2004). Subsequent surveys detected similar outbreaks in the Cooper Creek at Cullyamurra, with the same species affected, with the vast majority of golden perch and Barcoo grunters infected with severe ulcerations but found no incidence of disease in the Neales and only a single diseased individual from the Diamantina (McNeil *et al.* 2008). These authors also reported infestations of the parasitic copepod *Lernaea* on many diseased fish and noted ulcerations radiating from attachment sites.

The principal pathogen was not identified from the ARIDFLO surveys, but ulcerations were associated with the *Saprolegniacea* fungal mats causing secondary infection. Similarly, disease detected in Lake Hope in the lower Cooper were found to have secondary bacterial infections from *Aeromonas hydrophilla* suggesting combinations of fungal and bacterial infection (Costelloe *et al.* 2004). In both cases, the outbreaks were associated with post flood/flow conditions and may relate to the stress associated with flooding disturbance or with the overcrowding of fish population back into refuge waterholes following recessions of inundation. Disease is also associated with cold water temperatures (<16°C) rather than hot summer conditions. More recent surveys have detected further disease following large floods (Cockayne *et al.* 2012, 2013, Sternberg *et al.* 2014) with PCR analysis identifying the water mould *Aphanomyces invadens* (SARDI unpublished data).

This fungus is behind Epizootic Ulcerative Syndrome (EUS) which has been linked to epidemics of fish disease in the neighbouring Murray-Darling Basin (Boys *et al.* 2012) where many of the same species are similarly infected. Whilst these authors point out that the disease has been recorded only from coastal catchments suggesting a recent spread to the Murray-Darling, Costelloe *et al*. (2004) point out the high likelihood of this disease being an indigenous part of a healthy ecosystem. Literature on the disease however, suggests that infections have spread globally from an initial outbreak in Japan in 1971 (OIE 2014) and have been known in northern Australian fish since at least 1986 (Humphrey and Pearce 2006). Certainly, if the disease has been anthropogenically introduced into coastal, Murray-Darling and subsequently the Lake Eyre Basin ecosystems, then there is cause for alarm and further research is required to determine the invasiveness of this bacteria across Australian ecosystems.

It is clear, however, that EUS has been embedded into the ecology of fish in the Lake Eyre Basin or at least the fish of the Diamantina and Cooper catchments for at least fifteen years. A possible vector for the disease could be through the introduction of goldfish which carry the disease (OIE 2014) or through the intentional translocation of fish from outside the Basin [including Murray cod (*Maccullochella peelii*) and golden perch, both known to carry the disease in the Darling catchment (Boys *et al.* 2012)] by the Queensland government for the purpose of enhancing recreational fishing stocks (Peter Jackson *pers. comm.*). An additional white parasite has been recorded from Finke River pools (SARDI unpublished data) during the late *Dry* phase, however, this is believed to be unrelated to the fungal and bacterial infections prevalent in the eastern catchments. Figure 30 summarises the conceptual magnitude and timing of these disease outbreaks for various fishes from the Lake Eyre Basin.

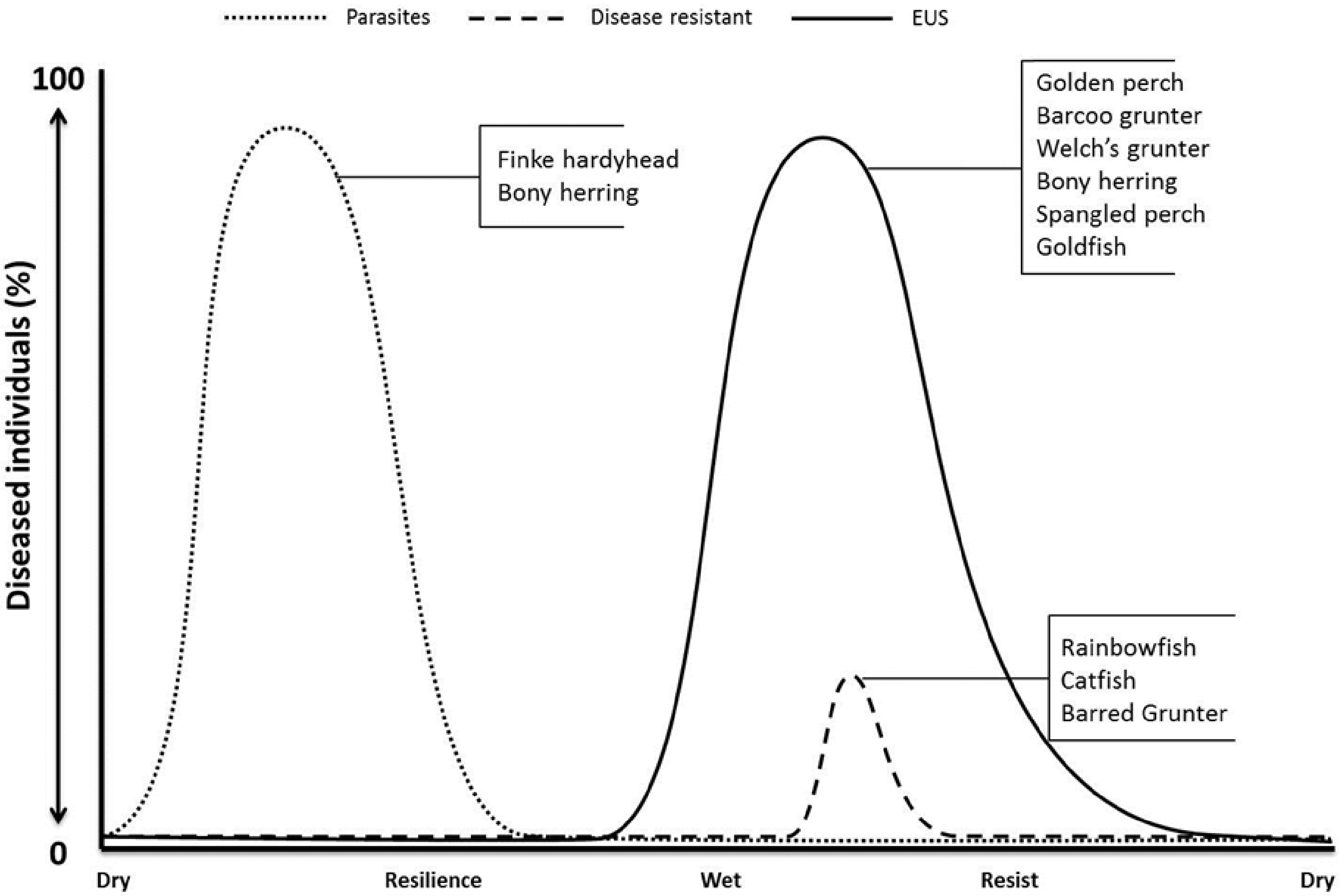


Figure 30. Conceptual model for disease rates of various species highlighting late wet – *Resistance* phase outbreaks of epizootic ulcerative syndrome (EUS) and an unknown white parasite occurring in two species from the Finke River during the late *Dry* phase. Species for which only very low incidences of disease have been recorded are hypothesised to be disease resistant

Discussion

Integrating conceptual modelling for the Strategic Adaptive Management of the Lake Eyre Basin

The development of conceptual models has a number of clear objectives relating to the focusing of knowledge around Lake Eyre Basin waterways, their hydrology, the role of critical habitats and the ecological responses that can be expected of biota across the range of climatic and hydrological variability. Understanding how these ecosystems can be expected to function, and the patterns that can be expected from monitoring and assessment programs at various places and times, is a critical first step towards being able to predict and monitor the response of the aquatic ecosystem to any potential impacts of climate or human disturbance that may develop in the future.

With this in mind, specific aims of the conceptual models are to validate and critique broader conceptual framework models such as the hydro-climatic model that seek to:

- Summarise a wide range of influences, processes and responses at the core of ecosystem function, and to
- Provide a range of more detailed conceptual models that:
    - represent the individual components and process
    - demonstrate how various ecosystem components and process function over space and time, and
    - Identify specific ecological indicators and thresholds to which assessment data can be applied
- Validate conceptual models with data analyses
- Elucidate more detailed indicator and threshold values to inform Strategic Adaptive Management (SAM)

In performing these roles, the conceptual models provide a number of key steps that are central to the effective delivery of scientific knowledge into SAM (Kingsford and Biggs 2012) process through which the Basin is managed under the cross jurisdictional Ministerial Forum (LEBMF 2012). The Lake Eyre Basin Integrated Science and Management Framework (ISMF) outlines the processes for bringing together scientific knowledge and management activities within the SAM framework (McNeil and Wilson 2014). This framework (Figure 31) is useful for communicating how the current conceptual model development and subsequent analysis of available data to identify hypotheses, indicators and thresholds, sit within the broader SAM framework for delivering NRM in the Lake Eyre Basin. Although initially constructed to manage impacts of coal seam gas and coal mining developments in the Lake Eyre Basin, the framework can be applied to any environmental pressure or NRM issue.

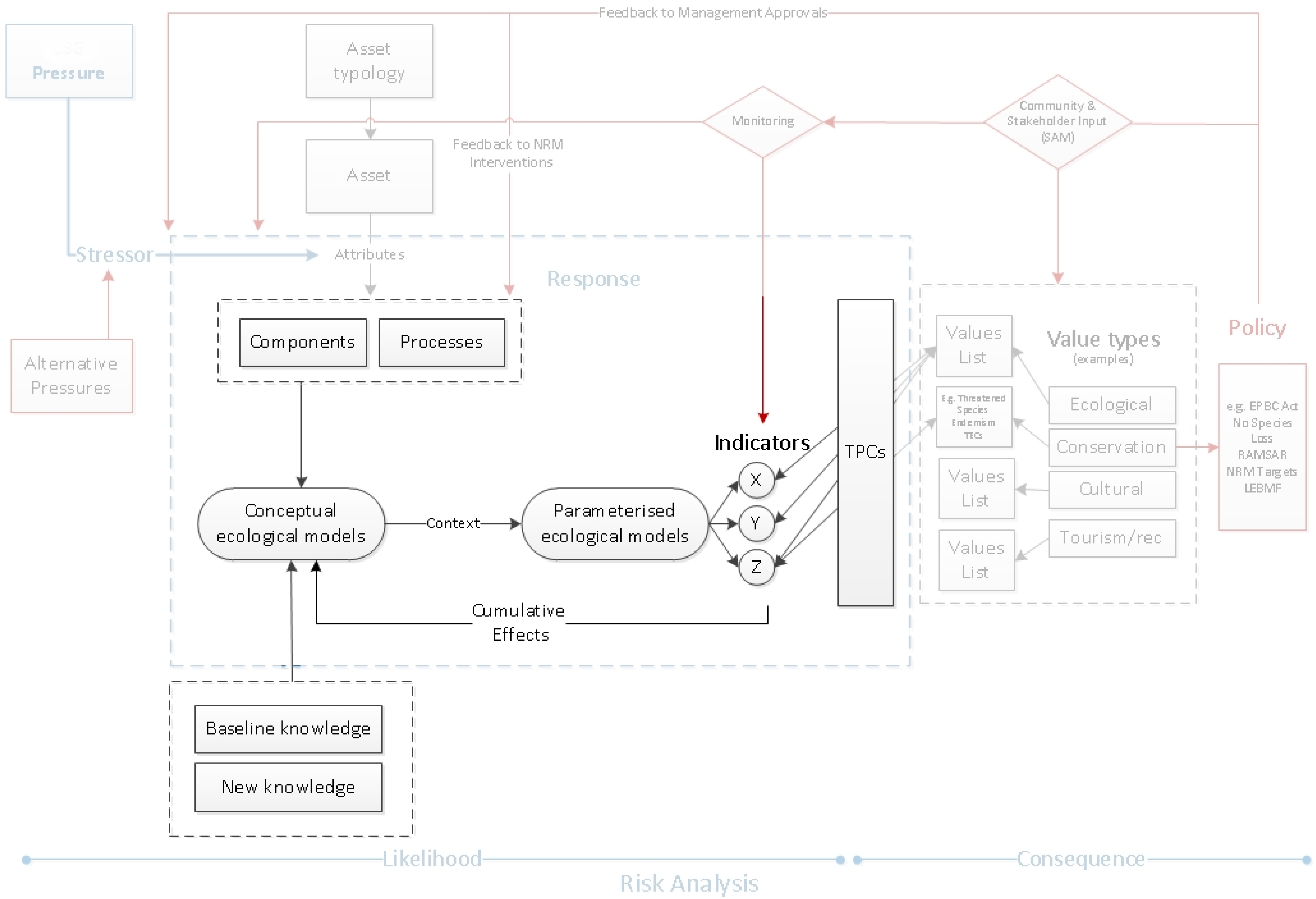


Figure 31. Lake Eyre Basin Integrated Science and Management Framework outlining the mechanistic of applying scientific knowledge to the Strategic Adaptive Management of threats and risks to ecological assets (adapted from McNeil and Wilson 2014). The part of the framework covered under the scope of the current Goyder LEB project is highlighted in bold text.

The development of conceptual models is a critical step in understanding how the ecological structure (habitat assets, components) and function (ecological processes) respond to drivers such as climate, hydrology or stressors associated with human pressures and impacts. Conceptual modelling is an important step for bringing together knowledge about ecological assets (habitats, ecosystems, etc.) and the way that the attributes of assets (components and processes) respond to natural drivers such as climate and hydrology, or anthropogenic stressors that may influence those drivers in a way that causes an ecological response. The processes of developing conceptual models for the current report has led to an improved understanding of how the drivers, habitats and ecosystem components and process respond within the natural variability of the system, specifically, within a framework of climatic and hydrological variation outlined under the overarching hydro-climatic model.

This approach provides an important counterpoint to models that only represent how the impacts of human pressures and stressors might in turn drive ecological responses. Importantly, the approach provides a conceptual understanding of how the Lake Eyre Basin ecosystem responds naturally to hydro-climatic drivers. Conceptual models of natural processes can then be compared to models representing an altered system where human drivers might change the ecosystem components and processes in an undesirable direction, or to an unsustainable or unacceptable degree. This synthesis and conceptualisation of core of knowledge is essential to developing a condition assessment approach that has the power to differentiate between natural variability and human induced change. Achieving this, however, is a difficult process (Arthington *et al*. 2014).

The conceptual modelling represents the first step in developing a natural set of conditions from which undesirable trajectories of influence may be identified, presuming that ongoing monitoring, data collection and assessments are designed and undertaken appropriately. This concept is crucial to the effectiveness of the SAM process whereby stakeholders and managers can easily understand how the system functions and what indicators can be used to inform them of undesirable change. To this end, the conceptual models must be further broken down into analysable components that can effectively use available and ongoing monitoring data to report on the status of condition indicators, and to test for the approach or violation of identified thresholds of potential concern.

The ISMF sets out the cycle of value assessment, management response and feedbacks to address the processes behind these changes. Reliable scientific data are essential for informing conceptual and empirical models and accurately defining indicators and thresholds. A higher standard of scientific knowledge leads to better informed managers and stakeholders. In particular, the ISMF sets out how important conceptual and empirical modelling is for establishing the likelihood of ecological responses informing risk assessment processes that are increasingly important to natural resource management processes.

Integration of Conceptual Models under the Hydro-Climatic Framework

Each conceptual model described in the report contributes to our understanding of how the Lake Eyre Basin ecosystems operate. The models attempt to take complex ideas and represent them in a general and simplified manner. Many of these models were then further simplified to present basic relationships or response variables that can in turn be used to generate hypotheses that are directly testable using data that is currently available. The relationship between general models and basic relationship models is presented in Figure 32.

Models at the top of the network inform models below, ultimately leading to the fish community assemblage model at the base of the network. Models on the left-hand side of the network begin with fish species traits and move through to ecological responses. Models on the right-hand side of the network relate to hydrology and habitat availability. General models are displayed on the outside of the network and lead to basic relationship models in the middle of the network (yellow area). These basic relationship model then lead to specific hypotheses outlined below.

Example Hypotheses

1. Fish Community Assemblage

Tested using cluster analysis and ordination (Figure 23).

1) After prolonged disconnection (bust), there will be only a few refugia and there will be two distinct fish assemblage clusters: an ark cluster associated with water depth (and other waterhole features) and a polo club cluster associated with poor water quality (e.g. salinity).
2) Upon flooding, there will be a large number of inundated refugia and fish assemblages in previously ark refugia and polo club clusters will become more similar (differences between clusters will be associated with flow, depth and other waterhole features).
3) During prolonged connectivity (boom), fish assemblages at in all refugia will be similar with no strong correlation with environmental variables.
4) After cease-to-flow, the number of refugia will diminish and two clusters will form and become dissimilar as they become ark refugia associated with depth and polo clubs associated with salinity.

2. β vs Habitat Availability Model

Variability in diversity between habitats (β) will be inversely related to habitat heterogeneity and availability (Figure 20). When habitat heterogeneity and availability are low during the *Dry* phase, β will be high (i.e. very different species assemblages in the resulting Ark and Polo Club habitats (Figure 21). During *Wet* phases, habitat availability will be higher, the habitat will be more homogenous and species assemblages will be similar in all refugia (Figure 21).

3. Fish Life History Model

Fish life history traits will be related to hydrologic variability and predictability as proposed by Winemiller (2005). Specifically: opportunistic strategists will be abundant and widespread in catchments or reaches during periods characterised by environmental disturbance and unpredictable flows; periodic strategists will be abundant and widespread in catchments or reaches during periods of predictable flows; equilibrium strategists will dominate in catchments or reaches during periods of stable flow.

4. Recruitment vs Flow Model

Low flow spawning species (gobies, hardyheads, mogurndas, carp gudgeon and smelt) will have high recruitment during low flow phases of the hydro-climatic regime (Figure 22). Flow response spawners (spangled perch, bony herring, golden perch, silver and Hyrtl's tandans, rainbowfish and glassfish) will have high recruitment in response to high flow phases of the hydro-climatic regime (Figure 22). The two different strategies will be inversely related and low flow spawners will reach a threshold of flow above which they won't show any signs of recruitment (Figure 22). Under low flow conditions, flow spawners will show little or no level of recruitment.

5. Salinity Tolerance Model

Each fish species will have specific salinity tolerances that predict the upper (and lower) limits of survival in saline waters (Figure 12). The model will also predict the impact on species abundance within the range of salinity tolerance. The maximum predicted number of species present in any waterhole will decrease in a linear fashion as salinity increases from freshwater to extremely hypersaline (Figure 13).

6. Resilience vs Resistance Model

In polo club refugia, resilient species abundance should be inversely related to resistant species abundance as proposed in Figure 16. Resilient species will peak in abundance during *Wet* phases, but will be absent from polo club refugia toward the end of *Resistance* phases and in *Dry* phases (Figure 16). Resistant species will peak during the *Resistance* phase, decline during the *Dry* phase and crash during the *Wet* phase (Figure 16). Resistant species will be present throughout the Hydro-climatic regime but may be lost at local scales.

7. Fish Disease Model

Occurrence of parasitic infections will peak during the *Dry* phase and primarily affect Finke hardyhead and bony herring (Figure 28). Several species (golden perch, Barcoo grunter, Welch’s grunter, bony herring, spangled perch and goldfish) will be infected at high rates by Epizootic Ulcerative Syndrome (EUS) on receding floods (Figure 28). Other species (rainbowfish, catfish and barred grunter) will be infected at the same time by EUS but at very low rates (Figure 28).

8. Exotic Fish Model

Invasive species with opportunistic life history traits (gambusia and goldfish) will increase their geographic range with increasing levels of hydrological disturbance (Figure 29). Once present in a habitat, gambusia abundance will be high at low levels of hydrological disturbance, decreasing to a low asymptote at high levels of disturbance (Figure 29). Goldfish abundance will be very low under low levels of hydrological disturbance and high in response to very high levels of disturbance (Figure 29).

9. Flow vs Depth Model

Waterholes with a cease to flow depth greater than the depth of water lost to evaporation between flows will be permanent ark refugia (Figure 8). The deeper the waterhole, the longer it will persist between flows. The more frequent the flow, the shallower the waterhole needs to be to provide permanent aquatic habitat. Waterholes with a cease to flow depth less than the depth of water lost to evaporation between flows will be disco or stepping stone refugia. Polo club refugia are omitted from this model because they rely heavily upon groundwater inputs to maintain adequate depth to persist between flows. Polo club refugia will persist if the cease to flow depth combined with the groundwater input is greater than the depth of water lost to evaporation between flows. Habitat structure may regulate the effect of waterhole depth and drying on assemblage change.

10. Flow magnitude outcome model

The matrix of flow types and outcomes (Table 6) predicts a range of categorical and continuous outcomes under a hierarchy of flow types. This matrix forms the basis for predicting the outcomes of generalised linear models or generalised linear mixed models.

Expanding the LEBRA Fish Trajectory Model

The LEBRA fish trajectory model (FTM) was developed in 2006 by a group of expert fish biologists with experience in the Lake Eyre Basin, the design of scientific monitoring programs and the development of condition assessment methodologies (Humphries *et al*. 2007). The FTM was designed to inform the methodology and assessment approach for a fish monitoring program under the LEBRA program. The model conceptualises a range of biological responses that could be expected under the regime of hydrological conditions encountered in the Lake Eyre Basin. It was subsequently tested under two pilot programs in South Australia (McNeil *et al*. 2008) and Queensland (Balcombe and Kerezsy 2009) with recommendations and modification from the pilot studies reporting back to the final FTM presented in Humphries *et al*. (2007). As the current LEBRA fish monitoring methodology (McNeil and Cockayne 2010) is targeted towards reporting on information relevant to the FTM, findings from the LEBRA monitoring program can be used to validate the various aspects of the FTM using the data collected since 2009.

As a first step towards expanding the FTM, we have undertaken a process for updating and expanding the model based on the information collected and presented under the conceptual models in the current report (Table 7). This integrates the concepts of the hydro-climatic model and addresses the anticipated responses under the various hydro-climatic phases, and considers how the responses are likely to differ across the various functional refuge habitat types. This information significantly expands the detail presented in the FTM and will optimize the application of the current monitoring data to inform on the condition and health of the Lake Eyre Basin rivers.

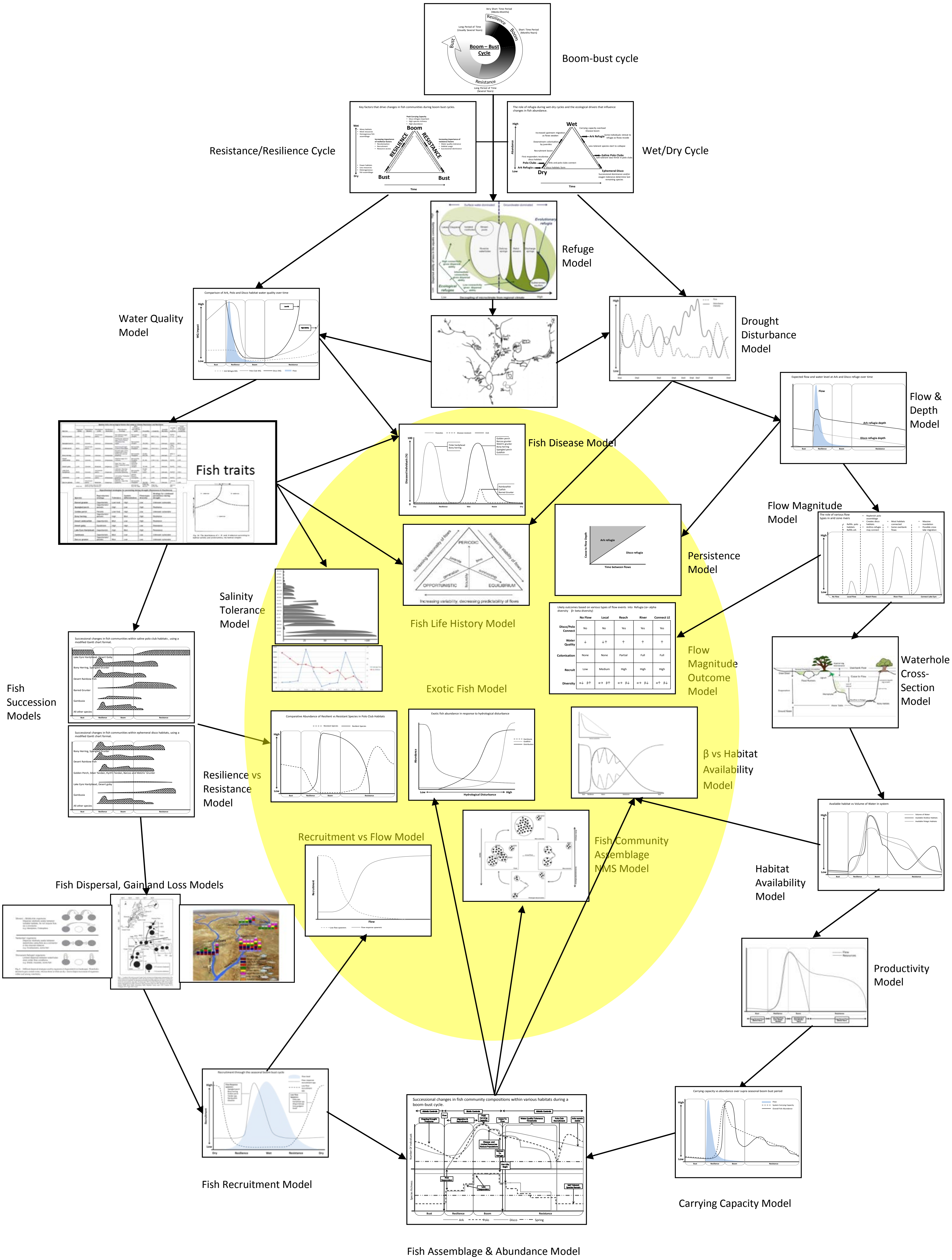


Figure 32. Network of conceptual models contained within the report. Models on the outside of the network lead to models in the middle of the network (yellow area) which answer specific hypotheses outlined in the report text. Models at the top of the network inform models below, leading to the Fish Community assemblage model. Models on the left of the network relate to fish species traits and ecological responses. Models on the right of the network relate to hydrology and habitat availability.

Table 7. Expanded LEBRA Fish Trajectory Model (Adapted from Humphries *et al.* 2007) incorporating Hydro-climatic phase and refuge specific responses consistent with the current conceptual modelling.

Antecedent Flow Condition (updated with Hydro-Climatic Phase)																																
	Dry/Bust (No recent flood)								*Resilience* (Recent 'super' flood)								*Wet/Boom* ('Super' flood in last 12 months)								*Resistance* (No flood in last 12 months)							
Fish Response Indicators	Humphries *et al.* 2007	Ark Refuge	Spring Polo Club	Saline Polo Club	Disco Refuge	Anthropogenic Refuge	Casino Refuge	Stepping Stone Refuge	Humphries *et al.* 2007	Ark Refuge	Spring Polo Club	Saline Polo Club	Disco Refuge	Anthropogenic Refuge	Casino Refuge	Stepping Stone Refuge	Humphries *et al.* 2007	Ark Refuge	Spring Polo Club	Saline Polo Club	Disco Refuge	Anthropogenic Refuge	Casino Refuge	Stepping Stone Refuge	Humphries *et al.* 2007	Ark Refuge	Spring Polo Club	Saline Polo Club	Disco Refuge	Anthropogenic Refuge	Casino Refuge	Stepping Stone Refuge
Species richness	N	N	N	N	A	D+		A	N	N	I++	I	I+++	I+		I++	N	N	I+	I	I++	I++		I++	D+	N	D	D+	D+++	D+		D+++
Abundance	I	D++	N	D++	A	D+		A	I++	I+++	I++	I	I+++	I+		I+	I+++	I++	I+	I+	I+++	I+		I++	D	D+	D	D+	D+++	D+		D+++
Biomass	D	D++	N	D++	A	D+		A	I+	I+++	I++	I	I+++	I+		I++	I+++	I+	I+	I+	I+++	I+		I++	D	D+	D		D+++	D+		D+++
Movement	-	A	A	A	A	A		A	-	Em+++	Im+/Em+	Im+/Em+	Im+++	Im+/Em+		Im++/Em+	-	Em+	Im+/Em+	Im+/Em+	Em+++	Im/Em		Em+++	-	N	N	N	N	N		Em+
Abundance of Alien Species	N			A	A	I		A	D								D-								N			D/A	D+++			D+++
Recruitment	I	D+	N	N	A	D++		A	I	I+++	I++	I++	I+++	I+++	I+++	I+++	I+++	I++	I+	I+	I++	I		I+	I	D+	N	N	D+++	D+		D+++
Abundance of herbivores	D-	N/I	D/A	A	A	D		A	I++	I+++	I	I	I+++	I+		I++	I++	I++	I	I+	I++	I		I++	N	D	D	D	D+++	D+		D+++
Abundance of macrocarnivores	D	I	A	A	A	D/A		A	I++	I++	I+	I	I++	I		I+	I++	I+++	I/A	I/A	I+	I		I	D-	D++	D+	D+	D+++	D+		D+++
Abundance of microcarnivores	D-	D	N	D	A	D++		A	I++	I+++	I+++	I+++	I+++	I		I++	I++	I+	I	I+	I+++	I		I++	D	D++	N	N	D+++	D+		D+++
Prevalence of disease	I				A	I+		A	I								A								I							

Im = immigration

Em = emigration

A = absent

N = no change relevant to average scenario

I = increase relative to average scenario

D = Decrease to average scenario

+ = moderate

++ = large

+++ = enormous

Conclusions

This report was intended to provide a range of information for guiding future analysis of data to inform assessments of ecological condition based on current LEBRA monitoring of fish, water quality and hydrology. The range of conceptual models and ideas represent the most comprehensive collation of knowledge regarding the influence of climate and hydrology in driving Basin-scale refuge dynamics and fish ecology patterns in the Lake Eyre Basin. However, many of the models require significant development before they can be applied to informing condition assessments through well-defined indicators and thresholds. Limitations may be based on the quality of data used to develop ideas and models, restricted spatial or temporal applicability of models, or lack of suitability for validation or analysis using the current suite of available monitoring data. These limitations are to be expected given the ambitious scope of the work and requirement for innovative thinking in developing new models.

The review of existing models is a significant step towards building a whole-of-basin approach to condition monitoring and assessment, as many of these studies are focused on single reaches, tributaries or catchments, or restricted areas of catchments. For example, a disproportionate number of existing models are based on studies of the Coongie Lakes and Windorah floodplain sections of the Cooper Creek. Care must be taken in generalising these to other catchments and even to other reaches within the Cooper as the high degree of variability in the Basin dictates that patterns derived in specific areas are likely to differ from those present elsewhere. This is especially an issue in generalising models from the more hydrologically stable (in terms of dynamic equilibrium) or predictable parts of the Basin, to areas where environmental pressures may be more extreme. Alternatively, new models are largely based on accumulated knowledge from a range of programs that have regional objectives, and Basin-scale monitoring that has limited local resolution to validate patterns.

The development of this suite of models has also highlighted a number of knowledge gaps that are important in understanding the existing variability of the system and in predicting what impacts of anthropogenic change may look like. One in these is the role of Lake Eyre itself in facilitating or preventing the dispersal of fish across catchments during periods of very high flow. Genetics studies are likely to be most informative to addressing this question (Murphy *et al.* 2014), however, as described above; genetic data are limited when not matched with a high degree of on-ground knowledge about the factors that may influence fish dispersal (e.g. human assisted movement). Actual movement data for fish in the Lake Eyre Basin is limited to a handful of tagged fish recaptures in the LEBRA program. All other movement data are inferred from observations of dry catchments possessing fish stocks following the resumption of flow.

The limitations of hydrological data and modelling are a pervasive and ubiquitous issue in the interpretation of hydro-ecological patterns in the Lake Eyre Basin. Modelled flow data are restricted to the Neales River in South Australia and Cooper Creek in Queensland. The limited number and distribution of rated hydrometric gauging stations creates difficulties in developing specific indicator rules and thresholds with high resolution, even though ecological responses may be well understood or modelled.

This report undertakes an important step in developing a scientific basis for the Strategic Adaptive Management of Lake Eyre Basin waterways (McNeil and Wilson 2015). The development of conceptual understanding provides a platform for further analysis and modelling of monitoring data. These scientific outputs can subsequently be used to identify ecological responses to human pressures and stressors and identify indicators of the key human values necessary for the protection and management of the Lake Eyre Basin (Morton *et al.* 1995).

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Appendices

Appendix 1

Attributes, components and subcomponents of Lake Eyre Basin Waterways used in the LEBRM modelling. Adapted from Imgraben and McNeil (2013a).

Attribute	Component	Sub-component
Hydrology	Flow regime	Timing
		Seasonality
		Volume
	Water regime (persistence, within waterbody)	Evaporation loss
		Waterbody volume
		Groundwater inputs
	Connectivity	Longitudinal (in-channel)
		Latitudinal (out of channel)
		Vertical (groundwater – surface water)
		Cross- catchment
		Phreatic evaporation
Geomorphology	Landform type	Basin
		Riparian/shore line
		Channel
		Floodplain
	Landform characteristics	Size
		Surface area
		Shape
	Valley boundaries	Confinement
		Valley floor and edges
	Cease-to-flow depth	
Physical habitat	Substrate	Permeability
		Structure/texture
		Contaminants
	Vegetation structure types	Woody debris
		Floodplain and watercourse vegetation structure (macrophytes etc.)
		Riparian structure
	Bank and shore stability	Stability
		Morphology
		Rock bars
		High adjacent terrain
Water quality	Natural chemical	Salinity (EC)

regime	components	Ionic composition
		pH
		Dissolved Oxygen
		Dissolved Organic Carbon
	Sediments	Turbidity
	Climatic influences	Temperature
	Nutrients	Nutrients
	Chemical pollutants	Contaminants
Wetland biota	Fauna	Microinvertebrates
		Macroinvertebrates
		Amphibians
		Reptiles
		Fish
		Birds
		Mammals
	Flora	Algae
		Biofilms
		Macrophytes
		Riparian vegetation
	Fungi	
Terrestrial biota	Fauna	Macroinvertebrates
		Reptiles
		Birds
		Mammals
	Flora	Terrestrial responders
		Algae
	Fungi	

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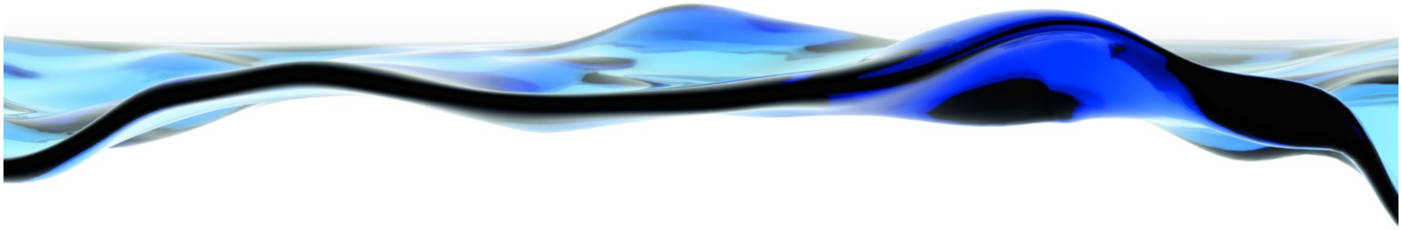

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