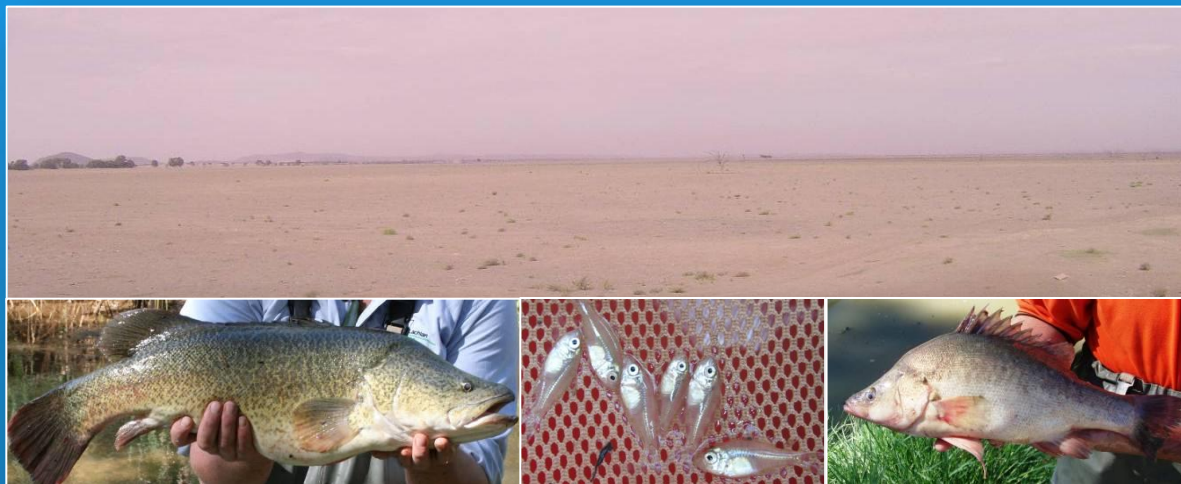


Resistance and Resilience of Murray- Darling Basin Fishes to Drought Disturbance



Dale McNeil¹, Susan Gehrig¹ and Clayton Sharpe²

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PO Box 120 Henley Beach SA 5022

April 2013

Final Report to the Murray-Darling Basin Authority - Native Fish Strategy Project MD/1086 "Ecosystem Resilience and the Role of Refugia for Native Fish Communities & Populations"



Government
of South Australia



Australian Government



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Executive Summary

This report summarises a review of published and government literature relating to the impacts of drought on freshwater ecosystems, and specifically upon fish species and assemblages in Australia's Murray-Darling Basin (MDB). The responses of aquatic ecosystems and native fishes to drought impacts are addressed and utilised for the development of conceptual frameworks to enhance understanding of *resistance* and *resilience* of fish population in the MDB. The framework uses a seasonal string approach to conceptualise how drought disturbances of varying intensity, and protracted climate change, impinge on native fish populations and assemblages over successive seasons. Empirical data may then be applied to this framework to identify: drought resistance/resilience attributes and thresholds of native fishes, potential species losses, changes to fish assemblages and populations susceptibilities under a range of climate change and/or drought scenarios.

The fundamental aim of the conceptual model was to evaluate the transition (possible success and/or failure) of a species in response to various drought scenarios. Success (or failure) was found to be dependent upon a number of species-specific life history traits, environmental tolerances and ecological characteristics that related to a species' resistance or resilience. Thus, a number of resistance and resilience factors were identified that notably influenced the transition of a particular species through drought. Resistance and resilience factors were then scored for 30 native and exotic MDB fish species; for which sufficient data and expert knowledge was available regarding life history traits and ecological characteristics.

Drought resistance and resilience factors were further analysed to determine whether specific guilds (or groups) of fishes exist that possess similarities in their responses and tolerances to drought impacts. A positive linear relationship between drought resistance and resilience factors was found; where particular species were distributed along a gradient of strongly resistant/strongly resilient to poorly resistant/poorly resilient. A small group of species were of particular interest, showing moderate resistance, but relatively low resilience scores. Further analysis showed that this group contained the majority of conservation dependent species and species that have presently become of conservation concern, following the recent drought.

Multivariate analysis identified three separate Drought Response Groups (DRGs). Fish species were grouped as a result of shared resistance and resilience traits; thus each DRG was statically differentiated from the other. In lieu of existing literature and expert opinion, and based upon the resistance and resilience traits and ecological characteristics identified, these three DRGs were differentiated into: DRG 1, which consisted of all of the conservation dependent species and species of recent conservation concern (except for the long-lived Murray cod and silver perch); DRG2, which contained either large-bodied or long-lived species and DRG3, which consisted of a group of common and widespread native and exotic species.

In particular, three key resistance/resilience factors characterised DRG1; namely poor dispersal ability, limited distribution and high patchiness within the natural range. These traits were significant in differentiating the threatened DRG 1 group from the other DRGs, which suggests that large spatial scale population structure, associated with an inability to rapidly recolonise following drought (or other disturbances) are likely to be key factors threatening the resilience of this vulnerable group to drought within the MDB. As such, this report recommends that management attention be focused upon the restoration of large spatial scale population processes for native fish within DGR1, in order to mitigate the impacts of drought disturbances upon the long term viability of populations. Importantly, it is highlighted that management investment during non-drought periods is likely to be the most effective approach to ensure the survival of threatened native fish populations during future drought disturbances in the MDB.

1.0 Introduction and Background

1.1 Drought and the Murray-Darling Basin

In the recent decade, spanning 1996 to 2010, the Murray-Darling Basin (MDB) experienced drought conditions (Murphy and Timbal 2008; Ummenhofer *et al.* 2009) of such duration and intensity it was referred to as a 'mega-drought' (Lake *et al.* 2008). Within this decade, mean annual rainfall and run-off were approximately 16 and 39% lower respectively, than the long-term average from 1895 to 2006 (Murphy and Timbal 2008; Potter *et al.* 2008). The unprecedented reductions in run-off appeared to be a combination of factors relating to low annual rainfall, increased temperatures, increased potential evaporation, decreased autumn and winter rainfall (in a region with largely winter-dominated runoff) and decreased inter-annual variability of rainfall (Potter *et al.* 2008).

While detectable in the north-east region, lower rainfall and runoff averages were mainly concentrated in the southern most regions of the MDB. In particular, parts of South Australia and Victoria that usually experience a winter rainfall peak (May to October) (Timbal and Jones 2007) experienced extended drought conditions. While such a 'big dry' has been recorded once before in the 20th century (i.e. 1936–1945; see Potter and Chiew 2009), drought conditions of the recent decade were exacerbated by elevated average daily temperatures (Murphy and Timbal 2008).

Recent drought conditions noticeably impacted MDB water resources. In general, inflows to the River Murray system over the 1996-2007 decade were approximately 42% below average; an amount approximate to inflows recorded during earlier extended droughts in the 1900's and 1940's (CSIRO 2010). Due to the combination of ongoing drought and current anthropogenic demands for water resources, it is predicted that it will take a number of years before inflows and water storages return to pre drought levels, even with a return to average rainfall (Lintermans and Cottingham 2007).

The impacts of drought have been further exacerbated by the high level of water resource use in the MDB and associated impacts of river regulation. Since European settlement, modifications of the natural hydrological regime have become dominated by very low flows (< 5000 GL per annum), and occasional high flows (>25000 GL per annum) and mid-range flows have noticeably decreased with a near elimination of natural spring floods (Maheshwari *et al.* 1995). The result is unnatural water regimes that lead to un-seasonal inundation of floodplains and a reduction in flooding (Norris *et al.* 2001, McMahon and Finlayson 2003), all of which have been linked to a decline in the abundance and distribution of many native fishes (Gehrke *et al.* 1995; Humphries *et al.* 2002). The large number and close proximity of regulating structures throughout the Basin, (especially along the lower Murray River, downstream of the Darling junction) leads to a series of

weir pools with relatively constant water levels that never dry out (Maheshwari *et al.* 1995).

1.2 Climate and the Murray-Darling Basin

In considering the impacts of drought, it is important to note that climatic conditions vary substantially across the MDB; the western plains are semi-arid to arid, while the southeast is temperate. Indeed, 86% of the Basin's land area is situated in semi-arid to arid landscapes, where rainfall is low (~240 mm per annum) and highly variable (Walker *et al.* 1995). Nearly 50% of the annual average inflow of the river system is contributed by merely 11% of the catchment area; the upland regions of NSW and Victoria for the Murray River and the monsoon-influenced headwater tributaries for the Darling River (Walker *et al.* 1995; Crabb 1997). The allogenic nature of inflows and the predominance of arid and semi-arid conditions suit classification of both the Murray and Darling as dryland rivers (Walker *et al.* 1995; Kingsford 2006).

The long term average annual rainfall across the MDB is ~440 mm, and is conspicuously variable on a year-to-year basis. This inter-annual variability is largely thought to be due to the Pacific Ocean and the impact of the El Niño Southern oscillation (ENSO) on southeastern Australia (see Bureau of Meteorology). Yet the periodic extended dry spells across the MDB may be primarily driven by Indian Ocean Dipole (IOD), especially in the southeastern regions (Ummenhofer *et al.* 2009). As a result of these marked differences in temperature, rainfall and evaporation across the basin, flow in the MDB river system is noticeably more variable than most of the world's major river systems (Puckridge *et al.* 1998). Furthermore, area-averaged total rainfall in some regions has decreased since pre-European times, with a 5.2% drop in rainfall in Queensland and a 2.5% drop in New South Wales and Victoria (Syktus *et al.* 2007).

Thus, large differences in temperature, rainfall and evaporation occur on a seasonal, annual and/or year-to-year basis. At local scales, these climatic differences may be even more distinct and may become more variable under changing climatic conditions.

1.3 Report Aims and Scope

In response to the increasing desiccation of aquatic habitat (through the combined impacts of water resource management, drought and climate change) the Murray-Darling Basin Commission (MDBC) under the Native Fish Strategy (NFS) convened a "Drought Expert Panel" to consider in detail the management of native fishes during drought. Water and natural resource managers were asked to begin the process of identifying, categorising, and protecting drought refugia for fishes, particularly those refugia with substantial depth and volume (including weir pools), high fish diversity, or those containing populations of threatened species (Lintermans and Cottingham 2007). A key objective of the Native Fish Strategy (MDBC 2003) in response to the recent drought is to ensure an adequate network of drought refugia to maintain native fish populations and provide

a fighting chance for survival, if not recovery.

The ability for native fishes to deal with drought disturbance is critical in determining the eventual impacts that drought will have on native fish populations in the MDB. It is acknowledged that not only are fish physically required to tolerate the impacts associated with drought (termed *resistance*) but that fishes must also be able to respond and recover following drought and maintain *resilient* populations that are able to recover once the pressures of drought have eased. Maintaining resilience is a complex issue and one which has not been closely investigated regarding drought and Australian freshwater fish species. A key focus of the current report is therefore to explore the mechanisms through which native fish are able to tolerate drought conditions and build resilient populations that can allow viable fish populations to persist in the face of regular drought disturbances. As an excellent surrogate of overall river health, this study of drought and native fish can infer broader ecological impacts across aquatic systems and biota in the MDB.

To address these issues, the MDBC (now the Murray Darling Basin Authority - MDBA) have commissioned two separate projects. The first of these, MD1087: 'The Protection of Drought Refugia for Native Fish in the Murray-Darling Basin' aims to establish clear criteria for characterising drought refugia, including their spatial distribution and key threats to their long-term viability, complemented by a framework for protecting and managing critical refugia during recent and future drought conditions. The second, MD1086: 'Ecosystem Resilience and Importance of Refugia for Native Fish Communities and Populations' aims to improve our understanding of how fish populations and species respond to and recover from drought. Hence, this review is the first phase of the ecosystem resilience project, providing an analysis of current literature surrounding the concept of ecosystem resilience and the importance of refugia for native fish communities and/or populations, with particular emphasis on the MDB, Australia.

This review addresses 6 primary themes:

- 1) review the impacts of drought on freshwater systems and, in particular, fish assemblages in the MDB
- 2) summarise the environmental conditions and processes operating within drought refugia,
- 3) the synthesis of current life history and tolerance threshold data of MDB fish species,
- 4) the development of Conceptual frameworks for modelling drought impacts and responses of native fish,
- 5) the determination of possible response guilds (i.e. functional groups) of MDB fish species to within drought refugia conditions and/or processes.
- 6) the identification of key factors important to drought susceptibility in MDB fishes.

2.0 The Impact of Drought on freshwater ecosystems in the MDB

2.1 What is Drought?

Drought is generally viewed as a disturbance causing primary resource limitation (i.e. decreased water availability), which in turn disrupts key ecological processes; with the potential to affect aquatic biota in a number of direct and indirect, complex ways (Lake 2003). Response to drought by aquatic biota will vary, as it depends on individual resistances and/or life stages (Geissler and Gzik 2008; Magoulick and Kobza 2003; Marques *et al.* 2007; Matthews and Marsh-Matthews 2003) and the influence of drought components such as timing, frequency, duration and magnitude (Wood and Pfitzer 1960).

In freshwater systems where seasonal drought is a predictable occurrence, the associated biota are often well-adapted; however if these systems are subjected to extended periods of drought (i.e. spanning decades to centuries) there may be losses, if not local extinctions (Boulton 2003; Magalhaes *et al.* 2007). This may be particularly so for species already approaching their resistance threshold limits because of other compounding impacts such as habitat loss, water abstraction, river regulation, damming, pollution and the spread of exotic species (Collares-Pereira *et al.* 2000; Cowx and de Jong 2004). Thus there is potential for ongoing droughts to reduce and simplify fish assemblages, which could have serious implications for fish conservation (Magalhaes *et al.* 2002; Magalhaes *et al.* 2007).

Nevertheless it is possible for ecosystems to recover once a drought has lifted (Caruso 2002), but at present there is a paucity of data relating to the resilience of ecosystems during drought, and in particular whether an adequate network of drought refugia (e.g. flowing perennial river reaches, deep waterholes) remain to preserve native fish species/populations in the MDB (Magalhaes *et al.* 2007). Additionally, there is limited data on the responses of fish assemblages to drought and the use of drought refugia (Arthington *et al.* 2003; Closs and Lake 1995; Humphries and Baldwin 2003; King *et al.* 2003).

Drought needs to be understood within the bounds of the natural climatic variability in a region, and therefore presents a challenge to biologists. Like all disturbances, drought can vary in intensity, magnitude, duration and extent (Boulton 2003; Lake 2003; Poff 1997; Sparks *et al.* 1990). The American meteorological Society defines '*meteorological drought*' as the occurrence of 'low' rainfall that lasts 'months to years' (Gawne and Gigney 2008); whereas the Encyclopaedia of Climate and Weather (1996) defines meteorological drought as "...an extended period – a season, a year or several years – of deficient rainfall relative to the statistical multi-year mean for a region" (cited in Lake *et al.* 2008). These definitions are temporally vague, occurring over months to years and relative to 'normal or mean' conditions over some undetermined timeframe.

Other definitions relate to the impact of meteorological drought on human society such as ‘*agricultural drought*’ or ‘*socio-economic drought*’ or impacts on aquatic systems – i.e., ‘*hydrological drought*’ (Gawne and Gigney 2008). In particular, hydrological droughts are characterised by the reduction in lake storage, lowering of groundwater levels and decrease of streamflow discharge, which may occur over one year or over several consecutive years, and often affect large areas (Smakhtin 2001). Definitions relating to meteorological and hydrological drought are the most useful for applying to ecological systems, since they acknowledge periods of exceptionally low rainfall, and subsequent reductions in volumes of freshwater available to aquatic systems.

The distinction between ‘*seasonal*’ and ‘*supra seasonal*’ drought has been used to distinguish between two key aspects of climatic drying (Lake 2003; Lake *et al.* 2008; McNeil 2004). Seasonal drought describes the extended periods of low rainfall and water resource scarcity that occur seasonally as part of annual climatic cycles. Supra seasonal drought describes longer-term expressions of climatic dryness that may last many years or decades, resulting in consecutive seasons of reduced rainfall and water resource availability (Gawne and Gigney 2008; Lake 2003). These supra seasonal droughts are driven by large scale global weather events (Timbal and Jones 2008) and are relatively unpredictable in terms of duration, spatial extent, severity or intensity (Boulton 2003; Humphries and Baldwin 2003; Sparks *et al.* 1990).

Supra seasonal drought can extend over large time-frames - the current ‘millennium’ drought in south eastern Australia has persisted, so far, for twelve years, prompting the additional classification of ‘*megadrought*’ to capture the most severe and extended drought periods (Lake *et al.* 2008b). While this distinction is useful, the two are intrinsically linked. Supra seasonal drought operates through the lens of seasonal drought; with longer term climatic dryness resulting in extended and more severe periods of seasonal drought. This reduces the effectiveness of intermittent wet seasons to normally ‘break’ seasonal drought periods through the provision of increased flows and floods (Gawne and Gigney 2008; Timbal and Jones 2008). In this way, supra seasonal drought can be viewed as a period where the magnitude, extent and severity of dry seasons are increased, while the magnitude and extent of wet seasons are greatly reduced.

2.2 How does drought impact aquatic habitats?

Just as hydrological drought is essentially an expression of meteorological drought; reduced river flows and groundwater recharge are expressions of reduced rainfall. By their nature, the function of most freshwater ecosystems in the MDB is dependent on precipitation, which, in turn, can feed ground and surface water systems (Gawne and Gigney 2008). In the early phases of drought, the associated lack of rainfall will reduce soil moisture, surface-water inputs and run-off. Furthermore, groundwater recharge will influence both groundwater and rainfall driven aquatic systems across a number of spatial and temporal scales (Bond *et al.* 2008; Dahm *et al.* 2003; Jones *et al.* 2002;

Lake 2003; Matthews and Marsh-Matthews 2003).

Australia's inland river systems are among the most hydrologically variable in the world, with large extremes of flood and drought regular features of riverine hydrographs (Walker *et al.* 1995; Puckridge *et al.* 1998; Puckridge *et al.* 2000). Under normal climatic regimes, intermittent streams and isolated floodplain habitats and wetlands are frequently subject to seasonal droughts during the dry season (Arthington *et al.* 2005; McNeil 2004; Perry and Bond 2009). When aquatic habitats begin to desiccate, those that are shallow or have porous substrate will dry, leaving only deeper, retentive or spring-fed pools, which themselves will begin to contract and desiccate under evaporation. The result is that habitats in these systems exist across a gradient of environmental severity, with the most impacted habitats desiccating completely and the least impacted maintaining intact aquatic communities, even after long hot summers (Closs *et al.* 2006; McNeil 2004; Ostrand and Wilde 2001; Sparks *et al.* 1990; Wiens 1977). Although seasonal drought disturbance is often viewed as somewhat predictable, it is rarely consistent on an inter-annual basis, because of the overriding and somewhat chaotic influence of large-scale climatic variability (Thoms *et al.* 1999).

Under supra-seasonal drought, the influence of the drying season gains ascendancy over that of the intermittent ("wet") season, resulting in an increased scarcity of fresh water in the landscape, particularly at the end of the dry season. While seasonal drought is seen as a *press* type disturbance, supra seasonal drought creates a *ramp* type disturbance; gradually increasing in severity over an extended period (Lake 2003) (Figure 1). Under these conditions, even perennial and regulated permanent systems suffer reduced flows that can lead to the formation of isolated pools within normally very hydrological stable waterways (Metzling *et al.* 1995), and stranded water bodies may disappear completely (Boulton 2003; Lake 2003).

Under the recent millennium mega-drought (Lake *et al.* 2008), even the largest wetland systems in the MDB (e.g. Lake Alexandrina and Lake Albert), are under significant threat of drying beyond habitability (Bice 2008; Bice and Ye 2009). Similarly, groundwater levels may deplete to such an extent that base-flows to groundwater dependent systems cease altogether. These impacts potentially threaten normally dependable upland waterways and exacerbate low inflows to downstream reaches (Van Lanen and Peters 2000).

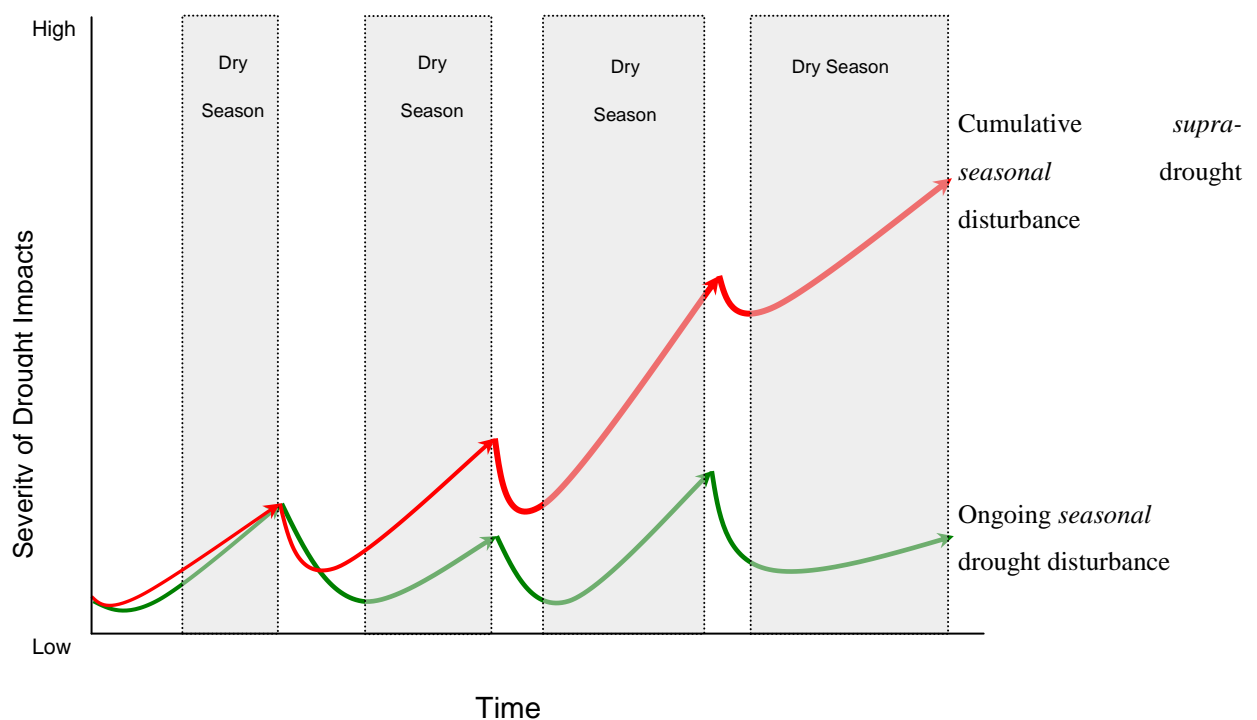


Figure 1. Seasonal drought disturbance increases throughout each dry season under the normal range of climatic variability, alleviated to varying degrees by intermittent wet seasons. Under supra-seasonal drought (red line), seasonal drought impacts become cumulative, with increasing impacts over time.

Under these conditions, a key process of increasing drought is the progressive disconnection between remnant waterbodies, both longitudinally within river channels, tributaries and distributaries, and laterally across riverine, floodplain and wetland habitats (Bond *et al.* 2008; Gawne and Gigney 2008). This process of spatial disconnection is incredibly important, especially following drought when pathways must be re-instated to reconnect fish populations. In a highly fragmented landscape such as the MDB, reconnection may be extremely complicated.

As isolated waterbodies continue to dry, *in situ* physical changes take place. These include a reduction in a) water depth and surface area, and b) the availability, complexity and variety of structural habitat (i.e. as water levels recedes below littoral vegetation, woody structures and shallow benches) (Arthington *et al.* 2005; Balcombe and Closs 2004; Closs *et al.* 2006; McNeil 2004). Depending on the type of water body affected, the nature and magnitude of drought impacts on water quality is expected to vary (Wood and Pfitzer 1960).

Reduced water inputs and increased evaporation under drought conditions lead to a number of changes in the physicochemical nature of those habitats, including water quality (Closs *et al.* 2006; Kodric-Brown and Brown 1993; McMaster and Bond 2008; McNeil and Closs 2007; Ostrand and Wilde 2001; Wallace *et al.* 2008; Winemiller *et al.* 2000). Drying is often linked with dramatic increases in water temperatures and increased incidence of thermal stratification in systems that

are otherwise well-mixed (e.g. isolated pools in lotic systems (Bormans and Webster 1997)). Changes in the thermal environment are often accompanied by dramatic decreases in dissolved oxygen (DO) (McNeil and Closs 2007; Wallace *et al.* 2008), combined with increased salinity (Lake 2003), organic load (McMaster and Bond 2008), and concentrations of the chemical by-products associated with algal activity and organic matter decomposition. Dissolved oxygen and salts can also stratify, further reducing the volume of aquatic habitat for all but the most exceptionally tolerant biota, within already shrinking waterbodies (Bormans and Webster 1997; Maier *et al.* 2001; Wallace *et al.* 2008).

Organic inputs to streams are typically seasonal and benign in nature (Barlocher and Graca 2002; Boulton 1991; Gasith and Resh 1999) and may be crucial components of overall ecosystem productivity (Vannote *et al.* 1980). However, during severe drought conditions, organic loads can increase dramatically as a result of leaf abscission from stressed and/or dying vegetation (Escudero *et al.* 2008; Williams and Ehleringer 2000), a problem exacerbated by a lack of flushing flows to export this material.

Decomposition of this material not only further reduces oxygen levels to the point of hypoxia (Towns 1985), but also results in the leaching of toxic compounds to the water (e.g. polyphenolic compounds found in *Eucalyptus* spp. leaves). These toxins are associated with 'blackwater' episodes which may cause fish kills (Boulton and Lake 1992; McMaster and Bond 2008, Gehrke *et al.* 1993; Townsend and Edwards 2003). By-products from anaerobic respiration (e.g. ammonium and sulphide), which may become increasingly concentrated as the water volume in remnant waterbodies shrinks, may also exacerbate these kills (Rodrigues *et al.* 2007).

With the majority of the MDB under heavy flow regulation and/or subject to the impacts of agriculture and/or urban development, the natural relationship between drought impacts and the response of aquatic systems are further complicated by anthropogenic changes to the pattern of flow, the nature of connectivity and the position of permanent water across the landscape.

Unregulated reaches, such as smaller or upper altitude streams/tributaries of major rivers, are still subject to more natural patterns of precipitation driven flow. However, the construction of instream barriers, changes to land use and abstraction of flows for agricultural and other human uses, mean that flow rates are generally lower than historically, with flashier catchment runoff patterns, (sharper hydrographs, shorter flow duration) and large volumes of flow captured in upper catchment dams, especially during lower flows (Teoh 2002, Heneker 2003).

Collectively, anthropogenic impacts on unregulated streams reduce flow duration and remove large volumes of flow from medium to low flow events, leading to longer cease to flow periods. The presence of dams and instream-weirs leads to habitat fragmentation and can impact on the ability of biota to move between reaches and recolonise periodically dry or impacted reaches (Mackay

2007).

Flow regimes of regulated streams and rivers in the MDB now differ considerably from historical natural regimes; with an overall reduction in flow volumes and peak flows occurring in summer (to meet irrigation demands) (Gehrke and Harris 1999). Overall, regulated reaches are now far more stable through time; where for some reaches water levels are almost static across time, regardless of natural climatic patterns. In particular, the lower River Murray downstream of Mildura is often considered a series of stable weir pools that exist in a state of 'anti drought' (Norris *et al.* 2001). More specifically, high water levels are maintained for far longer periods than they would have been historically.

Regulated reaches characteristically have unseasonal flow regimes and higher levels of permanency than historically; although the habitat value of these permanent waterbodies is likely to be far lower than under previous hydrological diversity. The increased stability in these systems leads to a far lower incidence of floodplain inundation and filling of off-channel wetlands and lakes, with many off channel habitats independently regulated by individual control structures (Smith and Fleer 2007).

Under drought conditions, the importance of regulated waterbodies, including weirpools, dams and river reaches, is likely to increase significantly due to their comparatively high degree of permanence. Research has barely focused on the role, or relative habitat quality of weir pools compared to natural habitats. However, the benefit of such habitats is conveyed through those species that are well adapted to the stable, low flow conditions that prevail in these man-made systems. As drought progresses, the implementation of irrigation and water resource restrictions can lead to the reduction of inflows into these reaches, subsequent declines in water level and water quality and further reductions to flow levels.

The impact of drought on regulated reaches is therefore complex, and likely to vary considerably across sites and systems. For example, the Wimmera River has become highly desiccated despite regulation. Similarly, the River Murray (below Lock 1) and the Lower Lakes/Coorong region have also become desiccated, while upstream reaches enjoy relatively stable water levels as a result of water pooled behind weir structures (albeit without floodplain and wetland connectivity).

Alternatively, anabranch systems such as the Wakool and Edward rivers have dried as a result of diversions of available water to the Murray River main channel (following the postponement of irrigation allowances that normally drive flow management into those systems). It is anticipated that monitoring and research programs conducted through the recent drought will significantly add to our understanding of the way regulated systems respond to drought. Hence, attention should focus on project outcomes that specifically collate and describe the responses of variously managed systems to drought impacts.

In addition to the natural cyclical nature of climate in the MDB, broad scale climate changes may lead to a *phase shift* where climatic conditions are reset at some different levels to recent historical records (Murphy and Timbal 2008). Although we will not enter a detailed discussion of climate change and phase shifts here, the predictions for drier climatic conditions across the MDB require that we consider the possibility of a changing climate. Under predicted patterns (Potter *et al.* 2008) the outlined cyclical nature of climatic harshness is likely to shift further towards the drought scenario; where a “normal” seasonal regime occurs, leading to a decreased influence of wet seasons and increased impacts of seasonal drying (Figure 1). In addition, the year to year ramping nature of drought disturbance may lead to increased drought-like impacts on aquatic ecosystems in the MDB. Under these scenarios, the drought impacts outlined in this report may become increasingly prevalent and resilience will become more important in determining long term viability of native fishes in the MDB.

3.0 How are Aquatic Biota Impacted by Drought?

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 resources 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 (the ability to persist) and resilience (the ability to recover) to impacts such as desiccation and/or habitat contraction (Lake 2000). 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.

3.1 Resistance Factors

Resistance relates to the ability of biota to survive the various direct/indirect impacts of drought and to achieve this, biota must tolerate or avoid those impacts (Lake 2003). In the MDB, many habitats are subject to the seasonal impacts of the climatic cycle and often undergo regular periods in extremely harsh environments during hot summers (Closs and Lake 1995; McNeil 2004). As a consequence, aquatic biota has evolved a range of strategies and adaptations for tolerating drought conditions. This section of our review will deal with these factors in more detail and, in particular, provide specific information regarding native and introduced fishes of the MDB.

3.1.1 Distribution, abundance and patchiness

The distribution and abundance of fishes is often highly individualistic, reflecting life history patterns, physiological tolerances and population fluctuations in terms of introductions, invasions, and local extinctions. While certain fish inhabit fast flowing, highland habitats (Pyron and Lauer 2004) and possess morphological adaptations such as excellent swimming abilities (Brazner *et al.* 2005), other species dominate lowland habitats on the valley floor or foothills displaying a tolerance to environmental variables such as turbid, silty conditions or warmer temperatures. Other species are more generalist, able to opportunistically modify their life history at local levels in order to persist in highly variable, unpredictable environments (Chapman *et al.* 2006).

For instance, in the MDB, the barred galaxias (*Galaxias fuscus*) is entirely restricted to fast flowing, cold montane reaches. Other species are restricted to the upper-mid reaches of the MDB where flows are moderately fast and temperatures are cooler (i.e. Macquarie perch (*Macquaria australasica*), mountain galaxias (*Galaxias olidus*), two-spined blackfish (*Gadopsis bispinosus*), river blackfish (*Gadopsis marmoratus*)), but whether this is due to an intolerance to thermal conditions or low flows is not clear. It is more than likely that those species that are at the northern

or southern extent of their range in the MDB are merely limited by thermal conditions, and are therefore most likely to respond to drought-related thermal shifts. Either way, under drought conditions it is highly probable that mortality as a result of thermal intolerance will also be closely linked to reduction in flow rates, which have a greater impact in higher altitude waterways (i.e. loss of two-spined blackfish from upper reaches of the Ovens Valley due to flow cessation) (Gawne and Gigney 2008).

Across the landscape, as flows continue to decrease under drought pressure, habitats begin to disconnect and fragment (Lake 2003, Matthews and Marsh-Matthews 2003). Higher floodplain habitats such as billabongs and anabranches become disconnected and begin to desiccate, followed by shallower habitats within main channels such as riffle reaches. Eventually, desiccation spreads to shallower runs and then pools, leading to widespread desiccation of a range of aquatic habitats. The extent and duration of disconnectivity is dependent on the extent and severity of drought; however, the process of reduced flows and habitat drying has a clear and direct impact on aquatic biota, and in particular native fish.

Eventually, aquatic habitats that receive direct inputs from groundwater become confined to remnant pools or 'waterholes' and fish populations become patchy. Arthington *et al.* (2005) demonstrated that while the overall abundances of fish persisting within waterholes on the Cooper Creek (Lake Eyre Basin) were low during protracted dry phases, it was the combination of flow history (area of adjacent floodplain inundated, period of inundation and time since last flood), interconnectedness of waterholes (proximity, and probability of connection) and physical habitat available during the dry phase (woody debris, boulders, scour holes, root-masses, leaf litter, aquatic vegetation) that were crucial to the persistence, or resistance of fish populations during periods of drought. Thus, the eventual resilience of fish populations to drought in dryland, lowland rivers was influenced by antecedent flood history and the quality of habitat available during the drought phase. In the case of lowland rivers, the high degree of anthropogenic disturbance in the MDB, in particular a reduction in flood frequency and magnitude may disrupt these resilience attributes when severe drought reduces regulated rivers to a series of waterholes, as occurred in many large rivers, their tributaries and anabranches during the most recent drought phase.

3.1.2 Low flows

The prevalence of low flow conditions during drought will have various impacts on aquatic dependent biota because even the development of low flows without severe drying (e.g. at the onset of drought) may impact on native fishes. For example, the loss of flowing reaches across the MDB may cease spawning and recruitment in the fluvial species, Murray cod (*Maccullochella peelii peelii*), which under current management scenarios are restricted to flowing anabranches such as Chowilla Anabranch (Zampatti *et al.* 2011). This section therefore specifically relates to the

traits of fishes that tolerate and function under conditions of low flow; that is, their ability to carry out necessary functions such as feeding, growth and under extended periods, reproduction and recruitment.

The majority of MDB fish species have evolved to persist through prolonged periods (multiple years) of low flow conditions, which as described earlier are enforced by the allogenic nature of inflows and prevailing hydrological variability (Puckridge *et al.* 1998). In general, the fish species of dryland Australian rivers tend to persist in low numbers during prolonged periods of zero flows and/or the contraction of rivers to isolated waterholes (Arthington *et al.* 2005), but respond to flooding with increased recruitment and offspring survival; leading to productivity levels comparable to some of the world's key freshwater fisheries (Bunn *et al.* 2006; Balcombe *et al.* 2007). It is generally considered that populations of most species found in dryland Australian rivers are maintained by flexible life history strategies such as the ability to tolerate and reproduce during low or zero flow conditions (Balcombe *et al.* 2006) and during floods. Furthermore, they benefit from extensive floodplain inundation and increased food resources, corresponding to flood-pulse models of fisheries function (Arthington *et al.* 2005; Balcombe *et al.* 2006; Balcombe and Arthington 2009).

In order to maintain populations of fish species native to dryland rivers, the low-flow-recruitment (LFR) hypothesis (Humphries *et al.* 1999; King *et al.* 2003) outlined a model that identifies that while rivers are highly variable (where flooding is unpredictable, or prolonged periods of drought are common), fishes will time reproduction to coincide with more predictable low flow periods (i.e. when temperatures are elevated), rather than align reproductive output to unpredictable floods. Indeed, these low flow conditions naturally occur throughout the MDB and even dominate the MDB lowland rivers (Humphries *et al.* 1999). Research from Humphries and Lake (2000) and later King *et al.* (2003, 2009) supports the LFR model; demonstrating that many MDB fish species will spawn in the absence of flooding. Favourable habitats that are abundant with prey, such as those found in the littoral areas and backwaters of river main channels, are often conducive to the survival of larvae during both low flow and high flow conditions. Although the ability for fishes to persist throughout protracted periods of low to zero flows (as often occurs during droughts), has only received limited attention in the MDB (Balcombe *et al.* 2006), it is believed that the ability to reproduce during drought conditions may be viewed as a critical resistance trait. Especially as low flows may, and often do, persist for periods far greater than the known longevity of many species native to the MDB (e.g. Australian smelt (*Retropinna semoni*), carp gudgeons (*Hypseleotris* spp.)). Hence, providing resistance to water quality conditions are met, it is the quality and availability of the physical habitats for fish to forage and avoid predation that effect resistance during drought periods when aquatic habitats are isolated to remnant pools (Arthington *et al.* 2005).

Declining water levels in regulated reaches can stimulate management concern and drive

interventions to provide managed flows to restore waterhole depth and water quality (Gilligan *et al.* 2009). These interventions are largely focused on iconic, angling species such as Murray cod and golden perch (*Macquaria ambigua*), and do not always consider broader ecosystem benefits or the impacts of delivering water to alleviate low flow issues, which can occasionally lead to ecological impacts such as hypoxic blackwater events and increased stress for remnant biota leading to fish kills (Pritchard *et al.* 2010). Alternatively, enforced periods of summer low flows that result from a drought related loss of irrigation supplies may in fact be beneficial in providing low flow summer spawning habitats for native fish adapted to reproducing in low flow periods. For instance, the highly threatened olive perchlet (*Ambassis agassizii*) in the lower Lachlan River, for which drought provided an opportunity to rebuild populations formerly decimated through river regulation impacts (McNeil *et al.* 2008a).

3.1.3 Desiccation

The complete desiccation of habitats represents the most extreme and obvious impact of drought on water-dependent organisms; however, many aquatic organisms have adaptations that allow them to persist through periods of desiccation. These include desiccation-resistant life stages such as eggs (Brock *et al.* 2003; Jenkins and Boulton 2007; Lake 2003; McNeil 2004; Paltridge *et al.* 1997; Snellen and Stewart 1979), seeds (Welling *et al.* 1988) or spores (Dodds *et al.* 1996) that can lie dormant without water for decades and rapidly recover upon re-inundation. Similarly, some aquatic organisms are able to aestivate in torpor of metabolic arrest as adults and tolerate desiccation within substrates; often utilising constructed burrows that minimise water loss (Brainwood *et al.* 2006; Christian *et al.* 1996; Fordham *et al.* 2008; Roe and Georges 2007).

While some fish species also produce desiccation resistant life stages and undergo aestivation in response to the loss of surface water, only one Australian fish species (from outside of the MDB), the salamanderfish (*Lepidogalaxias salamandroides*) is capable of aestivation (Berra and Allen 1989; Pusey 1990). In the MDB, no native fishes are currently known to be capable of aestivation or possess desiccation resistant life-stages, even though this has been suggested (i.e. spangled perch). The recently introduced oriental weatherloach (*Misgurnus anguillicaudatus*), however, regularly aestivates within soil substrates during periods of desiccation (Koster *et al.* 2001; McDowall 1996; McNeil and Closs 2007). As a result, the ability for MDB fish species to survive drought impacts relies largely on resistance mechanisms within aquatic habitats where they are subject to changes in water quality, habitat and biotic parameters without the option of avoidance.

3.1.3 Water Quality

As obligate aquatic organisms, fish in the MDB are dependent on the quality of the aquatic medium for individual-based, physiological processes, such as respiration, osmoregulation, excretion, thermoregulation, and reproduction; all of which are strongly impacted by water quality. However,

our understanding of the impact of water quality on the biology and ecology of MDB fishes is limited (Closs *et al.* 2006; Gehrke 1988; Gehrke 1991; Thompson and Withers 1999) and understanding of the tolerance of native fish species to key water quality impacts has been highlighted as a priority knowledge gap relating to our understanding of fish habitat use in the MDB (SKM 2003).

Not only is fish survival directly dependent upon being able to tolerate ambient water quality conditions, but also their ability to tolerate increasingly adverse impacts of drought on water quality (e.g. decreased dissolved oxygen, increased water temperature and increased salinity). As a result of drought, water quality parameters may reach potentially lethal levels, long before the threat of desiccation becomes likely (McNeil 2004). A range of pollutants and toxins may build up in aquatic ecosystems and threaten native fish. The predominant water quality parameters that are most likely to be associated with drought and to impact upon native fish and habitat are dissolved oxygen (DO), salinity, water temperature and pH (SKM 2003)

Oxygen

Oxygen is an essential component of the basic metabolic function of almost all living organisms (Hochachka 1980). The occurrence of oxygen levels below that which are required for normal activity is termed hypoxia (McNeil 2004). Within the aquatic medium, oxygen is far less soluble than it is in air, and is far more likely to limit the distribution of aquatic organisms than terrestrial ones (Kramer 1987). Under normal conditions, warm water temperatures limit the saturation of dissolved oxygen in water, thereby reducing the amount and volume available for respiration, while increasing the biological demand for oxygen (Beamish and Mookherjee 1964; Cech Jr *et al.* 1994; Davis 1975; Jackson *et al.* 2001; Smale and Rabeni 1995).

During drought, low or cease-to-flow episodes reduce the turbulent mixing of water bodies; thus limiting the mixing of oxygen at the air-surface interface. This can lead to severe stratification of dissolved oxygen throughout a waterbody and restrict the amount of available oxygen in the surface layers (Rahel and Nutzman 1994; Wallace *et al.* 2008). Under drought conditions, lentic waterbodies often undergo frequent diel fluctuations in dissolved oxygen as increased autotrophic respiration (particularly at warmer temperatures) during the night contributes to the oxygen demands from aquatic organisms (Gehrke 1988; McNeil and Closs 2007; Saint-Paul and Soares 1987; Smale and Rabeni 1995). The nature of hypoxia in aquatic habitats and its subsequent impact on fish assemblages during drought varies widely across habitats. The spatial extent and severity of hypoxia is highly dependent on the physical structure (i.e. depth, surface area), the hydrological regime and the isolation period of each waterbody (Closs *et al.* 2006; McNeil 2004).

Fish have evolved a number of behavioural strategies and physiological mechanisms for tolerating hypoxic episodes. Air breathers (facultative or obligate) have an obvious advantage in avoiding

hypoxia through use of atmospheric oxygen, often by means of a highly vascularised swim bladder or intestinal lining (Burggen and Johansen 1986). For water breathers, a common adaptation is aquatic surface respiration (ASR), whereby fish respire at the fine water surface layer that is maintained near to saturation by diffusion of oxygen from the atmosphere. The ability to utilise the surface layer effectively is maximised by possessing a small body size and morphological features such as an upturned mouth, flat head and neutral or positive buoyancy (Dean and Richardson 1999; Gee 1986; Gee and Gee 1991; Kramer 1987; McNeil and Closs 2007; Rosenberger and Chapman 2000).

Other physiological and morphological adaptations for surviving hypoxia include a) increased gill surface area (Galis and Barel 1980), b) capacity for anaerobic metabolism (Blazka 1958; Burton and Sephar 1972; Hochachka 1980) and c) the ability to regulate gill ventilation rate, aerobic respiration and oxygen consumption. These adaptations in response to hypoxic conditions all help to maximise oxygen uptake by the blood (McNeil 2004; McNeil and Closs 2007; Rosenberger and Chapman 2000; Verheyen *et al.* 1994). In lentic freshwater systems, oxygen is arguably the most influential of all abiotic factors that influence fish community structure (Jackson *et al.* 2001; Magoulick and Kobza 2003; Robinson and Tonn 1989; Suthers and Gee 1986).

Our understanding of the impact of hypoxia on fish in the MDB is largely based on a few recent studies (i.e. Gee 1986; Gee and Gee 1991; Gehrke 1988; Gehrke 1991; Gehrke and Fielder 1988; McNeil 2004; McNeil and Closs 2007). These studies are primarily based around the northern MDB, lowland or floodplain fish/communities, with almost no detailed assessment of fish from fast-flowing or upland habitats, even though species adapted to these systems are more likely to be intolerant of hypoxic conditions (McNeil 2004). The pioneering work of Gehrke (1988) and Gehrke and Fielder (1988) provide the most rigorous assessment of the physiological respirometry of the spangled perch (*Leiopotherapon unicolour*).

In these studies, spangled perch were found to tolerate oxygen levels down to 5% saturation, enabling them to persist in isolated pools during drought; under oxygen saturation levels of less than 20% (Gehrke 1988). Although the studies were limited to only one species, this work serves as a useful template for understanding the resistance limitations of native MDB fishes to drought conditions. In particular, Gehrke (1991) observed experimentally that juvenile golden perch avoided habitats that were low in oxygen (<15% saturation) and high in polyphenols (e.g. tannin and lignin; $4.5 \pm 0.12 \text{ mg L}^{-1}$) despite abundant food resources. However, tolerance values for these parameters were not obtained.

Gee (1986) and Gee and Gee (1991) assessed the thresholds for aquatic surface respiration and the use of buccal bubbles in a range of eleotrids including the flathead gudgeon (*Philypnodon grandiceps*), common to the MDB. McNeil (2004) established behavioural and physiological

laboratory methods for assessing hypoxia tolerance in MDB fish and provided comprehensive tolerance values for an entire community of floodplain fishes from the Ovens River (McNeil and Closs 2007). Under seasonal drought conditions, hypoxia combined with physical factors, such as waterhole depth and surface area, interact upon unstructured fish assemblages to create distinct assemblage groups over the course of seasonal drought (Closs *et al.* 2006). Furthermore, the impact of drought related hypoxia was implicated in a range of important biotic processes such as predation and competition (McNeil 2004).

Invasive species such as common carp (*Cyprinus carpio*), goldfish (*Carassius auratus*), oriental weatherloach, mosquitofish (*Gambusia holbrooki*), common in the MDB, were among the most hypoxia tolerant and may gain a competitive advantage over native species due to their ability to withstand drought impacts (McNeil 2004; McNeil and Closs 2007). Other information on the impact of hypoxia on MDB fishes is primarily derived from field observations. It is clear, however, that hypoxia is likely to be a key factor in the impact of drought on freshwater fish communities in the MDB. Tolerance to hypoxic conditions represents a significant resistance mechanism for surviving drought periods and therefore deserves further and more complete investigation.

The volume of dissolved oxygen is closely linked to water temperature (Coutant 1987; McNeil and Closs 2007; Secor and Niklitschek 2001), dissolved organic compounds (Gehrke 1991; McMaster and Bond 2008), and salinity. Under drought conditions the combined impact of these factors is likely cumulative and interactive (McNeil 2004). To understand their applicability to drought conditions the knowledge of the temperature and salinity at which various hypoxia tolerance data are collected is essential. For instance, in order to maximise the relevance of available tolerance data to drought conditions, it is recommended that investigations of hypoxia tolerance include measurements made in warm water conditions so that they are consistent with drought scenarios.

Alternatively these measurements are made as close to the thermal limits of test species (which also need to be further investigated) (McNeil and Closs 2007). Furthermore, under anoxic conditions (i.e. 0 mg L⁻¹), certain bacterial species may switch to use other compounds (e.g. nitrate, iron, manganese, sulphate and carbon dioxide) for respiration (Achnich *et al.* 1995; Liu *et al.* 2009). As a result, ammonium and sulphide concentrations may reach levels that become toxic to aquatic organisms, particularly juvenile fish, and further exacerbate the impacts of hypoxic drought conditions (Rodrigues *et al.* 2007).

Finally, thresholds for dissolved oxygen levels may be used as trigger points for management responses to prevent fish mortality under drought conditions. For example, in Rodwell Creek in the Eastern Mount Lofty Ranges, hypoxic thresholds for DO, including an alarm (4.5 mg L⁻¹) and Critical (2.0 mg L⁻¹) threshold were set as part of the state's Drought Action Plan (M. Hammer, unpublished data) to sustain a threatened population of river blackfish. When thresholds were

exceeded, management responses such as trucking additional fresh water into the site and installing aerators were implemented as a means of restoring and maintaining water quality above the threshold limits (Bice *et al.* 2010).

Nevertheless, drought management interventions can also pose a threat to native fishes through depletion of dissolved oxygen and hypoxia. For example, during the recent drought, the provision of some flows (provided to alleviate drought impacts and prevent desiccation and water quality decline), caused hypoxic 'blackwater events' that added additional stress to fish already impacted by drought.

As a consequence, the delivery of water resources to address impacts of drought must take steps to minimise additional impacts. For example, flow volumes must be significant enough to flush organic materials and poor quality water from remnant habitats, particularly where the inundation of dry reaches is concerned. Furthermore, the delivery of flows need to be planned in advance, as reactive flow provisions, delivered at the height of summer, when water quality and fish condition are lowest, are more likely to result in catastrophic impacts (Gilligan *et al.* 2009).

Salinity

Salinity is a widespread and common factor across the MDB (Jolly *et al.* 2001), and is predicted to worsen as the impacts associated with drought increase under future climate scenarios (MDBC 1999). During low flow and drought episodes, salinity levels may increase due to evaporative concentration or, in some circumstances, inflows of saline groundwater (Bond *et al.* 2008; Lake 2003). The severity of these impacts often depends upon the extent of the water level recession, the timing of the episode and its duration (Wood and Pfitzer 1960).

Under drought conditions, increasing salinity levels in shrinking pools can provide a direct threat to the survival of freshwater fishes and strongly influence assemblage structure in ephemeral stream pools (Ostrand and Wilde 2001). The MDB freshwater fish species are largely tolerant of high levels of salinity due to their recent marine ancestry (Hart *et al.* 1991); however, little data is available on the occurrence of drought-related salinity impacts, even in highly saline inland systems (Chessman and Williams 1975).

While comprehensive tolerance data does not exist for many fishes of the MDB, a review by Clunie *et al.* (2002) provides an excellent summary of data available at that time, and outlines key knowledge gaps. The collection of LC₅₀ values (under gradual acclimation) are the most relevant threshold values to inform predictions of field distributions and ecological scenarios (Kefford *et al.* 2004). However, for short lived life stages such as eggs and larvae, direct transfer LC₅₀ values may be necessary (McNeil *et al.* 2009a; McNeil *et al.* 2009b).

One of the primary knowledge gaps regarding salinity tolerance is the almost complete lack of data

for larval and egg stages (Hart *et al.* 1991; Kefford *et al.* 2004; Nielson *et al.* 2003), with most tolerance LC_{50} data collected from adult or juvenile fish (Bacher and Garnham 1992; Hart *et al.* 1991; Jackson and Pierce 1992; Williams and Williams 1991). Recent studies have revealed that for a range of MDB species common to the Lower River Murray, larval life stages are far more susceptible to salinity than eggs, juveniles and adults of the same species (McNeil *et al.* 2009a; McNeil *et al.* 2009b; McNeil *et al.* 2009c; McNeil *et al.* 2009d). This has important implications for some fishes in the MDB where drought related salinities already approach or exceed the tolerance threshold for larval life stages. In the Lower Lakes of the River Murray, Yarra pygmy perch (*Nannoperca obscura*) failed to recruit over three years (2007-2009) since refuge salinity rose above their recently determined LC_{50} threshold of 6.3 ppt (Bice *et al.* 2008; McNeil *et al.* 2009a).

Chronic and ecosystem-level impacts of salinity are largely unknown for MDB fishes. "Tolerable" levels of salinity can have sub-lethal effects, including reduced growth and condition and changes in feeding behaviour and activity; this can have a cumulative impact on fish fitness and cause extensive mortality after many months (McNeil *et al.* 2009d). Finally, reduced hatching rate of diapausing zooplankton eggs under saline conditions upon rewetting (Bailey *et al.* 2004) may also lead to reductions in key food sources for small-bodied fish, particularly those with highly specialised zooplanktivorous diets such as Australian smelt (Lieschke and Closs 1999).

Low freshwater inflows into estuarine systems may also cause salt water incursion into lowland freshwater habitats and drive an assemblage shift towards marine species (McAnally and Pritchard 1997). In the MDB, however, the Lower River Murray Barrages prevent this intrusion under current drought management scenarios (Bice 2008; Bice and Ye 2009). These barriers also limit the movement of native diadromous and euryhaline fishes and hence potentially limiting natural drought-response movements. These barriers thus may be, in effect, worsening the impact of the present drought conditions upon diadromous and euryhaline species by decreasing their access to obligate freshwater habitats and their ability to compete with marine generalist species (Jennings *et al.* 2008). As the only population of coastal, diadromous and estuarine fishes in the MDB, the combined impact of barrage operations and water management under the recent drought represent a dramatic threat to the resilience of these species.

Water Temperature

Following a general increase in ambient temperatures, water temperatures generally become higher under drought conditions (Lake 2003; Welcomme 1979). Mechanisms include reduced surface water, and cooling groundwater inputs, reduced shading due to increased leaf abscission, and loss of water volume, which reduces the insulating capacity of the waterbody against atmospheric temperature. Increased ambient temperatures during drought conditions may cause thermal stratification of water bodies, where surface waters become warmer and less dense than

bottom water layers (Bormans and Webster 1997). Stratification is a common occurrence in deep standing water bodies (i.e. reservoirs, deep pools) during low flow and/or drought conditions, but is less likely to occur in flowing or large, shallow water bodies (Bormans *et al.* 1997; Maier *et al.* 2001; Westwood and Ganf 2004). Temperature stratification is almost always linked to stratification in other chemical parameters, particularly dissolved oxygen (Rahel and Nutzman 1994; Wallace *et al.* 2008). The extent of the impact on water temperature associated with drought is dependent on the physical nature of individual habitat factors such as habitat isolation, depth, groundwater and/or rainwater inputs, substrate type, wind exposure and vegetation cover (Magoulick and Kobza 2003).

It is widely accepted that, under drought conditions, increased water temperatures often approach the upper thermal maxima for fish survival (Rummer *et al.* 2009; Smale and Rabeni 1995; Tramer 1977; Wallace *et al.* 2008; Welcomme 1979) and these tolerances are directly linked to the survival and distribution of fishes in the wild (Currie *et al.* 2004). Available thermal maxima values for MDB fishes are largely based on observations made in the field, aquaria or aquaculture ponds, (see Koehn and O'Connor 1990), with few dedicated laboratory assessments of lethal upper critical temperature (i.e. upper $T_{critical}$). As a result, critical thresholds for minimising fish deaths are difficult to estimate with confidence, a problem experienced across a range of ecosystem types including drought susceptible marine systems (Rummer *et al.* 2009).

However, thermal tolerance data collected overseas for invasive species (now established in the MDB), may be useful in predicting native tolerances. For example, the thermal tolerance of rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) is around 27°C and 29°C respectively (Beitinger *et al.* 2000), which may be similar to thermal maxima for upland natives such as galaxiids (*Galaxias* spp.) or blackfish (*Gadopsis* spp.). Comparatively, the thermal tolerance of lowland invasive species, such as mosquitofish and goldfish (40°C and 36°C, respectively; Beitinger *et al.* 2000), are much greater. Hence, optimal temperature estimates for these invasive species may be useful in predicting sub-lethal temperature impacts for native species (Burchmore 1990).

Thermal intolerance affects fish behaviour (Lowe-McConnell 1987) and is linked to changes in fish assemblage structure and distribution during drought. This may occur through the mortality of less tolerant species (e.g. brown trout) benefitting species with slightly higher tolerance, or through the capability of less tolerant species seeking out cooler sections of rivers, such as springs and shallow tributary streams (e.g. mountain galaxias) (Closs and Lake 1995). It is important to note that sub-lethal temperature impacts are poorly understood in relation to MDB fishes, but are likely to have significant consequences for fish health, growth and reproduction and interactive pressures through physiological dependence on body temperature.

Thermal tolerances and/or preferences are often used to classify fish (Lappalainen and Soininen

2006), generally resulting in the division of fishes into three broad categories: cold, cool and warm water species (Magnuson *et al.* 1979). These classifications are used to predict species that may possibly gain or lose habitats due to climate warming (Lappalainen and Lehtonen 1997) and such classification may be equally applicable to the MDB. Without concise thermal tolerance data, upper thermal limits may be inferred from geographical distribution within the MDB (Lintermans 2007).

However, it can be difficult to differentiate thermal limitations from altitudinal limits and flow preferences, given the close link between flow rates, altitude and water temperature (Paller *et al.* 2006). Aquatic ecosystems are identified as some of the most high risk ecosystems in terms of susceptibility to drying climate (McNeil and Hammer 2007) and hence consideration must be given to how ecosystem processes and functions are likely to be strongly impacted by dryer climate regimes. Under broad scale ecosystem changes, factors such as productivity and food availability are likely to exacerbate any direct impacts of climatic drying on fish in the MDB.

The impact of water temperature under drought conditions is, however, not restricted to absolute thermal tolerance. Many aspects of the life history and general biology of fishes are closely linked to water temperatures and to seasonal thermal regimes (Koehn and O'Connor 1990; McNeil and Hammer 2007; SKM 2003). For example, fish migration and spawning events are often closely linked with temperature cues (e.g. Humphries *et al.* 1999; King *et al.* 2003; Koehn and Harrington 2005; Mallen-Cooper and Stuart 2003; Malmqvist 2006; McNeil and Hammer 2007; McNeil *et al.* 2008a,b); Milton and Arthington 1983; Milton and Arthington 1984; Milton and Arthington 1985; O'Connor *et al.* 2005) and are timed with optimal temperature conditions for larval development, growth and feeding (Jobling *et al.* 1995; King *et al.* 2003; Magnuson *et al.* 1979). Therefore, changes to temperature regimes under drought conditions may have cascading impacts on the general biology and reproductive potential of MDB fishes.

Water temperatures are directly linked to a wide range of physiological processes in fishes. For example, warmer water temperatures result in increased metabolic rates and metabolic demands (McNeil and Closs 2007), while simultaneously reducing the amount of dissolved oxygen available to fish (Coutant 1987; Secor and Niklitschek 2001). As a result, the impacts of water temperature are often difficult to separate from associated factors, such as physical, chemical and biological variables, that compound the impact of high temperature on the resistance capacity of freshwater fishes.

For fish species that lack physiological resistances or behavioural mechanisms for surviving extreme temperature conditions, it might be possible to exploit microhabitats which provide cooler temperatures and higher DO levels, providing respite for brief periods (e.g. small, shaded areas or areas of groundwater or hyporheic input). In contrast, for tolerant species, higher temperatures may provide a beneficial environment for growth and food availability, and in turn provide release

from predation by larger, high temperature intolerant species (Anjos *et al.* 2008; Chapman *et al.* 2002; Rosenberger and Chapman 2000). However, regardless of thermal tolerance levels, as water bodies dry out, increasing water temperatures may exacerbate fish sensitivity to toxins. For instance, exposure to sublethal concentrations of agricultural pesticides, such as endosulfan and chlorpyrifos, decreased the critical upper lethal temperature of four MDB species: silver perch, Murray rainbowfish (*Melanotaenia duboulayi*), Western carp gudgeon (*Hypseleotris klunzingeri*), and rainbow trout, by as much as 2.5 – 5.9°C (Patra *et al.* 2007).

Acidity (pH)

Extreme acid and alkaline conditions are not common across the Murray-Darling Basin, and as a result, little is known about the acid or alkaline tolerance of native fishes. It is considered, however, that most native species are intolerant of pH levels below 5, or above 10 (Bice and Ye 2009). The exposure of sediments during the recent drought has presented a perceived risk of acid-sulphate development following desiccation and re-inundation of some soil types. In particular, the marine deposited sediments within the Lower Lakes, exposed for several years under drought, present a risk of widespread acidification upon rewetting and has drawn the attention of Natural Resource Managers.

Response interceptions have included the addition of limestone which can reverse acidification of waterways with low risk of impact on threatened fishes in the Lower Murray system (Gillanders *et al.* 2010). The potential for acid-sulphate soils to contribute to drought related fish kills is not fully understood, but the broad distribution of sulfidic sediments in wetlands across the MDB (Hall *et al.* 2006) suggest that there is a risk of widespread impacts resulting from the acidification of waterbodies as a result of drought.

3.1.4 Avoiding drought impacts-retreat to refugia

Many organisms possess wide-ranging avoidance mechanisms that enable them to avoid the impacts of seasonal and extended drought. For example, migratory birds undertake trans-continental migrations to avoid the seasonal impacts of harsh winters or drought. Migration cues and pathways are also strongly influenced by varying supra-seasonal regimes of drought and global climate change (Gordo 2007). African elephants seasonally travel thousands of kilometres in response to drought and water availability, continually moving to find new waterholes as each desiccates (Western and Lindsay 2008). Some freshwater organisms such as turtles possess the ability to emigrate and find new water-bodies where they can reside until more favourable conditions return (Bishop *et al.* 1995). However, many aquatic fauna, including the fishes of the MDB, are restricted to the aquatic medium.

While some MDB species may be able to avoid drought impact through movement into more benign estuarine or marine habitats, this movement has not been documented as a response to

drought. In addition, current management operations of the Lower Murray Barrages preclude the passage of refugee fish away from the drought impacted Lower Lakes. In addition, the closed Murray Mouth precludes access to near shore refugia for diadromous or euryhaline fish downstream of the Barrages (Bice and Ye 2009; Jennings *et al.* 2008). The ability for most MDB fishes to avoid drought impacts revolves largely around their ability to make potamodromous movements into relatively benign habitats within connected freshwater habitats, where their chances of surviving drought are higher (Magoulick and Kobza 2003).

At the onset of a predictable, seasonal drought, low flows and changing in-stream conditions may trigger emigration (i.e. movement out of a region) when low flows provide unsuitable habitat or limit resources for certain fishes (Love *et al.* 2008). For instance, some headwater fishes in southern North America have been reported to move downstream during extended dry periods (Ross *et al.* 1985). It is therefore likely that many fishes utilise flow and temperature cues to trigger migration at the onset of drought (Paller *et al.* 2006). However, the specific environmental cues driving fish movement to avoid adverse conditions are, as yet, unknown. One possibility is that drought related retreat to refugia habitats may be triggered by chemical induced, stress related cues, since many fishes often employ chemical communication for other purposes (Burks and Lodge 2002; van de Nieuwegiessen *et al.* 2009). Similarly, there are reported incidents of other moisture dependent organisms, like amphibians, use conspecific chemical cues to trigger moisture conserving strategies in response to drought (Rohr and Madison 2003).

Some MDB fishes are reported to undertake potamodromous 'dispersal' movements or migrations, as opposed to spawning migrations (Reynolds 1983) for the purpose of seeking refuge during drought using temperature and flow cues (Mallen-Cooper 1999). Again, it should be noted that the nature of these cues and their relationship to drought impacts has not been clearly demonstrated; although a few observations of possible drought and/or desiccation avoidance strategies exist. For instance, Wallace *et al.* (2008) observed Murray cod moving from shallow (<1.5 m) home range habitats into deep pool habitats (>3 m) when the Darling River ceased to flow and contracted to isolated deep pools during 2007/08.

While the cues to seeking drought refuge were not determined by Wallace *et al.* (2008); Sharpe *et al.* (2009a) has since determined that the distribution of Murray cod in the same study region is dictated by proximity to deep (>3m) refuge pool habitats. Sharpe *et al.* (2009a) also observed that Murray cod in the Darling River are more abundant in shallow run habitats immediately adjacent to deep pool habitats than they are in shallow run habitats of similar habitat quality, but which lack access to deep pool habitats. Similarly, Jones and Stuart (2007) observed Murray cod retreating from shallow inundated off-channel habitats as water level decreased in order to avoid desiccation, only to be isolated as a result of impassable regulatory structures. The above studies demonstrate that some fish species native to the MDB may have evolved behavioural adaptations to highly

variable flow regimes, which may in turn help them avoid desiccation during drought.

Any fish that do not possess the ability to detect cues that suggest oncoming desiccation, and then move into habitats with high persistence potential, or do not have the fortune to be located within the vicinity of a refuge habitat during the onset of drought, risk becoming stranded and dying. Equally, fish that possess the capability to select habitats with good potential to resist drought, may select habitats that eventually dry out anyway, depending upon the severity and duration of drought. On floodplains of the Ovens River (southern MDB), the majority of fish species, especially small bodied fishes, were widely and evenly distributed across most available habitats, regardless of physical habitat factors such as waterbody size or depth. Hence, following seasonal floods, many were left stranded in ephemeral pools. On the other hand, large bodied species such as golden perch, river blackfish, common carp and redfin perch (*Perca fluviatilis*) were not present in habitats that would potentially dry out following seasonal flooding, and were therefore lost from very few habitats as a result (McNeil 2004).

This pattern suggests some level of selection for deeper, more permanent habitats, where floodplain resources may offset any risk of stranding (Balcombe *et al.* 2009). The degree to which the risk of drying, or previous experience of seasonal drought (more likely in longer lived large bodied species) influences the selection of deeper habitats remains unknown. This raises the importance of refuge habitats and the role that they play in protecting fishes through periods of seasonal and supra seasonal drought.

3.2 The Role of Drought Refugia

Refugia are essentially habitats that protect organisms from the impact of disturbance, conveying resistance (a sanctuary from the impacts of the disturbance) and resilience (the capacity to sustain a supply of colonists following the disturbance) to inhabitant biota (Lake 2003; Robson *et al.* 2008; Sedell *et al.* 1990). The concept of aquatic drought refugia for freshwater fish, therefore, relates to habitats where fish can seek shelter from the impacts of drought and maintain a source population from which they can recolonise desiccated and/or impacted habitats and rebuild viable populations (Chapman and Chapman 1998; Magoulick and Kobza 2003; Rosenberger and Chapman 2000).

In general, refugia can be perceived as dispersal centres operating for the maintenance and resilience of depressed populations following a disturbance (Robson *et al.* 2008). They may be conceptualised as supporting metapopulations (Love *et al.* 2008) where physical attributes such as differences in refuge size, persistence and quality allow for the survival of resident biota and/or populations and ultimately shape immigration and emigration rates (Donovan and Thompson 2001; Hanski and Gilpin 1997; MacArthur and Wilson 2001; Taylor 1997; Taylor and Warren 2001). Within refugia, biotic predator-prey and competition dynamics (Williams *et al.* 2003) strongly shape local communities.

While the role that refuge habitats play during drought is relatively straightforward, the definition of what makes a refuge habitat is not. Predominantly, this is due to the highly complex nature of both drought disturbance and aquatic ecosystems, both of which operate across a range of temporal and spatial scales (Robson *et al.* 2008; Rohr and Madison 2003). To satisfy the above definition, a refuge habitat can only be identified once it has fulfilled its role in protecting and rebuilding populations throughout, and after, disturbance events. However, this does little to assist with the pro-active identification and management of key habitats that are likely to be important to fish populations during drought (Lintermans and Cottingham 2007). The current task is therefore to explore the nature and characteristics of aquatic drought refugia in the MDB and outline how they may operate in fulfilling their role under conditions of drought disturbance.

An important consideration in the determination of refugia is scale, as different parts of catchments may be differentially impacted by drought (Ross *et al.* 1985). Refugia operate at a number of spatial scales and function independently for various species or groups of fishes. Their role is inextricably linked with both abiotic and biotic factors that will determine whether they eventually serve their role in supporting fish populations through drought disturbance. At broad catchment scales the types of waterbodies available for fish refugia may include large reaches of the main river or stream channels, off-channel lakes, lagoons, and waterholes, wetlands, anabranches, and billabongs (Arthington *et al.* 2005; Bond *et al.* 2008).

Perennial streams, that continue to flow throughout a drought, might provide cool areas (i.e. through shading or cool groundwater inputs) that serve to protect certain biota from thermal extremes (Bond 2007). Cool flowing areas will also provide refuge for riffle-dwelling invertebrates such as mussels and hydropsychid caddisflies (Golladay *et al.* 2004), and some riffle-specialist fishes (Kennard *et al.* 2006). Floodplain billabongs may provide important refugia for wetland species such as flat-headed galaxias (*Galaxias rostratus*) or southern pygmy perch (*Nannoperca australis*) (Closs *et al.* 2006; McNeil 2004; McNeil and Closs 2007). Constructed refuges such as weir pools are likely to persist through time to a high degree, but their relative importance as habitats for native fish is likely to vary greatly compared to less stable habitats elsewhere in the catchment.

At larger spatial scales, important refuge areas often possess a greater degree of heterogeneity. Within local habitat areas or within a single river reach or floodplain, organisms may select refugia based on this heterogeneity. For instance, flowing anabranches of the Murray River such as Chowilla and Mullaroo Creeks may provide 'flowing' refugia critical for sustaining riverine species like Murray cod in anastomised reaches, even though connectivity remains with deeper, more permanent river channel habitats (Zampatti *et al.* 2008; Sharpe *et al.* 2009b). Large, deep pools (>3 m) within the main channel of large lowland rivers sustain large bodied species such as Murray cod, golden perch, and common carp during prolonged periods of cease to flow (months to years)

(Sharpe *et al.* 2009a; Wallace *et al.* 2008).

Large intermittent streams may break into a series of deep, isolated pools, some of which are far more permanent than others, that are used by species such as golden perch and freshwater catfish (*Tandanus tandanus*) (Balcombe *et al.* 2006). Large bodied fishes on floodplains utilise deeper, permanent billabong refugia within the spectrum of available habitats, while smaller bodied species may utilise smaller, environmentally harsher waterholes where predation pressure is low (McNeil 2004). Similarly in upland streams, trout may be confined to deeper downstream refugia while mountain galaxias can utilise shallower and environmentally harsher habitats in upper reaches where trout are excluded by barriers to movement (Closs and Lake 1995).

Still, these quasi-permanent refuge habitats are not always guaranteed sanctuaries for the fish that move into them because after colonisation, the impacts of drought continue to work on refuge habitats, often at even finer scales. As refuge habitats dry and shrink, over-crowding may occur, putting pressure on food and habitat resources and increasing intra- and/or inter-specific biotic interactions. Over-crowding in shrinking pools can exacerbate oxygen depletion and/or increase susceptibility to disease (Ostrand and Wilde 2001; McNeil *et al.* 2011c).

Further drying conditions may only serve to push physio-chemical parameters to extremes. Therefore, at an ever finer resolution of spatial and temporal scales, the unique physiological and behavioural attributes of organisms may force them to retreat to microhabitat “refugia-within refugia” (Anjos *et al.* 2008; Gomez and Lunt 2006; Matthews 1998). Small micro-habitat patches (cm to m’s) might provide cooler temperatures and relatively high DO levels, providing respite for fish for brief periods of time. In contrast, fish with higher physio-chemical resistances may use small habitat patches with poor water quality to escape predation from less tolerant predators (Anjos *et al.* 2008; Chapman *et al.* 2002; McNeil 2004; Rosenberger and Chapman 2000). Food resources may become confined to intolerable micro-habitats such as hypoxic depths and fish may need to use these intolerable microhabitats intermittently to meet energetic requirements (Rahel and Nutzman 1994).

As yet the microhabitat characteristics of aquatic drought refugia in the MDB and their use by fish have not been studied in detail (see Stoffels and Humphries 2003). Equally, the temporal nature of drought refugia is also poorly understood. Reaches of permanent water, such as those along the lower Darling River, can break into strings of isolated pools in some years, and return to a single pool in others; with starkly differing physio-chemical properties occurring both between pools and over time (Wallace *et al.* 2008). Exactly the same process occurs in floodplain pools and anabranches where single refuge units will break into several isolated pools (McNeil 2004).

In mid catchment lowland streams, the distribution and permanence of refuge pools varies greatly from year to year (Bond and Lake 2005; Bond *et al.* 2008). In all cases the temporal variability is

associated with changes in fish assemblage structure and drives very high levels of population variability for some species over extended time frames (Perry and Bond 2009, Balcombe and Arthington 2009).

In the neighbouring, arid Lake Eyre Basin, catchment scale contraction and expansion of fish populations occur in response to drought and floods. The Neales River contracted into two widely separated refuge pools in 2007, one of which protected the entire catchment population of all but one of the local species (McNeil *et al.* 2008b). Subsequent reconnectedness has led to recolonisation of the catchment rapidly by spangled perch and bony bream (*Nematalosa erebi*), more slowly by golden perch, Murray hardyhead (*Craterocephalus stercusmuscarum*) and Murray rainbowfish and not at all for barred grunter (*Amniataba percoides*), desert goby (*Chlamydogobius eremius*) and mosquitofish (McNeil *et al.* 2011c). The arid section of the Lake Eyre Basin is useful in providing fundamental information on natural impacts of drought and responses of fish unrelated to anthropogenic impacts such as river regulation and may be used to guide management objectives and trajectories for restoration of populations following drought in the MDB.

Aquatic drought refugia are found across a range of ecosystem types and are used by a wide range of species (Table 1; Robson *et al.* 2008). For instance, some refugia will contain a variety of species that are analogous with the aquatic biodiversity of the surrounding aquatic landscape, such as *ARK* refuges. ARKs are typically found in areas where the biota is well adapted to disturbance and typically experience mild environmental conditions. ARKs tend to have high species richness, secure habitat complexity, adequate food resources, low predation-competition interactions and the potential for more diverse gene pools. On the other hand some refuges are only suitable for a subset of species that are well adapted to the within- refugia environmental conditions, such as *polo clubs*. Polo clubs tend to experience harsher environmental conditions, have lower species richness, poor habitat complexity, limited food resources, high predation-competition interactions and restricted gene pools (although competition pressure can be lower due to loss of species).

Other areas may be left untouched by disturbance, forming *casino* type refuges through chance; which may be highly variable and therefore difficult to characterise. Also, as refugia tend to vary across temporal scales, some refuge habitats may also merely act as *stepping stones* (Loehle 2007) supporting some critical phase in the organism's life history. Hence the types of habitats that are used as refugia will depend on the preferences, resistances, life stages and other traits of the organism in question (Robson *et al.* 2008).

While these definitions are extremely useful when considering the function of refugia for various organisms at relevant scales, the generalisation of fish refugia as only an ARK type does not hold up under closer scrutiny. Specifically, the polo club type plays a particularly important role in

protecting fish under the impacts of drought. In particular, environmentally harsh refugia may persist throughout drought and indeed deteriorate to the extent where many or most fishes are excluded through intolerance. However, a small suite of highly tolerant fish species can persist within these harsh habitats until drought breaks. Generally, these polo club refugee species do not fare well in larger ARKs, where predation pressure and competition for resources are high. The polo club therefore serves not only as a refuge during drought, but may also provide an essential component in the resilience of these species to the impacts of 'normal' non-drought periods where they are not afforded the isolation and freedom to build populations free from biotic constraints.

Table 1. Summary of the characterised refuge types based on Robson *et al.* 2008 (and references therein) used by different biota including proposed additions for fish refugia.

Organism Type	Refuge	Refuge Type
Algae	<ul style="list-style-type: none"> Dry biofilm on stone and wood; dry leaf packs and perennial pools; channel and floodplain pools and dry sediment. 	ARK and/or Casino
Macrophytes	<ul style="list-style-type: none"> Soil seedbanks 	ARK
	<ul style="list-style-type: none"> Storage organs/propagule reserves 	Polo Club
Trees/shrubs	<ul style="list-style-type: none"> Aerial seedbanks; soil seedbanks or propagule banks 	Polo Club
	<ul style="list-style-type: none"> Survival of adults at riparian fringes and beyond 	Casino
Macro-invertebrates	<ul style="list-style-type: none"> Backwaters and slackwaters; hyporheos; bank-side stones, stable surface stones, interstices between stable stones and other microhabitats that retain slow flows (although many of these refuges may be absent from sandy streams); 	Casino
	<ul style="list-style-type: none"> Egg banks; 	ARK
Amphibians	<ul style="list-style-type: none"> Aestivation sites 	Polo club
	<ul style="list-style-type: none"> Logs, patches under banks, riffles, subsurface stream sediments, stream vegetation Ovipositing sites 	ARK and/or Casino Polo club
Fish	<ul style="list-style-type: none"> Perennial pools and sections of persistent flow in non-perennial rivers and streams 	ARK
Proposed additions for MDB Fish	<ul style="list-style-type: none"> Environmentally harsh perennial pools where biotic constraints (e.g. competition, predation) are removed/alleviated for tolerant species 	Polo club, Casino
	<ul style="list-style-type: none"> Waterbodies where all but one species are excluded due to disturbance 	Isolation Tank
	<ul style="list-style-type: none"> Non-permanent waterholes that provide refuge during seasonal drought under wetter climatic conditions. Important habitats for building resilience, may dry under supra seasonal drought. 	Disco
Birds, Reptiles and/or Mammals	<ul style="list-style-type: none"> Perennial wetlands and rivers during dry periods and/or aestivation sites 	ARK

On the Ovens River floodplain, polo clubs provided a refuge where flat-headed galaxias, southern pygmy perch and Australian smelt could persist in isolation from the pressures of redfin perch, which dominated larger ARK refugia (McNeil 2004). Equally, in the Lake Eyre Basin, polo club refugia exist during seasonal and supra seasonal drought periods in the lower ephemeral reaches of large rivers. In these habitats, Lake Eyre hardyhead (*Craterocephalus eyresii*) and desert goby are able to persist in minimal numbers in very low quality habitats where salinity approximates sea

water, sometimes joined by spangled perch or bony bream (McNeil *et al.* 2008b). Outside of drought periods, re connectivity leads to periods where fish from upstream ARK refugia recolonise and dominate the habitats where polo club survivors become scarcer under the changed biotic conditions (McNeil and Schmarr 2010).

In Victorian ephemeral streams, diverse regional fish species are reduced to polo clubs where mountain galaxias and carp gudgeons may persist to varying degrees during drought periods (Bond and Lake 2005). Furthermore, the polo club refugia for fish can deteriorate to conditions where only a single species is able to tolerate the conditions and persist through the drought period (Bond and Lake 2005; McNeil 2004). In this instance, refugia tend to operate as isolation tanks; hence the authors propose a new refugia type for fish, namely *isolation tank* refugia (Table 1). Isolation tanks may serve to provide opportunities for populations of isolated species to rejuvenate then, upon re-inundation, provide them with the advantage to gain early access to local resources and habitats, before other species arrive from more distant refugia to recolonise the area.

An additional category of *Disco* refugia, previously proposed for the Lake Eyre Basin by McNeil and Schmarr (2010), is also proposed for fish in the MDB (Table 1). Disco refugia represent refuges from seasonal drought disturbances. Often isolated by large distances from other refuge habitats, disco refugia protect freshwater biota within a highly desiccated landscape. However, unlike ARK refugia, during extreme drought, disco refugia will dry out; sometimes regularly, or for extended periods of time. Therefore, these refuges become especially important for conveying resilience to fish populations since they provide habitats where populations can rebuild following disturbances and provide stepping stones for recolonisation of potentially contracted ranges or distributions. As such, disco refugia are important refuges during “intra-drought” periods, allowing freshwater fish to rebuild viable populations and maintain resilience over the long term. During non-drought periods, disco refugia are likely to be numerous and widespread across the landscape, but may disappear (or decline in condition) to provide polo club refugia during extreme drought.

Recent discoveries of small pockets of otherwise regionally extinct fish species have demonstrated that spatially scattered *Casino* refugia also exist within the MDB (Table 1). For example, the single small refuges that harbour newly discovered remnant populations of southern purple spotted gudgeon (*Mogurnda adspersa*) in the Lower Murray (Hammer 2007a) and olive perchlet (*Ambassis agassizii*) in the Lachlan River (McNeil *et al.* 2008a) have, for as yet unknown reasons, been spared from whatever combination of impacts has led to the disappearance of these species in other habitats. While the impacts of drought may impact upon these casino refuges, as they do elsewhere, individual casino refugia that are free from anthropogenic disturbance may shift to become ARK or polo club refugia. Similarly, casino refugia may not be drought refugia after all, and

then the impacts of drought may be disastrous. This was demonstrated by the complete desiccation, and possible loss, of a refuge population of purple spotted gudgeon (Hammer 2007a). Additionally, during early stages of drought, fish will have differing inter- and intra-specific abilities in retreating to refuge habitats and are likely to become stranded due to natural or man-made barriers before they are able to reach suitable refugia.

3.3 Deteriorating refugia condition under drought

Drought refugia are constantly changing entities, continually subject to the ongoing impacts of drought, despite their increased resistance potential compared to other habitats. As a result, the physical, chemical and biotic conditions in refugia vary significantly over time and in proportion to the severity, timing and duration of the drought. In the initial stages of isolation, overall conditions for fish within refugia are likely to be good, particularly in systems that are adapted to seasonal drought. More specifically, within refugia conditions are likely to be largely controlled by biotic factors such as predation, competition for habitat, food and spawning sites (Gasith and Resh 1999). As conditions dry there may be distinct shifts in macroinvertebrate assemblages, with drought tolerant taxa becoming dominant and a general shift towards opportunistic 'r-type' species that are tolerant of warm, low flow conditions (Boulton 2003; Gamito and Furtado 2009; McMahon 2002). These assemblage changes may in turn impact fish; particularly those with highly specialised diets (see Section 9.0).

As refuge areas further dry and contract, habitat complexity may also start to simplify as instream woody debris and undercut banks are left exposed. This resultant loss of instream habitat complexity may affect fish assemblages (Bond and Lake 2005). Over-crowding of refuge areas may also increase the intensity of intra- and/or inter-specific predation and competition (Matthews 1998). Limited movement and reduced choice of cover may lead to increased predation pressure in refuges, since decreasing volume of water within water bodies may mean aerial and terrestrial predators have potentially easier access to prey (Copp 1992).

Increasingly, the impacts of drought will begin lowering water levels, impacting on habitat and water quality conditions and increasing levels of abiotic disturbance upon resident biota (Closs *et al.* 2006; McNeil 2004) as outlined in previous sections. Extreme environmental pressures, such as hypoxia, may compound these interactions, since fish may be driven to the water's surface to use behavioural response mechanisms such as, aquatic surface respiration (Kramer 1987; McNeil 2004; McNeil and Closs 2007). Competition for resources may be further exacerbated, as a decrease in the volume of inhabitable water, following stratification, may reduce the overall area of available habitat and therefore increase the amount of overlap in microhabitat use (Copp 1992; Ingram 2009). Food resources may become difficult to obtain, with highly tolerant prey species residing in deeper hypoxic zones intolerable to fish for extended periods (Rahel and Nutzman

1994), increasing the effort required to access food resources.

Over-crowded conditions within refugia may also increase exposure and susceptibility of fishes to pathogens, parasites and diseases (Dove *et al.* 1997; Dove and Fletcher 2000) and increase the concentration of nutrients, metabolic waste and the probability of harmful cyanobacterial blooms (Gehrke *et al.* 1993). Confinement to isolated refugia habitat patches may also increase exposure to other toxic compounds, such as agricultural herbicides and pesticides such as malathion, endosulfan and chlorpyrifos and industrial pollutants that may enter the system, either accidentally or deliberately (Pablo and Hyne 2009). As water bodies dry, these poisonous compounds may become more concentrated and increasing water temperatures may exacerbate toxicity for fish (Patra *et al.* 2007).

Under advanced drying conditions, abiotic parameters take precedence over the biotic, driven by physical features such as the size and depth of the refugia, extent of the isolation, groundwater/rainwater inputs, substrate type, wind exposure and vegetation cover (Magoulick and Kobza 2003). Eventually, abiotic conditions can deteriorate to levels that remove fish species from the refuge assemblage (Arthington *et al.* 2005; Closs *et al.* 2006; McNeil 2004; McNeil and Closs 2007), creating the polo club assemblages outlined earlier (Robson *et al.* 2008).

These habitats will serve as key refugia for tolerant, mainly small bodied species, but of great concern is the ability for many introduced species such as oriental weatherloach, common carp, goldfish and mosquitofish to tolerate the most extreme conditions, and therefore polo club refugia in the MDB may act as refugia for undesirable species as well as rarer native species (McNeil 2004; McNeil and Closs 2007). Across the landscape, the majority of habitats eventually dry completely under severe drought pressure (Closs and Lake 1995). In such a scenario many refugia will disappear and by definition cease to perform the roles of refugia (if indeed, they ever were). Perhaps, under this scenario in the MDB, only the oriental weatherloach may persist; dormant and buried within substrate refugia, pending re-inundation.

However, those fishes that were able to seek out and persist within suitable refuge habitats, resisting the impacts of drought, must now rebuild viable populations and recolonise suitable habitats across their range wherever they can access the resources required for feeding, spawning and recruitment. The factors that enable species to rebuild viable populations following drought disturbance contribute to their resilience potential (Arthington *et al.* 2005). The resilience potential of fish species to recover is influenced by a wide range of factors that occur before, during and after drought disturbance.

4.0 Resilience of fishes under drought disturbance

4.1 Pre drought condition and anthropogenic impacts

Many of the factors that influence the resilience of fish populations following drought disturbance take effect long before the onset of drought. Largely, these are factors that generally support the maintenance of robust and viable populations across their geographic range. Population growth is dependent upon the number of individuals at sexual maturity, which in turn are able to successfully mate and produce larvae that are then able to disperse, settle and recruit (McGlashan and Hughes 2001). Hence, access to habitat types that facilitate the connectivity between each demographic step is essential (see Steneck *et al.* 2009 and references therein). The more widespread a species is, the greater the potential for local persistence (Taylor *et al.* 2006), whereas small populations may become highly fragmented and therefore physical and demographic connectivity is potentially severed (Knight *et al.* 2009). Low abundances could also elevate population extinctions (Boxall *et al.* 2002) and slow rates of population recovery (Hutchings 2000), especially if prior population genetic erosion or limited gene flow already occurs (Faulks *et al.* 2008; McGlashan and Hughes 2000; Vrijenhoek *et al.* 1992).

In terms of community stability with a system, each species performs a diversity of ecological functions; hence high species richness is often correlated with high functional diversity, and therefore greater ecological stability and resilience (see Tilman *et al.* 1996). Greater stability and resilience is additionally dependent on the ecological history of the region and species-specific characteristics (Holling 1994; Sankaran and McNaughton 1999; Walker *et al.* 1995). For instance, although the introduction of exotic species has increased the species richness of fish communities within the MDB; the functional capacity of the system at local scales is potentially threatened by the presence of recently introduced exotics like redfin perch, common carp and goldfish (Closs *et al.* 2006; McCarthy *et al.* 2006; McNeil 2004; Smith *et al.* 2007).

In pre drought conditions, the resilience potential of fish is influenced by their life-history traits, assemblage structure, resource availability (i.e. habitat and/or food), genetic structure and population growth patterns (Hutchings 2000; Hutchings and Reynolds 2004). These factors affect the general distribution, extent and structure of fish populations prior to drought, and following drought. They are also factors that are overwhelmingly linked to anthropogenic impacts which have also affected the ability of MDB fishes to deal with additional disturbances such as drought (Bond *et al.* 2008; Turner *et al.* 1994). For instance, river regulations across the MDB has lead to a myriad of impacts such as: *i*) habitat degradation, *ii*) loss of floodplain and wetland habitat, *iii*) loss of connectivity to the sea, *iv*) creation of migration barriers, *v*) the introduction of exotic species, *vi*) floodplain and riparian deforestation, *vii*) increased stock and agricultural land use, *viii*) increased water resource development and irrigation activities, and *ix*) increased water storage. These

factors, along with the potential impacts of climate change, all impact upon the potential for fish populations to be prepared for, resist and regenerate following drought (Collares-Pereira *et al.* 2000; Cowx and de Jong 2004; Dove and Fletcher 2000; Gehrke and Harris 2001; Lucas *et al.* 2009; Miller *et al.* 2007).

While no pre-European records of fish distribution and abundances are available (although potentially exist within aboriginal middens if excavated and analysed carefully) it is generally accepted that current numbers of native fish across the Basin exist at somewhere around 10% of their pre-European abundances (Lintermans 2007). A number of species have undergone fragmentation and/or extreme contractions in their distribution across the basin since European settlement. These include species such as: southern purple spotted gudgeon, olive perchlet, flat-headed galaxias, Murray hardyhead, trout cod (*Maccullochella macquariensis*), Macquarie perch, freshwater catfish and at more local scales, the southern pygmy perch and Yarra pygmy perch, river blackfish and possibly estuary perch (*Macquaria colonorum*), congolli (*Pseudaphritis urvili*), common galaxias (*Galaxias maculatus*) and a range of estuarine species. For example, the southern purple spotted gudgeon has become locally extinct within the entire Murray drainage, with only a single small population persisting (pre drought) in South Australia (Hammer 2007a.). Similarly, the olive perchlet, once widespread across the entire MDB is now virtually extinct, with only a single small population remaining in the Lachlan River (McNeil *et al.* 2008a.). Across their ranges, many species have undergone high levels of fragmentation, with remnant populations persisting in small isolated communities (McNeil and Hammer 2007). For example Murray hardyhead persist in a very few small areas that are highly fragmented and isolated (Wedderburn *et al.* 2007; Wedderburn *et al.* 2008). Others still appear to be widely distributed, but have become far less abundant than historical records suggest, prompting leading state, territory and federal government agencies to list 26 of the 46 native MDB fishes as either rare or threatened species (Lintermans 2007).

Anthropogenic modification is already acting as a ramp disturbance on these species with the most impacted being restricted to anthropogenic-type refuge habitats (e.g. built habitats such as weirpools or artificial channels) where they can resist the impacts of this disturbance (Robson *et al.* 2008). The impacts that arise from drought are therefore likely to add a compounding pressure to habitats that have already become constricted and impoverished as a result of human-induced influences. Thus, drought has the potential to significantly diminish the quality of these critical refugia. For example, the last known population of southern purple spotted gudgeon in the Lower Murray were found restricted in a single drain as a result of human-induced modifications to their preferred habitats. However, this last refuge has now become completely desiccated during the recent drought (Hammer 2007a.).

Threatened, isolated fish populations in the Eastern Mount Lofty Ranges have little chance of

recolonisation from the wider catchment and are therefore a high conservation value community. In this region, isolated populations of river blackfish, southern pygmy perch and mountain galaxias, all significantly impacted by water resource development, have come under threat from drought (Hammer 2007b; Lintermans and Cottingham 2007; McNeil and Hammer 2007). In the Lower Lakes similarly isolated and anthropogenically impacted populations of Yarra pygmy perch and Murray hardyhead have come under the risk of local extinction through the recent drought (Lintermans and Cottingham 2007). Populations of Murray hardyhead, confined to only a few off-channel lakes through river regulation, have crashed under recent drought conditions (Lintermans and Cottingham 2007). There is a clear pattern emerging (under the recent drought) of drought impacts presenting a stronger threat to those species already heavily impacted by anthropogenic development. The impact that this will have on the recovery of these populations following the drought remains to be seen, but it is likely that the pre drought resilience potential of these populations has been greatly reduced by pre-existing anthropogenic impacts. This has been described as a 'double whammy' impact leading to the loss of innate resilience in fish populations and increasing the pressure of drought disturbance (Bond *et al.* 2008).

4.2 Within-drought resilience factors

The key factor influencing the resilience of fish during drought is their ability to resist its impacts within refugia (as previously outlined), as this determines the suite of species that are able to recover. However, a number of other within-refuge factors, influencing resilience potential, are not directly linked to resistance by traits of individuals and/or groups of fishes. These factors largely relate to the ability of fishes to maintain viable populations during drought, either within refugia, or by taking advantage of opportunities (such as small flows, or periods of local connectivity during diminished wet seasons), to relocate to more favourable waterbodies.

There may be some potential for fish to maintain resilience strength throughout drought as long as flow conditions (Humphries *et al.* 1999; Junk *et al.* 1989; Puckridge *et al.* 2000), seasonal factors, such as temperature (Danilowicz 1995; Humphries *et al.* 1999) and spawning site availability (King *et al.* 2003) coincide with the spawning requirements of a given species. Maintaining or increasing population-building capacity also depends on satisfying recruitment requirements such as the availability of suitable receiving habitat for larvae and juvenile rearing (King 2004; King *et al.* 2005), sufficient quantity and quality of food resources (Boulton 2003) and limited competitive and predatory interactions (Thome-Souza and Chao 2004). In connected systems, recruitment success is influenced by the number of locally produced larvae, plus larval settlement from elsewhere, minus the total number of locally released larvae (e.g. downstream larval drift) (Botsford *et al.* 2009). However, in isolated systems, larvae recruitment is solely reliant on locally produced larvae. Consequently, life history traits, such as rapid growth rates, early age to sexual maturity, high

fecundity and lower longevity allow some species to rapidly exploit available resources (Holling 1994; Lobon-Cervia 2009) and ensure opportunities are maximised for population growth (Larkin *et al.* 2009).

For some species, spawning is triggered during warm, low to no-flow conditions, which are common within drought refugia. In the MDB, olive perchlet have been found to spawn under very low flow conditions once temperatures exceed 23°C (McNeil *et al.* 2008a). A range of small-bodied species, particularly those that utilise floodplain and backwater habitats, have been found to spawn and recruit under low flow conditions (Balcombe and Arthington 2009; Humphries *et al.* 1999) and are more likely to possess within-refuge recruitment capacity. Fecundity however, is often lower for these species, which may result in relatively slow population growth potential. Alternatively, species such as bony bream and mosquitofish have generalist reproductive requirements and high fecundity and are therefore able to regularly produce large numbers of offspring within drought refugia (Growth 2004; Tonkin *et al.* 2011).

Being short lived these smaller bodied species are more likely to rely on within refuge spawning and recruitment capacity to persist throughout periods of drought. This high dependence on within refuge recruitment has implications in habitats where competition and/or predation pressures are particularly high, such as shrinking refuge pools. As a result, a range of interacting biotic variables become important for the maintenance of resilience capacity during drought periods and the cumulative impact of these variables within drought refugia are likely to be highly site specific. The potential for smaller species to maintain resilience potential during drought may require the presence of refuge habitats where predators and/or competitors are excluded or at a disadvantage (Closs *et al.* 2006; Rosenberger and Chapman 2000). Often, the mechanisms underlying such exclusion are abiotic (e.g. microhabitat structure) and therefore, the complexity of biotically determined resilience factors is made more complex by interacting environmental factors (McNeil 2004).

As opposed to low flow spawners, a range of species in the MDB possess spawning and recruitment traits that are closely linked to and often dependent upon high flow conditions (Humphries *et al.* 1999; Koehn and Harrington 2005; Koehn and O'Connor 1990; Puckridge *et al.* 2000). In this way, species such as golden perch and common carp are able to utilise flow cues to access newly inundated floodplain resources such as larval/juvenile habitat and food (Balcombe and Arthington 2009; Humphries *et al.* 1999; Humphries *et al.* 2002; King *et al.* 2003). Diadromous species in the MDB frequently rely on flow cues to trigger spawning, and to provide access to and facilitate movement into marine environments (Koehn and O'Connor 1990; McNeil and Hammer 2007b). Equally, some introduced species also utilise flow cues to trigger movement and spawning, for example redfin perch show large spikes in recruitment directly following winter flows (McNeil *et al.* 2011c), while common carp form large spawning aggregations in response to flow

increases (Smith and Thwaites 2007).

Within drought refugia, these cues are often not present or greatly reduced, requiring adaptability within these species to enable some level of spawning and low flow recruitment. In Lake Eyre Basin refugia, golden perch were found to recruit at low levels during seasonal drought, even though flood mediated recruitment events are far more significant (Balcombe and Arthington 2009). Equally, common carp are able to respond to very small pulses of flow within drought refugia and produce large numbers of offspring during these small events (McNeil *et al.* 2011a).

For longer lived species, the short-term need to spawn and recruit within refugia is reduced. However, species with inflexible or flow related spawning requirements, must possess the longevity required to wait out drought periods, and subsequently the ability to reproduce when appropriate high flow conditions return (Collins and Anderson 1999). However, extreme intervals between flooding and rewetting are likely to restrict reproduction and recruitment, potentially constraining the capacity to rebuild populations. Therefore, life history traits such as slow growth rates, late age to sexual maturity, low fecundity, higher longevity and adaptive traits such as gonadal re-absorption, allow for conservation of resources during drought periods (Baker *et al.* 2009) and may support the persistence of populations until rewetting. Combined with the resistance traits of fishes, these within refuge resilience processes determine the status of species within post drought assemblages and will largely govern the potential for species to recolonise and rebuild viable populations across their previous distribution range once connectivity resumes.

4.3 Post drought resilience factors

We have determined that many of the factors that influence the resilience of fish to drought disturbance relate to the pre drought condition and the degree of non drought disturbance as well as the capacity for species to resist drought impacts and maintain viable populations, and even low level recruitment, within drought refugia. These resilience factors relate to the capacity of refuge habitats to support the functional processes that sustain a supply of potential colonists (Robson *et al.* 2008). If these components are not satisfied and no recolonisation potential remains post-drought, then even if populations persist within refugia during drought, they may end up resembling isolated 'living museums' of past conditions (Robson *et al.* 2008).

Once the yoke of drought disturbance is lifted, improved conditions will generally allow previously isolated waterholes to become reconnected once more. Reconnection allows fish to disperse into newly inundated habitats, exploit food resources and rebuild populations (Balcombe *et al.* 2006). Yet few studies have investigated the mechanisms underpinning the resilience of fish communities following drought at broad, landscape scales. For most obligate-aquatic organisms, the ability to recolonise is dependent upon the species' vagility and their ability to disperse into newly inundated areas (Griffiths 2006). It is also dependent upon the spatial configuration and types of drought

refugia. In particular, the distance between refuge and receiving habitats, plus the degree and timing of connectivity, are important factors in the recolonisation and resumption of broader distributional ranges following drought (Davey and Kelly 2007; Sheldon and Thoms 2006a). In general, recolonisation tends to decline with increasing distance from refugia (Davey and Kelly 2007).

There are often great differences in the recolonisation pattern of freshwater fish species following drought disturbance and contraction to refugia, with each individual species possessing a distinct recovery pattern. For example, species such as bony bream and spangled perch are known to recolonise entire catchment areas immediately on reconnected, even under during relatively low levels of within channel flow (McNeil *et al.* 2008b). A range of other species, including golden perch, Murray rainbowfish and Murray hardyhead will respond much more slowly, requiring successive seasons and/or larger areas of connected habitat to recolonise the same area. Alternatively some species show very low potential for recolonising their former range even with successive years of reasonable connectivity (McNeil and Schmarr 2010). These findings are supported in the MDB for species such as carp gudgeon, which move very slowly across larger landscape scales, rendering them susceptible to local extinctions as a result of drought (Perry and Bond 2009). For some fish (and larger sized macroinvertebrates), it may take hours to weeks to travel into rewetted reaches, depending on their proximity to perennial waters (Larimore *et al.* 1959). Recolonisation may also depend on species specific behavioural responses to the direction of flow upon rewetting. Magalhaes *et al.* (2007) found that there is a marked tendency for species richness to increase in downstream reaches following rewetting, since downstream flow generally aids dispersal for most species. However some species are more likely to colonise upstream wetted reaches (Davey *et al.* 2006) and others may move out to colonise areas along lateral gradients (Balcombe *et al.* 2007; Roach *et al.* 2009).

Hence, the spatial arrangements and heterogeneity of habitat patches and the possibility of intervening barriers might further constrain fish recolonisation pathways in post-drought conditions. For example, waterfalls create natural physical barriers, restricting gene flow between populations of the fly-specked hardyhead (*Craterocephalus stercusmuscarum stercusmuscarum*) (McGlashan and Hughes 2000); while man-made weir structures hinder the movement of Murray hardyhead during normal (in-channel) flow periods in the Lower Murray (Wedderburn and Walker 2008). Large accumulations of migrational species below large weirs are a common occurrence across the MDB following seasonal flows (Mallen-Cooper 1999) leading to the widespread implementation of fish passage facilities throughout the MDB (Barrett 2008). Given that the recolonisation of catchments following drought is often linked with spawning responses, access to suitable spawning areas is important during this post-drought phase, particularly for species with highly specialised spawning habitat requirements. Examples include wetland or vegetation dependent spawners such as

southern pygmy perch, flat-headed galaxias, olive perchlet and gudgeon spp. (Closs *et al.* 2006; Humphries *et al.* 1999). In many cases, longitudinal connectivity must be linked with lateral pathways to access floodplain and wetland habitats for these species and this may require high flows and even flooding (Graham and Harris 2005).

Similarly, habitat and food resources must also become available within receiving habitats both for the immigrant adults and for newly spawned recruits. Presuming that most of these receiving habitats will have become completely desiccated during drought, the re-establishment of these resources will depend upon their own resistance and resilience mechanisms under drought disturbance. Dormant life stages such as eggs, seeds or rhizomes, or ability to utilise refugia such as moist subsoil and crayfish burrows that have resisted drought, may allow rapid response following re-inundation and the ability to rapidly become abundant (Boulton 2003; Brock *et al.* 2003; DWLBC 2006). Therefore, the area of inundation and the re-wetting of specific habitat types such as floodplains may be very important to the resilience of fish populations (Balcombe *et al.* 2007). These processes may also have temporal dimensions, with a number of seasons likely to be required for rebuilding population size, especially for less fecund species or those that emerge from drought with greatly reduced population numbers.

Even once former ranges are re-established, and populations are rebuilt, the impacts of drought may still be evident. For example, flannel mouth suckers (*Catostomus latipinnis*) still bear the genetic impacts of historical drought events that reduced their population to only a few individuals millennia ago (Douglas *et al.* 2003). Furthermore, recovering fish populations must once again contend with the anthropogenic impacts that impacted on pre drought communities. Potentially, new anthropogenic impacts may have occurred as a result of drought conditions, for example, firewood removal from newly desiccated habitats will reduce the amount of woody debris available as habitat and hence constrain the rebuilding of populations. The use of dry wetlands and floodplains for agriculture may greatly impact on seed banks, rhizomes and egg masses within the soil reducing the food and habitat resources available to fish post-drought (Bond *et al.* 2008).

5.0 Conceptualising resilience to drought disturbance

This review of literature has provided an array of information that enables us to begin conceptualising drought impacts on fish in the MDB and what factors are likely to be important influences in maintaining the resistance and resilience of fish populations. As outlined in a previous section, the nature of drought is not constant, but rather a seasonal press disturbance, with impacts that gradually intensify with the dry season until it is relieved, to varying degrees, during the intermittent wet season (if one occurs). Under supra-seasonal drought, the influence of these seasonal drought cycles become increasingly harsher, as a multi-year drought intensifies in a ramp disturbance (Lake 2000; Lake 2003). Equally, resistance and resilience factors that are important for fish are not constant in their nature, but come into play as these cycles of seasonal drought press disturbances accumulate, under successive cycles, as the supra seasonal drought ramps up.

In an effort to conceptualise the heterogeneity of impacts, resistance and resilience factors were attributed to the specific phases of the seasonal drought cycle (Figure 2). Variables that are important before a drought occurs are allocated as 'pre drought resilience' factors within the conceptual model. They are thus important during the preliminary phase (Wet Season 1) and include ecological characteristics such as: the general abundance of the species, the patchiness of a population across its range and the breadth of its distribution across the MDB. Overall, these variables tend to operate at large, landscape scales. These ecological characteristic factors are important for the viability of populations regardless of impacts of drought disturbance and can often be heavily impacted by anthropogenic impacts such as the modification of habitats and river flows, catchment land use, harvesting and the introduction of exotic species. Thus anthropogenic factors that influence the 'starting point' of conceptual models may heavily influence the ability of species to meet the requirements of resistance and resilience during drought.

Variables that are important early in the seasonal drought cycle are listed within the early drying phase (Figure 2). They predominantly represent key resilience factors, related to the ability of fish to passively or actively inhabit refugia and their susceptibility to biotic factors that influence the early stages of habitat contraction. Structural and biotic impacts are important factors during this phase, in particular, reduced availability and diversity of habitat and/or food resources, and increased predation and competition pressures as a result of overcrowding.

During the late drying phase, conditions within refugia deteriorate at varying degrees (depending on the nature of the refugia) and abiotic variables then become increasingly important in structuring the fish community (Figure 2). Equally, the individual traits of each species may strongly influence the way that drought impacts upon them. This phase is characterised by a dependence on resistance traits such as environmental tolerance to various water quality parameters and

susceptibility to disease. In addition, resistance traits related to ability to spawn and recruit under low or no flow conditions will be important for short lived species, meaning longevity itself is an important resilience trait for species confined to refugia.

The post drought phase (e.g. Wet Season 2) of the seasonal cycle is highly variable (Figure 2). Under normal seasonal cycles, this may provide widespread connectivity and catchment inundation and resilience factors will become increasingly important. Yet under supra seasonal droughts, connectivity may not happen at all and resilience factors will predominantly fail. However, even during supra seasonal droughts, small periods of re-connectivity, and possibly even re-inundation of key spawning and feeding habitats may occur, that help to build resilience. The capacity for fish to migrate rapidly and recolonise new habitats and to spawn/recruit become increasingly important during the post-drought phase. Therefore, post drought recovery depends upon recolonisation potential, specificity of spawning habitat and food resource requirements, and dependence on rarely inundated habitats, such as wetlands or floodplain habitats (Figure 2).

For each phase, the success or failure of each species to satisfy their resistance and/or resilience requirements will determine their ability to maintain viable populations either throughout and/or following drought disturbance. For instance, while species that are evenly distributed across a landscape and highly abundant may have a greater potential to access a range of refugia, they may still succumb to predation pressure or poor water quality as the drought progresses. Alternatively, other species may locate refuges, and then survive refuge conditions, but possess very poor abilities for rapid recolonisation, or the ability to wait for floodplain inundation episodes to occur before spawning and rebuilding populations. Hence, the satisfaction of the various resistance and resilience requirements and the interaction of biotic and abiotic impacts with species traits are critical to their overall resilience and ultimate recovery (Figure 2).

A second model has therefore been developed to account for continuity of seasonal cycles (Figure 3). Here success (or failure) of resistance and resilience processes still drive fish assemblage and population structure, but individual seasonal patterns also have the potential to *i*) force fish populations into extended periods of isolation (as under extreme drought), or *ii*) provide ongoing periods of good connectivity (as for wetter periods) or *iii*) to enable them to vary dynamically under more realistic patterns of variable degrees of connectivity and isolation. Under this conceptual model, failure to meet resistance requirements will lead to localised extinctions of certain species. On the other hand, success (or failure) in satisfying resilience requirements, both within- and/or during post-drought phases, dictates whether populations are likely to be maintained, expand or fail under any given sequence of seasonal cycles. This model can be then run for individual species to determine the likelihood of surviving drought impacts. This model can also be used for known assemblages in specific habitats (i.e. with a measured fish assemblage structure), or for fish functional groups and/or guilds that may have similar resistance and resilience traits.

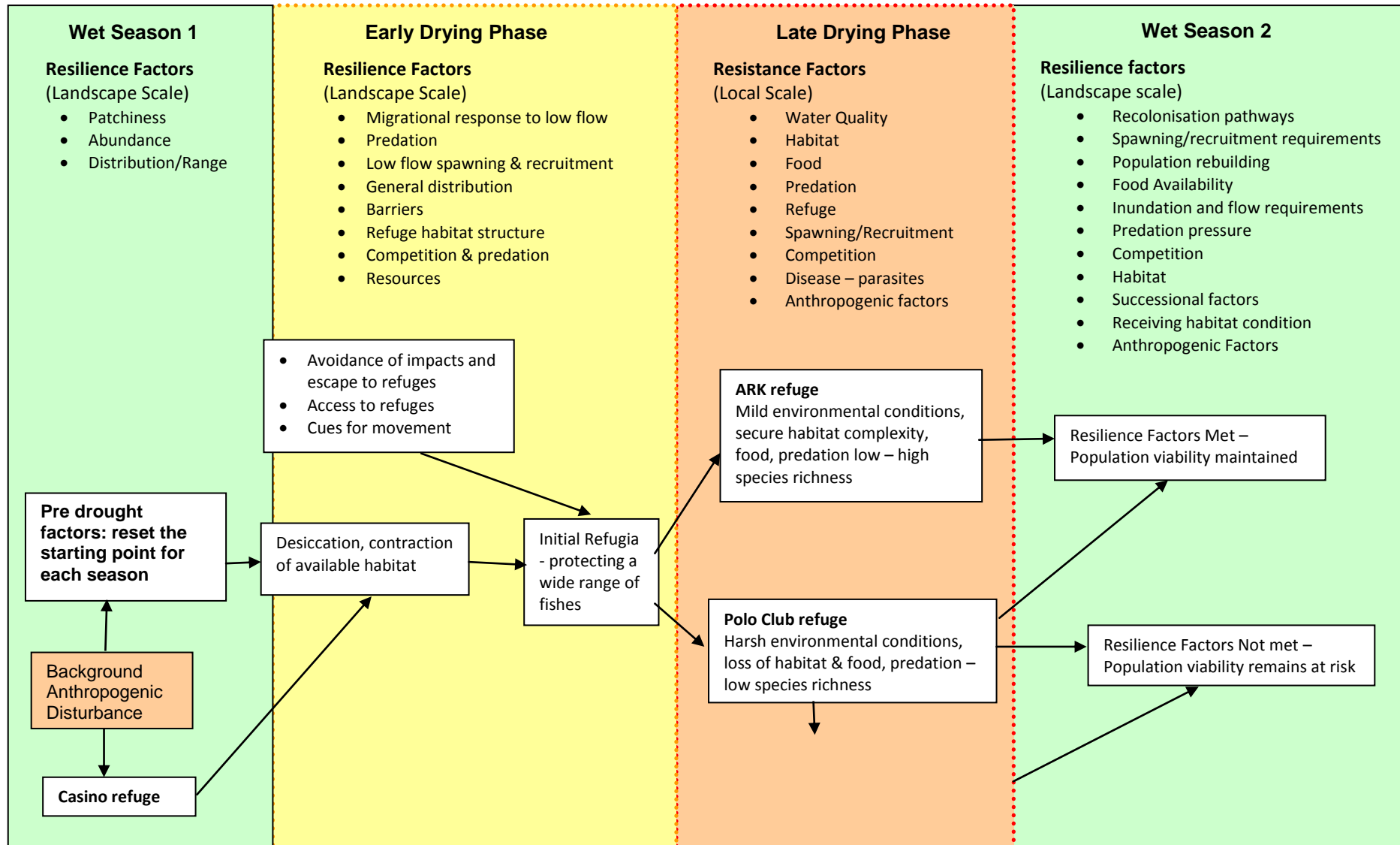


Figure 2. Conceptual framework outlining resistance and resilience factors through a seasonal drought period. A supra seasonal drought would string a series of these seasonal drought periods together with new starting points and accumulating impacts (greatly reducing potential) by the second wet season.

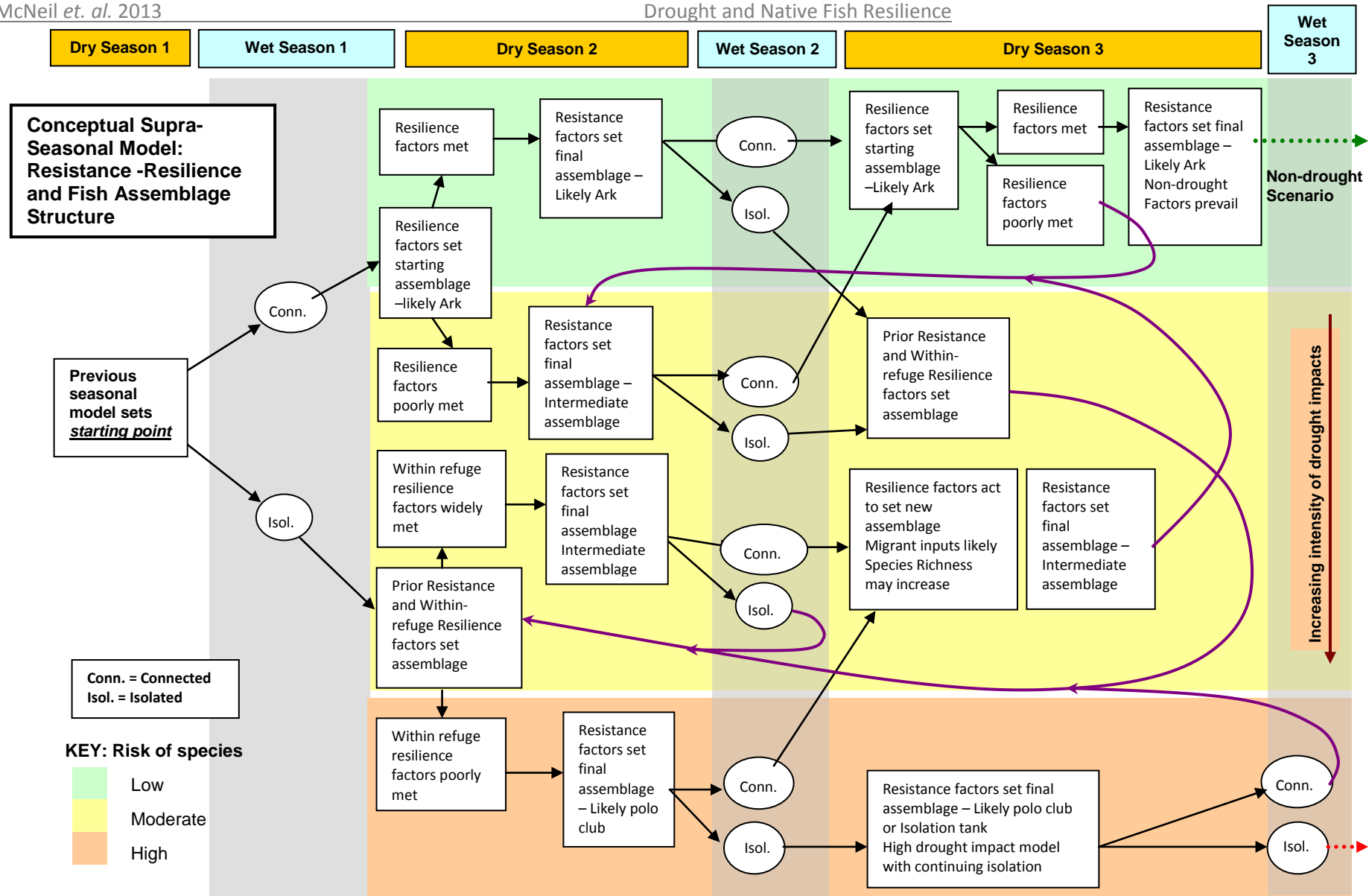


Figure 3. Conceptual diagram outlining the responses of fish assemblages through consecutive dry and wet seasons, including drought and non-drought sequences. Conn. = hydrological connectivity across habitats, Isol. = habitat isolation. Arrows show pathways through model.

Within this conceptual framework (Figure 3) more complex model units can then be constructed. By applying specific data related to species' attributes, traits and/or tolerance thresholds, more detailed estimates on the likelihood of populations and/or assemblages surviving various patterns of drought disturbance can be determined. If conducted for specific habitats (or collection of habitats), it should then be applicable across a wide range of scales, providing the potential to combine a number of individual models run for each refuge habitat; either within a catchment, and/or a management unit. Hence, the more detailed data available regarding resident fish species and local habitat and ecological characteristics, the better the predictions such a model may make in terms of determining the resilience of fish species, populations and/or assemblages under a range of possible scenarios.

This conceptual model (Figure 3) is based upon a series of multiple seasonal units, which are strung together under the duration of supra seasonal drought (n.b. with increasingly stronger drying phases and weaker intermittent, wet season influences). At the end of each cycle, various species may have either succeeded or failed to meet the various resistance and resilience requirements. Under 'normal' conditions, post drought resilience is more likely to be easily met. However, under supra seasonal drought, the diminishing or complete loss of connectivity of habitats between seasonal drought cycles means that the ability for species to meet their resistance and resilience traits will become much more variable. This will influence the final structure of refuge assemblages, effectively re-setting the next seasonal drought cycle to a new *starting point* (Figure 3). This new starting point will then be defined, not only by the structure of the final refuge assemblage structure, but also by the water quality conditions and resource availability that existed at the end of the previous cycle.

In reality, each successive seasonal drought cycle varies across this range. Some seasons may be defined by continual disconnectivity, while some seasons are defined by localised or lower levels of connectivity. Therefore, models of supra seasonal drought will be characterised by successive strings of particularly dry phases with poor connectivity, while wet phases will be characterised by strong periods of reconnectivity and a greater extent of inundation (subject to water availability and flow regulation). Conceptual models of resistance and resilience must be able to account for these extended strings of seasonal models, where each successive seasonal cycle is inherently linked to the previous cycle. In addition, each intermittent wet phase must consider the potential to either break the drought, or to force fish back into another cycle of within refuge isolation (and potentially anything in

between these extremes). Similar strings of wet and dry season factors have been successfully used to model native fish populations and climatic impacts previously for sites in the MDB (Perry and Bond 2009).

The impact of drought on fish assemblages can be modelled by running various drought scenarios and species assemblages through the successive phases and success (or failure) of resistance and resilience factors can be used to predict the impact for each species. The conceptual model (Figure 3) can be populated with specific assemblages and whatever data or level of information exists for the given assemblage or constituent species. Under any given scenario, threshold data from a specified site can be used to determine the success or failure of each species in meeting their requirements. The model therefore allows the testing of various scenarios and assemblages to determine potential susceptibilities and/or failure points for valuable species, or at a minimum to identify high risk species or thresholds that can assist in managing populations during drought.

Furthermore, the generalised nature of the conceptual model (Figure 3) allows it to be transferred across habitats and scales. For instance, it can either be applied to an individual waterhole, or to a broad scale network of habitats at the catchment or landscape level. Constituent fish species can be accordingly used or removed for different communities and local data can be used to develop thresholds and impacts as well as habitat variables and species' traits. The conceptual framework (Figure 3) is merely a first step in developing other models that can be informative and useful to scientists and managers. However, the population of these models with empirical data, as well as careful consideration as to the nature of various thresholds and responses, is still required. Long term data sets of fish assemblage and population structure, hydrology, habitat and water quality should be applied to this framework in order to validate and develop these models and to ensure applicability to modelling and predicting the impact of drought on MDB fish populations.

6.0 Qualifying drought responses in MDB fishes

6.1 Functional Response Groups and Guilds

While previous sections have outlined many of the important factors influencing the resilience of fish communities to disturbance, particularly drought disturbance, there is little information regarding general groups or suites of fish species that may be impacted by, or respond to, drought in similar ways. The presence of such groups for which particular factors may be generalised, is likely to be of significant interest to those who research, or manage, aquatic habitats under drought conditions (Lintermans and Cottingham 2007). While there is no known published attempt at investigating the presence of drought response groups in fish, significant effort has been made to develop guilds based on various life history traits, many of which are likely to be directly applicable for fish resilience (see Welcomme *et al.* 2006). Furthermore, researchers have made some attempts to classify and group other biota such as vegetation and aquatic invertebrate communities in terms of their response to drought.

The reasons that certain taxa respond in a predictable fashion to environmental changes, such as drought, is usually a function of their life history, behaviour, morphology, or other adaptations (Lytle and Poff 2004). Life history adaptations may include the synchronisation of life cycle events, such as reproduction and growth, to specific flow regime events. Other organisms have evolved morphological adaptations, such as anoxia tolerance, that allow them to persist throughout certain flow conditions. Alternatively, others use behavioural adaptations that allow an immediate reaction to certain flow conditions, via environmental cues. For example, resistance factors (e.g. physiological thresholds) and resilience factors (e.g. seed dispersal and germination characteristics) have previously been used to classify aquatic plant communities (van der Valk 1981; van der Valk and Davis 1980) and highlighted the significance of 'environmental sieves', or filters (see Lytle and Poff 2004; Poff 1997) in determining the survival and/or arrival of plants within marsh communities. Similar trait-based classifications were used to predict the responses of plant communities to disturbance (Noble and Slatyer 1980). Certain traits are expected to vary in response to environmental variability (e.g. changes in climate and/or precipitation), and can therefore provide a mechanistic understanding of their response to disturbance processes such as fire (Bradstock and Kenny 2003; Gasith and Resh 1999; Pausus 1999).

Drought, as a disturbance, can also be expected to inflict environmental filters on

aquatic communities from the onset, which will change and no doubt intensify as the drought develops. In particular, large-scale physio-chemical habitat filters may influence regional composition of organisms, whereas biotic interactions potentially filter the local community composition (Lytle and Poff 2004; Poff 1997). Magalhaes *et al.* (2007) described the recovery patterns of fish following drought disturbance in the Mediterranean Basin. In this study, the abundance of some species decreased within-drought, whereas the abundance of other species increased. There were also notable declines in the abundance of some species during post-drought conditions, whereas the abundance of others increased. However, the available biological information essentially failed to unify the species within each response group. As a result, it remains difficult to identify particular traits or groups of species, which may be especially vulnerable to the environmental filters imposed by drought.

Most organisms, including fish, have been characterised into guilds defining the way groups of species exploit environmental resources in the same way (Root 1967). For instance, when studying community shifts in estuarine assemblages that are exposed to drying conditions, fish are often assigned to guilds that describe various life history modes (Elliot *et al.* 2007; Franco *et al.* 2008; Martinho *et al.* 2007). Important biotic variables that shape the resistance of fish assemblages may simply be captured using feeding mode functional groups, especially at finer, local scales (Roach *et al.* 2009). Trophic guilds go further by providing information on feeding modes, geographic range and predator-competitor interactions (Main *et al.* 2007; Tales *et al.* 2004). Other guild types may be more applicable since they attempt to classify fish incorporating life history modes, feeding modes, specific habitat and microhabitat associations (e.g. flowing versus standing water bodies, pools versus riffles) and behavioural adaptations (e.g. migration and/or dispersal behaviour) (Welcomme *et al.* 2006). However, they are often highly technical and complex so it may be difficult to generalise or apply those guilds to ecological or management problems.

Classification of reproductive functional groups also considers the cues and conditions conducive to recruitment (Franco *et al.* 2008), which provides a means of determining the potential resilience of species. Several classifications of reproductive guilds of native MDB fishes are already proposed (Growth 2004; Humphries *et al.* 1999; Schiller and Harris 2001b). These reproductive guilds have been based on various life cycle adaptations such as cues required for spawning, timing and duration of the spawning period, fecundity, egg development, larval feeding and parental care.

McNeil (2004) produced drought tolerance 'clusters' using a range of MDB fishes

based on various behavioural and physiological tolerance indicators and respiratory modes. These groups represented different abilities for tolerating warm, hypoxic conditions and were directly related to the susceptibility of those species to the impacts of seasonal drought. Thermal guilds have been developed to capture physiochemical habitat variables that are likely to reflect species resistance strength (Lappalainen and Soininen 2006; Magnuson *et al.* 1979), although these generally relate to 'optimal' temperatures as opposed to limiting temperatures that are likely to be more important during drought (Lappalainen and Lehtonen 1997). Any use of guilds as an approach to drought modelling must be undertaken with caution due to the potential for differences in the individual traits, responses and impacts for each species, particularly under the cloak of unquantified anthropogenic impacts that may exist independently of drought, yet strongly influence survival and recovery. Any attempt to formulate guilds for this purpose must undertake a rigorous process of accumulating individual species data to verify their formation.

6.2 Drought response groups for fishes of the MDB

To investigate the possibility that distinct guilds (or groups) of fishes may exist in the MDB based on their susceptibility to drought impacts, the authors attempted to identify species' traits and key ecological factors that relate to drought impacts and the ability of species to survive and respond under a framework of climatic variability and harshness. The available literature, used to develop the current review, provides a range of information regarding the life history traits of MDB fishes that may contribute to, or detract from, their various potential in resisting the impacts of drought, and in recovering to re-establish viable populations following drought. The literature sources provide varying levels of detail on species' traits, ranging from specific biological and threshold data, through to estimations based on observational and expert opinion. While the available knowledge for some species is very poor, others have a relatively comprehensive and reliable degree of information regarding key traits and ecological factors. Therefore a range of available information on ecological characteristics, life history traits, tolerance thresholds and ecological threats has been collected for the entire native and exotic fish species recorded as present in the MDB (summarised in the tables found in Section 9.0).

Within drought periods, key biological *resistance* traits are likely to provide the greatest survival potential and tolerance to abiotic variables, such as *i*) low flows, *ii*) low dissolved oxygen levels, *iii*) high salinity, *iv*) high temperatures, *v*) greater adaptability to alterations in food availability and/or competition-predation

interactions. Accordingly, physiological traits related to these abiotic variables and a species' adaptability to food availability and competition-predation interactions are likely to be important factors determining whether or not a species can meet the 'requirements' for surviving drought impacts.

In addition, a number of non-drought (e.g. pre drought or post drought) factors relating to the initial ecological status of a species may influence species resistance and resilience. These factors reflect pre-existing factors, such as the presence of historical anthropogenic impacts that may interact with direct drought impacts on population survival. However, it is important to note that these are not species' traits, but instead relate to the ecological history of that species in the MDB and are included in this analysis because they may be influential in determining the success (or failure) of species in surviving drought impacts. Several key questions were therefore considered that addressed: species abundance (e.g. if a species is present does it tend to be highly abundant?); distribution (e.g. how widespread is the species across the MDB?) and patchiness (e.g. at any given site within its range, what is the likelihood of the species being present?) of populations. Furthermore, life history traits, such as longevity, age to maturity, spawning requirements, spawning specificity (e.g. general versus highly specific spawning requirements), dispersal ability and fecundity are also included, as they are factors that are likely to be particularly influential to species' resilience potential. During post- (and pre-) drought conditions, these resilience traits come to the fore, as they potentially provide the ability to recolonise and rebuild populations.

The success or failure for these factors to convey resistance and resilience are intricately linked with the characteristics of each specific environment, and therefore, in order to be integrated into conceptual and empirical models, must be linked to the specific environmental scenarios for the target system (see McNeil *et al.* 2011b). Equally, data such as population structure (the presence of recruitment and long lived, fecund individuals) is likely to be a strong determinant of survival at local scales. For the purpose of determining drought response groups, resistance and resilience factors are generalised at the scale of the MDB to support Native Fish Strategy (NFS) objectives. This approach also assumes that when populations are present, population structure is sound, although this may be precluded somewhat by the ecological factors of abundance, distribution and patchiness that are included here.

6.3 Scoring Resistance and Resilience Factors

Accordingly, drought factors were separated into resistance and resilience factors based on their contribution towards a population surviving the direct impacts of drought versus their contribution to the maintenance of viable populations. This approach allowed scoring to be integrated into the conceptual model outlined earlier (Figure 3), and supports the development of empirical scoring to establish success or failure of a species (or assemblage) throughout seasonal drought sequences.

A total of 30 common fish species from the MDB (Table 2) were selected because sufficient and reliable information existed in the literature (see Species Information Tables: Table 5). Species specific resistance/resilience traits and ecological characteristics were scored across a constant scale between 0 and 6 (Table 3).

The higher modality (i.e. score value of 5 or 6) was given to the expression of traits that were considered to enable better resistance and resilience to drought, while lower modalities (i.e. score values of 0, 1 or 2) represented poor potential for tolerating drought. This six-stage scoring system allowed the representation of high or low adaptation to drought (6 and 1), as well as providing representation of moderately high (4 and 5) and moderately low (2 and 3) adaptiveness. Importantly, a middle score value of 3 was used in the case of *i*) no data, or *ii*) for values with low confidence or *iii*) for situations where species' traits were neither adaptive nor prohibitive to their resistance and resilience to drought. This score was applied based upon the collective agreement of the authors and in consideration with data from congeneric species.

Resistance factors were defined as: physiological tolerances to low flows, high temperatures, low dissolved oxygen, and salinity and biological adaptabilities to predators and diet that may have impact within refuge habitats. *Low flows* scores range from 1 (intolerant of low-flow conditions) to 6 (prefer low flow conditions). *Temperature* scores range from 1 (upper temperature thresholds < 24°C) up to 6 (upper temperature thresholds > 38°C). *Dissolved oxygen* scores range from 1 (tolerate DO levels > 5 mg L⁻¹) up to 6 (tolerate 0 mg L⁻¹). *Salinity* scores range from 1 (< 12, 000 mg L⁻¹) up to 6 (> 38, 000 mg L⁻¹). Two biological parameters were also considered as resistance traits and include: *predator susceptibility* scores ranging from 1 (highly susceptible to predators) to 6 (key predator and non-susceptible) as well as *feeding specificity* where scores range from 1 (highly specialised diet requirements) to 6 (generalist diet requirements). In addition, pre drought ecological factors such as a measure of *abundance* included scores ranging from 1 (low

abundance if species is present) to 6 (high abundance if species is present); *distribution* includes scores ranging from 1 (not widespread across the MDB) to 6 (widespread across the MDB) and *patchiness*, which defines the level of population fragmentation and likelihood of a species being present within any given site across its MDB range with scores ranging from 1 (highly fragmented populations) to 6 (non-fragmented populations).

Resilience traits summarise ecological variables that describe the resilience of fish species in pre-, within- and post-drought conditions. Reproductive variables encompassed: *longevity* which defines typical maximum lifespan includes scores ranging from 1 (1-2 yr lifespan) up to 6 (> 15 yr lifespan); *age to maturity* where scores range 1 (< 6 months to breeding age) up to 6 (> 5 years to breeding age); *no-flow spawners* which defines the ability to spawn within low-flow or cease-to-flow conditions, with scores ranging 1 (no ability) to 6 (very capable); *spawning constraints* which provides a measure of species-specific spawning needs in terms of flow, seasonality, habitat type and so on, with scores range from 1 (highly specific needs) to 6 (no-specific needs); *dispersal ability* which defines a species' vagility with scores representing 1 (poor vagility) to 6 (very high vagility) and finally *fecundity*, which defines the number of potential offspring where scores of 1 (100's eggs) up to 6 (100, 000's eggs or 100's live young). These variables were based upon existing data.

Table 2. Common fish species of the Murray-Darling Basin (from Lintermans 2007). Conservation listings are: C = common; L = listed as state or federal conservation concern (vulnerable and higher), prior to 2006; R = recently identified as a conservation concern at IUCN workshop Adelaide, 2010; and I = introduced species.

Common name	Scientific name	Conservation status
Barred galaxias	<i>Galaxias fuscus</i>	L
Two-spined blackfish	<i>Gadopsis bispinosus</i>	L
Rainbow trout	<i>Salmo trutta</i>	I
Macquarie perch	<i>Maccullochella macquariensis</i>	L
River blackfish	<i>Gadopsis marmoratus</i>	R
Yarra pygmy perch	<i>Nannoperca obscura</i>	L
Trout cod	<i>Macquaria australasica</i>	L
Mountain galaxias	<i>Galaxias olidus</i>	C
Olive perchlet	<i>Ambassis agassizii</i>	L
Murray hardyhead	<i>Craterocephalus fluviatilis</i>	R
Common galaxias	<i>Galaxias maculatus</i>	R
Southern pygmy perch	<i>Nannoperca australis</i>	R
Purple-spotted gudgeon	<i>Mogurnda adpersa</i>	L
Dwarf flathead gudgeon	<i>Philypnodon macrostomus</i>	C
Flathead galaxias	<i>Galaxias rostratus</i>	R
Congolli	<i>Pseudaphritis urvillii</i>	R
Freshwater catfish	<i>Tandanus tandanus</i>	C
Silver perch	<i>Bidyanus bidyanus</i>	L
Australian smelt	<i>Retropinna semoni</i>	C
Murray cod	<i>Maccullochella peelii</i>	L
Redfin perch	<i>Perca fluviatilis</i>	I
Golden perch	<i>Macquaria ambigua</i>	C
Carp gudgeon	<i>Hypseleotris spp.</i>	C
Bony bream	<i>Nematalosa erebi</i>	C
Oriental weatherloach	<i>Misgurnus anguillicaudatus</i>	I
Common carp	<i>Cyprinus carpio</i>	I
Flathead gudgeon	<i>Philypnodon grandiceps</i>	C
Spangled perch	<i>Leipotheapon unicolour</i>	C
Goldfish	<i>Carassius auratus</i>	I
Mosquitofish	<i>Gambusia holbrooki</i>	I

Table 3. Scores for resistance and resilience factors (based on species traits and ecological characteristics) of a subset of native and exotic fishes from the Murray-Darling Basin.

Species	Resistance Factors									Σ -Resistance	Resilience Factors						Σ - Resilience	Total Score
	Abundance	Distribution	Patchiness	Low - Flow Tolerance	Temperature Tolerance	DO Tolerance	Salinity Tolerance	Predation	Feeding Specificity		Longevity	Age to Maturity	No flow Spawning	Dispersal Ability	Fecundity	Spawning Constraints		
Barred galaxias	5	1	0.5	0.5	0.5	0.5	1	1	5	15	2	1	1	2	1.5	1	8.5	23.5
Two-spined blackfish	2	3	2	1	1	2	2	3	4	20	3	2	1	1	2	1	10	30
Rainbow trout	4	1	1	1	1	1	3	6	5	23	3	3	1	3	2	1	13	36
Macquarie perch	2	1	1	3	3	3	3	2	3	21	4	4	1.5	2	3	2	16.5	37.5
River blackfish	4.5	3	3	2	2	2	2	4	5	27.5	3	2	1.5	1	2	1	10.5	38
Yarra pygmy perch	1	1	1	5	5	4	4	1	3	25	1	1	5	1	1	3	12	37
Trout cod	1	1	0.5	4	2	2	2	5	6	23.5	5	5	1	1	3	2	17	40.5
Mountain galaxias	3	4	3	3	4	4	4	1	3	29	1.5	1	2	4	4	3	15.5	44.5
Olive perchlet	4.5	1	0.5	5	4.5	4	3	1	5	28.5	1	1	5.5	1	2	3	13.5	42
Murray hardyhead	5	0.5	0.5	5	5	5	6	1	1	29	1	1	6	1	1	3	13	42
Common galaxias	6	1	1	3	3	3.5	6	1	5	29.5	2	1	2.5	3	3	3	14.5	44
Southern pygmy perch	3	2	2	5	5	5	3	1	5	31	3	1	2	2	1	2	11	42
Purple-spotted gudgeon	2	0.5	0.5	5.5	4	4	3	3	5	27.5	3	0.5	5	1.5	2	2	14	41.5
Dwarf flathead gudgeon	4	3	3	2.5	3.5	3.5	4	2	5	30.5	2	2.5	2	2.5	3	3	15	45.5
Flathead galaxias	2	1	1	6	4	4	3	3	5	29	2.5	1	6	1	2	2	14.5	43.5
Congolli	5	1	1	4	2.5	2.5	6	6	5	33	4	2.5	2	1	2.5	1	13	46
Freshwater catfish	2	4	1	5	4	4	3	2.5	3	28.5	4	5	6	2	3	2	22	50.5
Silver perch	3	3	4	4.5	5	4	3	1	5	32.5	4	4	1	5	5	2	21	53.5
Australian smelt	5	6	6	5.5	4	4	6	1	2	39.5	1.5	0.5	6	6	1	5	20	59.5
Murray cod	4	4	4	4.5	5	2	3	6	6	38.5	6	6	2	2	4	2	22	60.5
Redfin perch	3	6	6	5	5	4	3	6	6	44	4	1.5	3	4	4	3	19.5	63.5
Golden perch	4	4	5	4.5	5	4	3	5	6	40.5	6	5	1	6	5	2	25	65.5
Carp gudgeon	6	5	6	6	5	5.5	4.5	1	5	44	2	1	6	5	2	6	22	66
Bony bream	6	6	6	6	5	2	6	1	6	44	3	0.5	5	6	5	6	25.5	69.5
Oriental weatherloach	5	5	4	6	6	6	5	2	6	45	2.5	2	6	5	4	5	24.5	69.5
Common carp	6	6	6	6	6	5.5	5	3	6	49.5	5	1	1	5.5	6	1	19.5	69
Flathead gudgeon	6	6	6	6	5	6	6	4.5	5.5	51	2	1	5	2.5	3	5	18.5	69.5
Spangled perch	4	4	5	4	6	6	6	5	6	46	3	1	4.5	7	4.5	5	25	71
Goldfish	5	6	6	6	6	6	5	3	6	49	5	2	6	6	5	5	29	78
Mosquitofish	6	6	6	6	6	6	6	5	6	53	2	1	6	4	5	6	24	77

In order to explore preliminary patterns in overall resilience to drought disturbance, and to explore the existence of drought response groups, the total scores for resistance and resilience (Σ - resistance and Σ - resilience) traits determined for the sub-set of the MDB fish community from Table 3 were plotted against each other (Figure 4). The relationship between total resistance and resilience factors was analysed using a linear regression analysis. A significant, positive relationship was identified between the two factors (Linear Regression (df1); $F=34.018$; $R^2=0.549$; $P < 0.000$; Appendix 1).

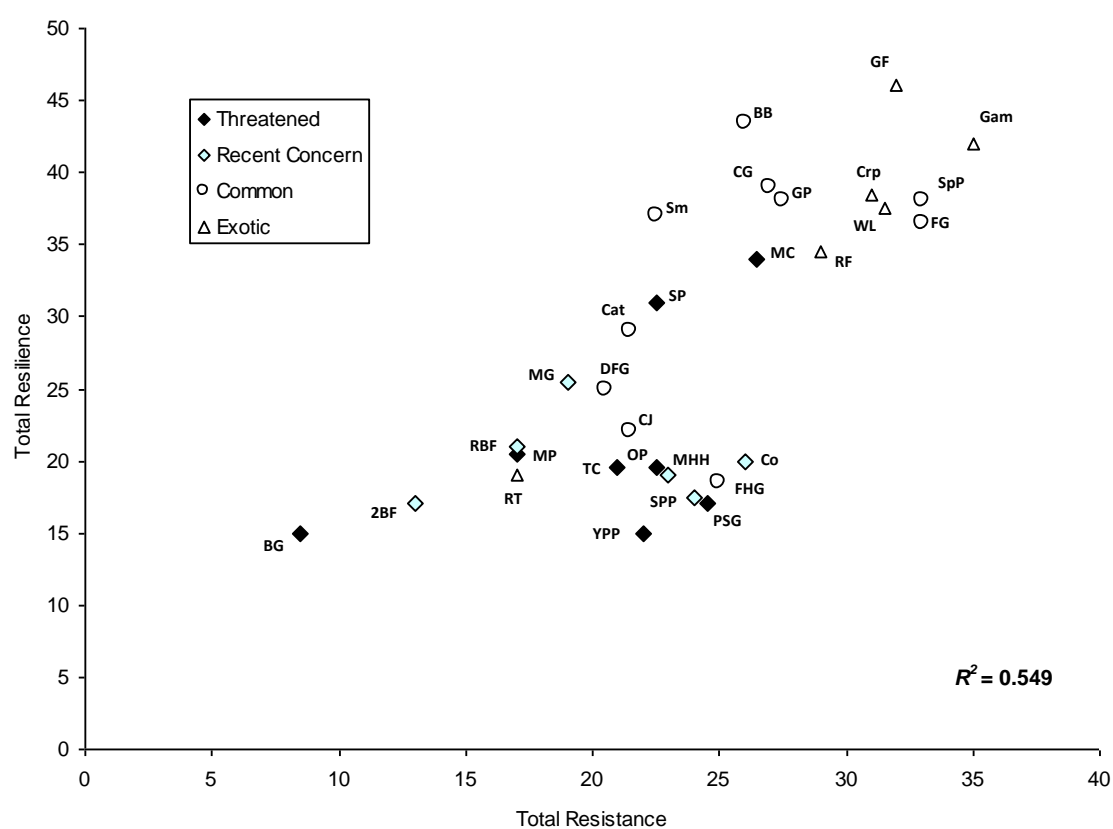


Figure 4. Preliminary plot analysis of total resistance versus total resilience for each of the 30 Murray-Darling Basin fish species. Scores were determined (where sufficient data existed) based on the sum total of individual resistance and resilience traits. Species identification follows: BG=barred galaxias, 2BF= two spined blackfish, RT=rainbow trout, RBF=river blackfish, MP=Macquarie perch, MG=Mountain galaxias, TC=trout cod, OP=olive perchlet, MHH=Murray hardyhead, SPP=southern pygmy perch, YPP= Yarra pygmy perch, CJ=Common galaxias (or common jollytail), PSG = purple-spotted gudgeon, Co = congolli, DFG = dwarf flathead gudgeon, Cat = freshwater catfish, SP=silver perch, RF=redfin perch, WL=oriental weatherloach, MC=Murray cod, Sm=Australian smelt, GP=golden perch, CG=carp gudgeon complex, BB=bony bream, Crp=common carp, FG=flat-headed gudgeon, SpP=spangled perch, GF=goldfish and Gam= gambusia (or mosquitofish).

The relationship indicates that highly resistant species also tend to be highly resilient species, and vice-versa. Species are distributed along an axis of low resistance/resilience, which are characterised by cool water, high flow specialists such as barred galaxias, two spined and river blackfish, Macquarie perch and rainbow trout; through to high resistance/resilience, characterised by highly tolerant, mobile and/or generally distributed species, such as introduced goldfish, oriental weatherloach, common carp and mosquitofish and natives such as bony bream, spangled perch, carp gudgeon, flathead gudgeon and golden perch (Figure 4).

However, despite the significant correlation between resistance and resilience factors, a small cluster of species are present that represents species with moderate resistance scores, but relatively low resilience scores (Figure 4). This group is dominated by species that are of high conservation value with restricted or patchy distributions, and includes southern and Yarra pygmy perch, olive perchlet, flat-headed galaxias, purple spotted gudgeon, trout cod, congolli and common galaxias. Hence, this cluster appears to represent a group of species that are highly susceptible to drought impacts (Figure 4).

7.0 Assessing Drought Factors and Response Groups

To explore and identify which particular resistance/resilience traits (or ecological characteristics) may be influencing the trends observed in the logistic regression analysis (Figure 4), further multivariate analyses were undertaken in order to determine: *i*) clusters of species within the data set that are influenced by similar sets of drought factors, *ii*) drought factors that may be more strongly associated with species and in particular certain clusters of species and *iii*) which factors may be more closely linked with threatened species, or those that have become a concern during the recent drought.

7.1 Analytical Methodology

For each species, the total drought factor score (i.e. total species' scores for resistance or resilience factors; (see Table 3)) were normalised. Euclidean distances were then used to calculate a similarity matrix between species' drought factor scores and then analysed using cluster analysis. Differences between cluster groups were then analysed using Permutational Multivariate Analysis of Variance (PERMANOVA) on unrestricted permutations of raw data.

A Principal Components Analysis (PCA) was run on the non-normalised data matrix, from which two PCA axes (PCA 1 and 2) were plotted. The direction and relative

correlation of each drought factor was also plotted to indicate the direction of influence that each has in relation to the PCA of species-based drought factors. Correlating drought factors were presented only if co-efficients scored in excess of 0.300 (i.e. other factors are considered to be of lower biological significance for the current study).

Data points for each species were also differentiated by their relative conservation status (see Table 2) to allow for a post hoc assessment of conservation status, relative to cluster analysis and PCA outputs. The percent contribution of each drought factor in determining cluster groupings were then analysed using SIMPER Analysis; where drought factors contributing over 10% to the formation of clusters were considered significant.

All analyses were run using Primer version 6.1.12 (Clarke and Gorley 2006).

7.2 Results and Discussion

Cluster analysis identified three distinct groups of fish species based on drought factors with a Euclidean distance of 4.9 (Figure 5). Group 1 consists of almost all of the smaller-bodied, conservation listed species, as well as those that have been listed as present conservation concerns under the recent drought conditions (based on Hammer *et al.* 2010) and the outcomes of the International Union for the Conservation of Nature (IUCN) Australian Native Fish Workshop held in Adelaide in 2010 (unpublished data) (Figure 5; Table 2).

An exception was the invasive rainbow trout which is highly dependent on high altitude cool water conditions for survival in the MDB (Koehn and O'Connor 1990, Lintermans 2007). Group 2 consisted of all large bodied, long lived species; including silver perch, golden perch and redfin perch, carp and Murray cod (Figure 5). This group of species exhibited a variety of conservation concerns, ranging from noxious (redfin perch) to threatened (silver perch) (see Table 2). Group 3 contained a range of common native and introduced species such as goldfish, mosquitofish, oriental weatherloach, spangled perch, flathead and carp gudgeon, smelt and bony bream (Figure 5; Table 2). All of these species each exhibited high resistance scores (see Table 3).

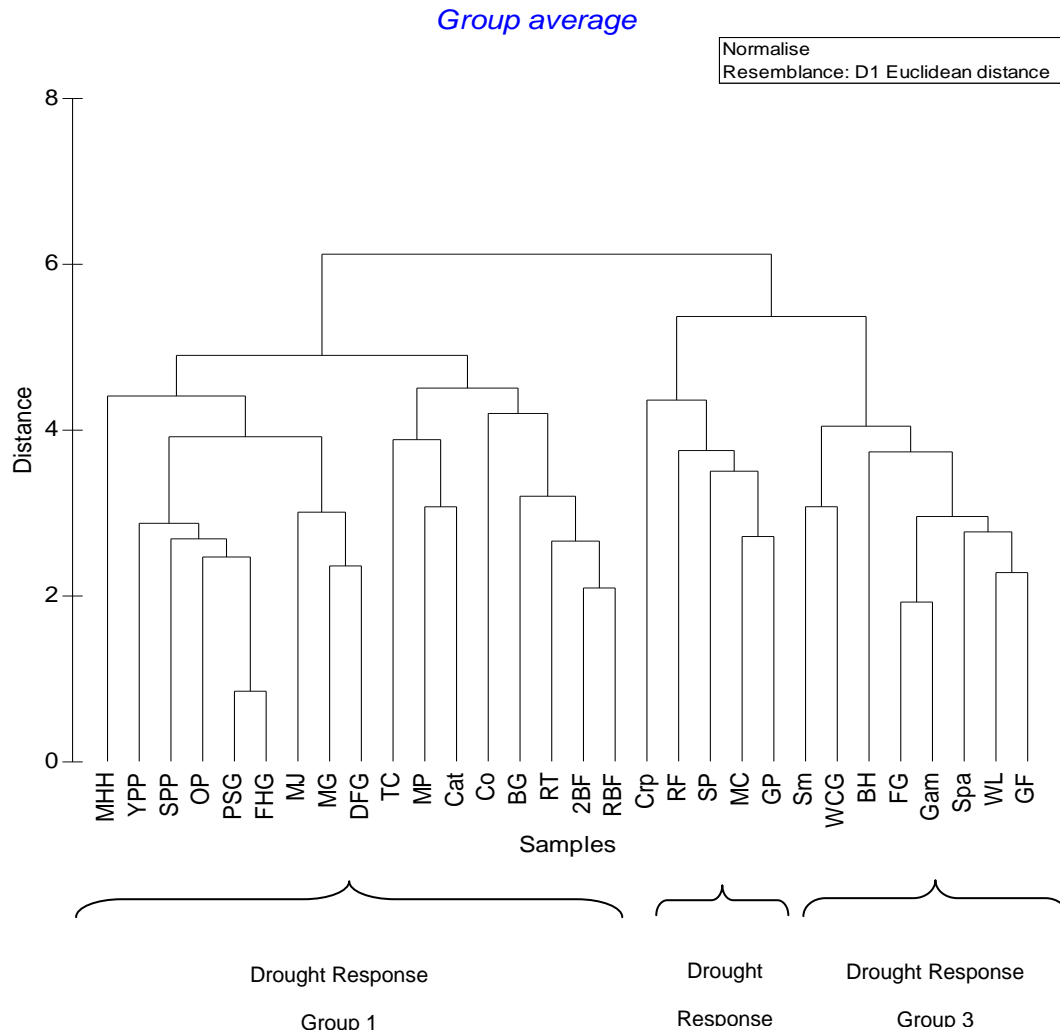


Figure 5. Dendrogram showing clustering of relative similarity between fish species' drought factor scores (i.e. total scores for resistance/resilience factors and ecological characteristics), using Euclidean distance measures. The cluster analysis shows three groupings of species or Drought Response Groups (DRG) at Euclidean Distance of 4.9. Species identification follows: BG = barred galaxias, 2BF = two spined blackfish, RT = rainbow trout, RBF = river blackfish, MP = Macquarie perch, MG = Mountain galaxias, TC = trout cod, OP = olive perchlet, MHH = Murray hardyhead, SPP = southern pygmy perch, YPP = Yarra pygmy perch, CJ = Common galaxias (or common jollytail), PSG = purple-spotted gudgeon, Co = congolli, DFG = dwarf flathead gudgeon, Cat = freshwater catfish, SP = silver perch, RF = redfin perch, WL = oriental weatherloach, MC = Murray cod, Sm = Australian smelt, GP=golden perch, WCG = carp gudgeon complex, BB = bony bream, Crp = common carp, FG = flat-headed gudgeon, SpP = spangled perch, GF = goldfish and Gam = gambusia (or mosquitofish).

Significant differences were found across cluster groups (PERMANOVA: *Psuedo-F* = 11.17, $P < 0.001$; see Appendix 2). Significant pair wise differences were also found across all three cluster groups (Table 4). These results support the classification of distinct groups or 'guilds' based upon individual species' resistance/resilience traits and ecological characteristics. The authors therefore propose that these cluster groups form *Drought Response Groups* (DRGs); given that they are the product of significantly different suites of drought related species' resistance/resilience traits and ecological characteristics. These DRGs may be useful in generalising drought impacts upon particular species and for guiding predictive management actions and responses. This is particularly so if each group responds differentially to various drought impacts, or possess similar collections of traits and ecological characteristics that may govern their responses and susceptibility to drought impacts.

Table 4. PERMANOVA results for drought response groups (DRGs). Statistically significant effects ($\alpha=0.05$) in bold type. Pair-wise comparisons for significant interaction effect $F^{\#}$ = permutational F value; t = t -test value; P (probability value).

PERMANOVA Pair-wise Comparisons.			
Cluster Groups	<i>Psuedo-F</i>	P	No. permutations
DRG 1 v. DRG 2	2.7306	0.001	980
DRG 1 v. DRG 3	3.9972	0.001	998
DRG 2 v. DRG 3	2.8417	0.003	691

The PCA (see Appendix 3) indicated that the two primary axes of separation (PC1 and PC2) accounted for 64.9% of the total variation in drought factors across species (41.8% and 23.1%, respectively; (Figure 6). PC1 was positively associated with drought factors, such as poor dispersal ability and distribution, patchy occurrence, poor tolerance of low flow, hypoxia and temperature and a high degree of spawning specificity. PC2 was positively associated with drought factors such as longevity, higher trophic level (carnivorous), high fecundity and high spawning specificity. The separation of species clusters against PC axes were largely due to a positive clustering of DRG 1 species with PC1; indicating that these species tend to be poorly distributed, have a high likelihood of patchiness, low tolerance for low flows and/or poor water quality, possess a low dispersal ability and have specific spawning requirements.

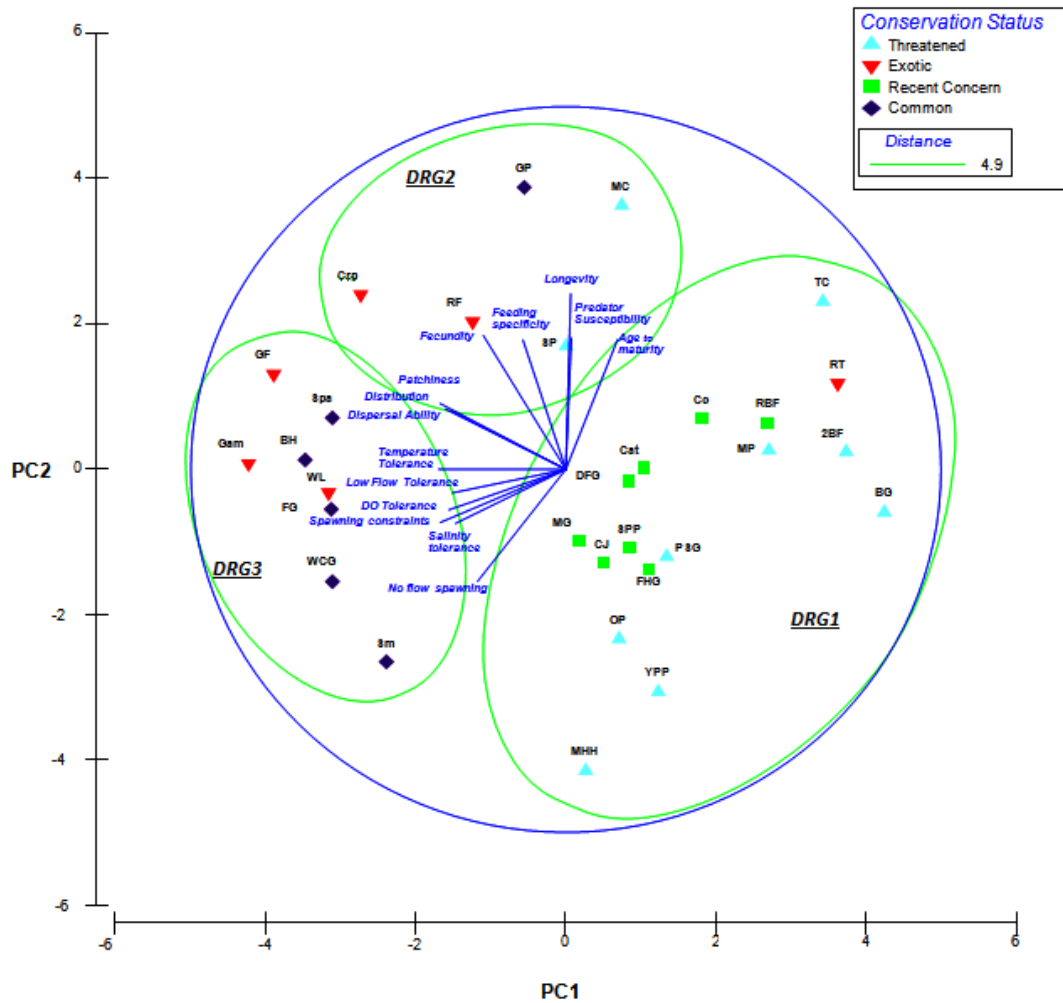


Figure 6. Principal Components Analysis plot showing the distribution of fish species' drought factor scores (total scores for resistance/resilience traits and ecological characteristics) along axes PC1 and PC2. Species identification follows: BG = barred galaxias, 2BF = two spined blackfish, RT = rainbow trout, RBF = river blackfish, MP = Macquarie perch, MG = Mountain galaxias, TC = trout cod, OP = olive perchlet, MHH = Murray hardyhead, SPP = southern pygmy perch, YPP = Yarra pygmy perch, CJ = Common galaxias (or common jollytail), PSG = purple-spotted gudgeon, Co = congolli, DFG = dwarf flathead gudgeon, Cat = freshwater catfish, SP = silver perch, RF = redfin perch, WL = oriental weatherloach, MC = Murray cod, Sm = Australian smelt, GP=golden perch, WCG = carp gudgeon complex, BB = bony bream, Crp = common carp, FG = flat-headed gudgeon, SpP = spangled perch, GF = goldfish and Gam = gambusia (or mosquitofish). The direction of influence for each of the significantly correlated drought factors are shown in blue. Distinct Drought Response Groups (DRG: 1, 2 and 3) are encircled in green. Conservation status follows: blue triangles = threatened species; red triangles = exotic species; green squares = recently listed species of conservation concern and purple diamonds = common species.

DRG 3 fish were separated from DRG 1, primarily along the axis of PC1, indicating that these species are widely and evenly distributed across their range, have a high tolerance of low flows and poor water quality and possess high dispersal ability (Figure 6; Table 3). DRG 2 species are positively distributed with PC2 and represent long-lived, highly fecund species that are usually flow dependent spawners and less susceptible to predation as adults. It should be noted that of the DRG 3 species, the two conservation listed fishes, silver perch and Murray cod were slightly more positively associated with PC1 than others in the group (Figure 6; Table 3).

Species of conservation concern (see Table 2) were predominantly associated with lower resistance (lower tolerance to low flows and water quality) and resilience factors (restricted and patchy distribution, specific spawning requirements and low dispersal ability) (Figure 6; Table 3). Of particular interest were species in DRG1, which are of recent conservation concern (i.e. those that have become threatened during the recent drought) as they were more negatively distributed with PC1, compared to the conservation listed species (i.e. those species that were threatened prior to the recent drought) within the same group (Figure 6). This suggests that the recent drought impact may be represented by a shift to the left along PC1, forcing historically more robust species to start failing resistance and resilience factors along this axis (Figure 6).

The results indicate that the factors that are causing historically common species to now present a conservation risk are similar to those historical factors that may have resulted in these species becoming endangered in the past. Under this hypothesis, drought largely re-emphasises the traditional anthropogenic impacts that have resulted in failure of resistance and resilience requirements in the past. It is therefore likely that the factors that render MDB fishes susceptible to drought are the very impacts that render them susceptible to the impact of other types of disturbance, particularly anthropogenic ones.

The main axis of separation between DRG 1 and DRGs 2 and 3 is diagonal to the PC1 and PC2 axes and associated with three key drought factors: dispersal ability, patchiness and distribution (Figure 6). SIMPER analysis shows that these three factors are significantly correlated with the separation of DRG 1 from the other two DRGs. The cumulative dissimilarity between DRG1 and DRG2 is 35.8%; while the dissimilarity between DRG1 and DRG3 is 38.7% (Appendix 4). These three factors are strongly linked to resilience traits and ecological characteristics, especially across larger scales. For instance, species with poor dispersal ability are likely to be very slow to recover, especially across broad spatial scales, following drought (Perry and

Bond 2009, McNeil and Schmarr 2010).

Consequently, impacts that reduce the distribution of species (and/or increase the patchiness of populations across that range) are likely to impact very strongly on species with a poor ability to re-disperse quickly, recolonise their range and rebuild population viability. Thus, species that exhibited patchy and restricted distributions prior to the recent drought may find it very difficult to rapidly respond to seasonal flows or temporary inundation and reconnectedness. Furthermore, those species with slow recolonisation ability may especially require extended periods (i.e. several years) of habitat connectivity and facilitative conditions before they are able to rebuild to pre drought distributions and population sizes.

The inclusion of diadromous species in DRG1, such as congolli and common galaxias, emphasises that barriers between critical habitats (in this case the Murray Barrages that separate marine and freshwater habitats) can impact on the resilience of fish species. With more than 4000 barriers to fish passage across the MDB (Lintermans 2007), recovering from localised population declines is likely to be a struggle for DRG 1 species, even during non-drought periods. This may occur via obstruction to movement and/or recolonisation following isolation and desiccation during drought. This loss of connectivity between habitats during the recent drought may be a critical reason for the recent conservation listing of species within this group, especially when historical perturbations that may include drought and a range of anthropogenic disturbances are considered.

The recent drought led to localised losses of many species, particularly within ephemeral streams, littoral riverine, wetland or floodplain habitats (Bice and Ye 2009). Therefore it may be that the lack of resilience potential for DRG1 species is driving their rapid decline and thus the recovery process may be slow and difficult in the coming post drought period. Management strategies and actions directed towards building resilience in these particular species needs to focus on *i*) rebuilding their distribution within the MDB and *ii*) facilitating long term hydrological connectivity across habitats (to facilitate even the slowest recolonising fish).

Furthermore, these results emphasise the importance of managing native fishes at a large spatial scale since drought impacts on native fish are significantly exacerbated by broad scale patchiness and limited distributions. This may be particularly relevant for species that are not rapid dispersers or are unable to recolonise due to barriers or loss of connectivity over larger spatial scales. These findings support recent research that suggests that the protection of drought refuges and key populations during

drought should focus on longer term, large scale management programs rather than relying wholly on responsive local scale interventions that afford resistance upon the lucky few recipient populations or individuals (Bond *et al.* 2008, Crook *et al.* 2010, McNeil *et al.* 2011b). Considerable care should be taken to protect this group of high risk species and in addition, management plans and water resource management should consider the long term process of providing suitable conditions to reconnect and rebuild populations following drought periods.

It is highly recommended that native fishes within DRG 1 be considered *acutely* susceptible to the impacts of drought as a result of their relatively poor ability to meet the resilience requirements necessary for surviving and responding in post drought conditions.

8.0 General Conclusions

This review has captured the major mechanisms through which drought impacts upon aquatic ecosystems and freshwater biota. Native freshwater fish were used as a surrogate for all freshwater biota owing to their strong value as an indicator of ecological condition, and their susceptibility to the impacts of drought and climatic disturbance. The literature depicted the cyclical, seasonal nature of drought in the MDB, and differentiated regular season cycles of drought and wet seasons within supra-seasonal, progressive drought conditions. While the impacts of seasonal, climatic cycles are effectively the same as for supra seasonal drought, the impacts occur across much broader scales of time and space. Accordingly, models conceptualising the impacts of drought on native fish should be based on consecutive seasons of wet and dry periods, although the various levels of climatic harshness should be determined separately for each season.

Scenarios of supra seasonal drought represent an accumulative impact created through an increasingly harsh string of seasons; with each subsequent season dependent upon the impacts of the preceding season. Under this model, the impacts of dry seasons amass compared to the diminishing potential for recovery under poorer wet seasons. This *seasonal string approach* of conceptualising drought impacts develops a framework for outlining the responses of native fish to a range of seasonal climatic scenarios. The success (or failure) of individual species to progress through each consecutive season depends on *i*) the species' ability to tolerate and survive the impacts of drought applied during each dry season, and *ii*) on their ability to recover and rebuild population viability during intervening wet seasons where climatic impacts are reduced and habitats are potentially reconnected or impacts

alleviated to some degree.

The success (or failure) of fish to meet these resistance/resilience requirements will determine their ability to survive drought and maintain viable populations, by either resisting impacts in harsh environments, or by recolonising impacted habitats from refuges located elsewhere in the MDB (prior to rebuilding population structure). Failure to meet resistance requirements removes species from a given habitat, therefore only by meeting resilience requirements (e.g. recolonisation and recruitment into previously 'vacated' habitats) can species be restored to a particular reach in question. In subsequent seasons, a number of resilience factors may need to be met before the population viability is effectively restored, especially over large spatial scales.

The conceptualisation of the impacts of drought on aquatic habitats and the responses of native fish, presented herein, provides a solid basis for developing more empirical models and hence should be tested and applied using ecological data and species/ecosystem thresholds. This platform would assist in the management of fish assemblages and species during drought, or periods of climatic change, particularly if local assemblage and environmental data collected at the appropriate scale (i.e. population, catchment or local refuge) is used for each scenario.

In order to assess the likely responses of various MDB fish species to the impacts of drought, a review of species' life history traits, tolerance thresholds and key threats were identified. This information was used to determine resistance and resilience factors that best characterise the key mechanisms through which fish may be impacted by, or respond to drought. Species were then scored relative to each factor and it is envisioned that these scores can then be used determine the success (or failure) for species and/or assemblages in fulfilling each of the resistance and resilience requirements presented by the specific environmental data set or scenario provided. The approach is therefore transferrable and adaptable to any species and/or assemblages, and can be applied to habitats across a broad range of scales; although some of the resistance and resilience factors may change over various scales (e.g. multiple catchments).

Hence the subsequent analysis of drought factors for a subset of fish species common to the MDB (for which sufficient and reliable data and literature was available), established some interesting patterns regarding the relative resistance and resilience potential of many MDB fishes. It also highlighted *1*) some of the species traits and ecological characteristics that threaten the resilience of native fish

to drought disturbances and *ii*) the anthropogenic impacts (that may work through similar mechanisms to drought disturbances).

In general, a positive linear relationship was identified between resistance and resilience factors and hence species were generally either highly resistant/resilient species through to poorly resistant/resilient. However, there was a small group of species that possessed only moderate levels of resistance and lower than expected resilience (Figure 4). Further analysis revealed that this group was the core of a broader group of species that not only included the majority of conservation listed species, but also species that have lately become a conservation concern during the recent drought. Species that are listed as either common and/or exotic (with the exception of rainbow trout) formed other groups that were separated from the aforementioned vulnerable group of species based on respective drought factor scores.

The classification of different groups based on drought factors therefore led to the proposal of Drought Response Groups (DRGs) to differentiate between the susceptibility of member species to the impacts of drought. In particular, it was identified that drought factors, such as poor dispersal ability and limited, patchy distributions were the main drivers separating the DRGs. These factors are therefore the likely drivers corresponding to the poor resilience potential identified for the majority of threatened and high risk species in the MDB.

These results highlight a need for management strategies and actions that address large scale issues relating to population viability, since the restoration of species distributions and connectivity are the principal mechanisms through which native fish can be protected from the impacts of drought. Although a concentrated effort will be required to restore resilience potential in species throughout non-drought periods, it has the added benefit of addressing factors that have historically lead to declines in vulnerable species across the MDB, particularly for those species with poor dispersal potential. While, short term, immediate drought response interventions may still be required to protect very high risk populations; the long term vision for the MDB should be the restoration of large scale patterns of population connectivity across the Basin.

9.0 Species Information Tables

Table 5. Species' life history traits, tolerance thresholds and threats information for native and exotic species common to the Murray-Darling Basin (MDB). Tolerance data is relevant to adult fish only (i.e. excludes: eggs, larvae and juvenile data). Unless otherwise stated, blank spaces represent information either not known or not applicable. All relevant reference number and details succeed tables.

Southern pygmy perch (<i>Nannoperca australis</i>) Family: Nannopercidae		
Life History	Abundance and distribution across MDB	Small, limited populations with patchy, scattered distribution (Lower Murray/Murrumbidgee catchments)
	Adult Habitat	Slow flowing or still waters
	Adult micro-habitat association	Habitat specialist: associated with dense stands of vegetation/abundant cover
	Home Range	Not known
	Longevity	5+ years
	Reproductive age	12 months
	Duration of spawning	Short
	Spawning style and timing	Single spawning - Late Winter or Summer
	Spawning cues and habitat requirements	None known, low flow or zero flow trigger? low flow/in-stream cover
	Spawning migration	No
	Spawning site	Over open structures (vegetation, leaf litter) or substrate
	Courtship display	Yes
	Number of eggs	100-4,000 eggs; multiple or protracted spawner
	Size and type of egg	3 - 4 mm diameter; round, transparent and non-adhesive
	Egg Laying site	Scattered over the bottom or aquatic vegetation
	Time to hatching	2- 4 days
	Tolerance	Parental Care
Dispersal ability		Low
Larvae Size		3.2 – 3.9 mm length
Larvae/Juvenile functional feeding group		Zooplankton / early instars of insects
Adult Functional Feeding group		Carnivorous: e.g. cladocerans, copepods, ostracods and chironomid larvae, mayflies, mosquito larvae and water bugs
Adult size		Maximum length = 85 mm; usually less than 65 mm
Schooling behaviour		Yes
Tolerance to cease-to-flow periods		High
Temperature		High (upper $T_{critical} = 38^{\circ}C$)
Conductivity		Low (10, 000 $mg L^{-1}$)
Threats	Dissolved Oxygen	High (< 1 $mg L^{-1}$)
	Turbidity	High
	Predators	Trout, redfin, mosquitofish
	Competitors	
	Other	Loss of lateral connectivity & vegetation cover; destruction of in-stream habitat; flow alteration; cold-water pollution;

References: 1, 2, 3, 4, 5, 6, 7, 153

Yarra pygmy perch (<i>Nannoperca obscura</i>) Family: Nannopercidae		
Life history	Abundance and distribution across MDB	Locally abundant, limited distribution (e.g. Lake Alexandrina; coastal streams Victoria)
	Adult Habitat	Restricted to slow-flowing water, wetland or drainage channel habitat (Lake Alexandrina)
	Adult micro-habitat association	Habitat specialist: associated with dense stands of vegetation/abundant cover
	Home Range	Not known
	Longevity	5+ years
	Reproductive age	12 months
	Duration of spawning	Short
	Spawning style and timing	Single spawning - Late Winter or Summer
	Spawning cues and habitat requirements	None known, low flow or zero flow trigger? low flow/in-stream cover
	Spawning migration	No
	Spawning site	Over open structures (vegetation, leaf litter) or substrate
	Courtship display	Yes
	Number of eggs	100-4,000 eggs; multiple or protracted spawner
	Size and type of egg	3 - 4 mm diameter; round, transparent and non-adhesive
	Egg Laying site	Scattered over the bottom or aquatic vegetation
	Time to hatching	2- 4 days
	Parental Care	Yes
	Dispersal ability	Low
	Larvae Size	3.2 – 3.9 mm length
	Larvae/Juvenile functional feeding group	Zooplankton / early instars of insects
Adult Functional Feeding group	Carnivorous: microcrustaceans, molluscs and aquatic insects, such as mosquito larvae	
Adult size	Maximum length 75 mm; usually < 65 mm	
Schooling behaviour	Found in small groups, often mixed with Southern pygmy perch	
Tolerance	Tolerance to cease-to-flow periods	
	Temperature	Found in locations where temp ranged 19-21.1°C (upper $T_{crit} = 30^{\circ}C$)
	Conductivity	Found in locations where salinity ranged 14.6 - 17.3 $\mu S\ cm^{-1}$
	Dissolved Oxygen	Unknown (possibly medium)
Threats	Turbidity	Found in locations where transparency up to 20 cm
	Predators	Redfin, mosquitofish
	Competitors	
	Other	Vegetation loss; alienation of wetland habitats; over-extraction of water

References: 2, 7, 8, 153

Darling River Hardyhead (<i>Craterocephalus amniculus</i>) Family: Atherinidae		
Life history	Abundance and distribution across MDB	Limited, locally common populations primarily in upper tributaries of Darling River at NSW/Qld border
	Adult Habitat	Slow flowing, clear, shallow water
	Adult micro-habitat association	Aquatic vegetation at edge of waters
	Home Range	Not known
	Longevity	Not known
	Reproductive age	Not known (likely 0 – 12 months)
	Duration of spawning	Spring-Summer
	Spawning style and timing	In Macintyre River – (September – February)
	Spawning cues and habitat requirements	Not known
	Spawning migration	Not known
	Spawning site	Vegetation, woody debris
	Courtship display	Yes
	Number of eggs	20-120
	Size and type of egg	1.3 - 1.5mm eggs; transparent and demersal with filamentous adhesive strands
	Egg Laying site	Vegetation, wood, substrate
	Time to hatching	4-7 days
	Parental Care	No
	Dispersal ability	High (drift)
	Larvae Size	3-5 mm length
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		Carnivorous, eating small insects such as mosquito larvae, and microcrustaceans
Adult size		Maximum length 55 mm
Schooling behaviour		Found singly or in small or large schools (50+ fish)
Tolerance to cease-to-flow periods		Unknown (possibly high)
Temperature		Unknown (possibly medium)
Conductivity		Unknown (possibly medium)
Dissolved Oxygen		Unknown (possibly medium)
Turbidity		Unknown (possibly medium)
Threats		Predators
	Competitors	
	Other	Unknown

References: 5, 10, 11, 12,153

Unspecked hardyhead (<i>Craterocephalus stercusmuscarum fulvus</i>) Family: Atherinidae		
Life history	Abundance and distribution across MDB	Restricted populations in southern Basin; abundant and widespread in northern Basin
	Adult Habitat	Found at lake margins & slow-flowing lowland rivers, backwaters and billabongs
	Adult micro-habitat association	Aquatic vegetation and sand, gravel or mud substrates
	Home Range	Not known but unlikely
	Longevity	Not known (likely 1-3 years)
	Reproductive age	0-12 months
	Duration of spawning	Medium
	Spawning style and timing	Multiple spawning, October to February (peak in spring when water temp >24°C)
	Spawning cues and habitat requirements	Water temperature, daylength. Adhesive eggs on vegetation, wood, substrate
	Spawning migration	None observed
	Spawning site	Littoral zone, slow flowing
	Courtship display	Yes
	Number of eggs	20 - 2,000 eggs
	Size and type of egg	1.3 - 1.5mm eggs; transparent and demersal with filamentous adhesive strands
	Egg Laying site	Vegetation, wood, substrate
	Time to hatching	4-7 days
	Parental Care	No
	Dispersal ability	High (drift)
	Larvae Size	3-5 mm length
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		Carnivorous, eating small insects such as mosquito larvae, and microcrustaceans
Adult size		Maximum length 78 mm; usually 50-60 mm
Schooling behaviour		Form schools around September to March
Tolerance to cease-to-flow periods		High
Temperature		High (up to 36°C)
Conductivity		High (up to 61, 000 mg L ⁻¹ ; LC50: 43, 700 mg L ⁻¹)
Dissolved Oxygen		High (0.1 mg L ⁻¹)
Turbidity		Medium to High (190 NTU)
Threats		Predators
	Competitors	Mosquitofish, (possibly redfin perch)
	Other	Possibly increased salinisation; habitat degradation; coldwater pollution

References: 2, 9, 11, 13, 14, 153

Murray Hardyhead (<i>Craterocephalus fluviatilis</i>) Family: Atherinidae			
Life history	Abundance and distribution across MDB	Limited populations in lowland areas of southern Basin and less common mid-Lower Murray	
	Adult Habitat	Adults in shallow habitats such as lake margins	
	Adult micro-habitat association	Open sand banks and submerged and emergent vegetation	
	Home Range	Not known	
	Longevity	Mostly 12 months; although some live for 2 years	
	Reproductive age	Males when 27-34 mm caudal fork length and females at 41-43 mm (0 – 12 months)	
	Duration of spawning	Long	
	Spawning style and timing	Serial spawner, peak in spring and early summer	
	Spawning cues and habitat requirements	Increasing water temperature and daylength; vegetation	
	Spawning migration	Not observed	
	Spawning site	On vegetation, close association with <i>Ruppia</i> spp.	
	Courtship display	Yes	
	Number of eggs	30 – 90, (<2,000) eggs	
	Size and type of egg	Adhesive; 1.4 – 1.9 mm diameter	
	Egg Laying site	Vegetation	
	Time to hatching	2 – 4 days	
	Tolerance	Parental Care	No
		Dispersal ability	
Larvae Size		4 mm length	
Larvae/Juvenile functional feeding group		Facultative zooplankton (copepods, early instars of cladocerans)	
Adult Functional Feeding group		Omnivorous, primarily microcrustaceans but also aquatic insects and algae	
Adult size		Maximum length 76 mm, usually 40-65 mm	
Schooling behaviour		Found in schools of distinct size classes	
Tolerance to cease-to-flow periods		High	
Temperature		High (Upper $T_{crit} = 38^{\circ}\text{C}$)	
Conductivity		High (range: 45, 900 – 110, 000 mg L^{-1})	
Threats	Dissolved Oxygen	High (>2 mg L^{-1})	
	Turbidity	Medium	
	Predators	Mosquitofish, birds, piscivorous fish	
	Competitors		
	Other	Possibly increased salinity; habitat degradation; flow modification; loss of connectivity	

References: 9, 15, 18, 19, 20, 21, 22, 26, 27, 153

Small-mouthed hardyhead (<i>Atherinosoma microstoma</i>) Family: Atherinidae		
Life history	Abundance and distribution across MDB	Widespread and common in coastal streams (SE Australia); limited populations Lower Lakes (South Basin)
	Adult Habitat	Generalist: brackish lakes, lagoons, estuaries in still or slow flowing habitats and adjacent marine habitats
	Adult micro-habitat association	Lakes, Estuaries, lower freshwaters of rivers
	Home Range	No
	Longevity	1-3 years
	Reproductive age	0-12 months
	Duration of spawning	September - December
	Spawning style and timing	Batch spawner
	Spawning cues and habitat requirements	Serial spawner, peak in spring and early summer
	Spawning migration	Increasing water temperature and daylength; vegetation
	Spawning site	On Vegetation, close association with <i>Ruppia</i> spp.
	Courtship display	Yes
	Number of eggs	20 - 2,000 eggs
	Size and type of egg	Demersal, adhesive
	Egg Laying site	Vegetation
	Time to hatching	2-9 days
	Parental Care	No
	Dispersal ability	High
	Larvae Size	3.9 - 4.2 mm length
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		Plankton, microinvertebrates
Adult size		Maximum length = 107 mm; commonly < 80 mm
Schooling behaviour		Yes
Tolerance to cease-to-flow periods		High
Temperature		Unknown (possibly medium)
Conductivity		High (LC 50: 108, 000 mg L ⁻¹)
Dissolved Oxygen		Unknown (possibly medium)
Turbidity		Unknown (possibly medium)
Threats		Predators
	Competitors	
	Other	

References: 9, 11, 16, 23, 24, 25, 153

Bony Bream (<i>Nematolosa erebi</i>) Family: Clupeid		
Life history	Abundance and distribution across MDB	Very widespread and abundant; particularly in lowland river systems
	Adult Habitat	Lowland rivers, wetlands
	Adult micro-habitat association	Open water, pelagic species
	Home Range	Not known
	Longevity	Up to 5 years
	Reproductive age	Males 1-2 years; females 2 years
	Duration of spawning	Medium
	Spawning style and timing	Single?; October to February; temp > 20°C
	Spawning cues and habitat requirements	Increase in daylength and temperature, still waters of shallow, sandy bays
	Spawning migration	Possibly upstream
	Spawning site	Shallow backwaters
	Courtship display	Not known
	Number of eggs	33,000 - 880,000 eggs
	Size and type of egg	0.83 mm diameter; demersal then becoming buoyant
	Egg Laying site	Still waters of shallow, sandy bays and muddy lagoons
	Time to hatching	Unknown but likely to be rapid (<3days)
	Tolerance	Parental Care
Dispersal ability		High
Larvae Size		4 mm length
Larvae/Juvenile functional feeding group		Not known
Adult Functional Feeding group		Algae detritivore, consuming large quantities of detritus, microalgae and microcrustaceans
Adult size		Maximum length ~470 mm (commonly 120-200 mm)
Schooling behaviour		Large masses in open water
Tolerance to cease-to-flow periods		High
Temperature		High (upper T _{crit} = 38°C)
Conductivity		High (ranged: 24, 600 – 35, 000 mg L ⁻¹)
Threats	Dissolved Oxygen	Medium (down to 5 mg L ⁻¹)
	Turbidity	High (>300 NTU)
	Predators	Birds, Murray cod and golden perch
	Competitors	
	Other	Cold water pollution; fish barriers

References: 13, 14, 16, 27, 28, 29, 30, 31, 32, 153

Two-spined blackfish (<i>Gadopsis bispinosis</i>) Family: Gadopsidae		
Life history	Abundance and distribution across MDB	Locally abundant, fragment populations across MDB; populations declining in ACT and NSW catchments
	Adult Habitat	In-stream cover, rock and woody debris, slack waters
	Adult micro-habitat association	Woody-debris, rocks, undercut banks
	Home Range	Yes (acute)
	Longevity	Not known
	Reproductive age	Females in 2nd or 3rd year at > ~120 mm length
	Duration of spawning	Short
	Spawning style and timing	November – December
	Spawning cues and habitat requirements	Cobbles, rocks
	Spawning migration	No
	Spawning site	Usually in the gaps between cobbles or boulders
	Courtship display	Not known
	Number of eggs	80 – 420 eggs
	Size and type of egg	~3.5 mm diameter; demersal and adhesive
	Egg Laying site	Attached to the upper surface of a rock
	Time to hatching	After 16 days
	Parental Care	Yes
	Dispersal ability	Low
	Larvae Size	Not known
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		Predominantly aquatic insect larvae (e.g. mayflies, caddisflies and midges) and rarely fish and crayfish
Adult size		150 - 450 mm
Schooling behaviour		Not observed
Tolerance to cease-to-flow periods		Medium
Temperature		Unknown (possibly medium)
Conductivity		Unknown (possibly low)
Dissolved Oxygen		Unknown (possibly medium)
Turbidity		Unknown (possibly high)
Threats		Predators
	Competitors	
	Other	Cold-water pollution; sedimentation over egg and/or spawning sites

References: 5, 33, 34, 35, 36, 37, 153

River blackfish (<i>Gadopsis marmoratus</i>) Family: Gadopsidae		
Life history	Abundance and distribution across MDB	Locally common in mid-Basin, absent in northern Basin, now very rare southern Basin (i.e. boom & bust)
	Adult Habitat	Deep permanent pools, cool- flowing water
	Adult micro-habitat association	Good instream cover such as woody debris, aquatic vegetation and boulders
	Home Range	Restricted-home range is estimated at 10-26 m; hunt in open water at night
	Longevity	>5 years
	Reproductive age	1 - 4 years
	Duration of spawning	Short
	Spawning style and timing	Single spawning, same time each year, Oct-Dec
	Spawning cues and habitat requirements	Circannual and min temp > 20°, low flow/in-stream cover
	Spawning migration	No
	Spawning site	Usually inside hollow logs, although rocks and undercut banks may also be used
	Courtship display	Yes
	Number of eggs	Usually < than 500 eggs up to 2,500 eggs
	Size and type of egg	~4 mm diameter; demersal and adhesive
	Egg Laying site	Laid in low to zero- velocity sites
	Time to hatching	> 14 days
	Parental Care	Yes
	Dispersal ability	Low
	Larvae Size	6-8 mm
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		Opportunistic carnivore: aquatic insect larvae, crustaceans, terrestrial insects & occasionally other fish
Adult size		Maximum length = 350 mm, usually 200-250 mm
Schooling behaviour		Not observed
Tolerance to cease-to-flow periods		Medium
Temperature		Medium (upper $T_{crit} = 28^{\circ}\text{C}$)
Conductivity		Low (10, 000 mg L^{-1})
Dissolved Oxygen		Medium (down to 4 mg L^{-1} ?)
Turbidity		High (up to 300 NTU)
Threats		Predators
	Competitors	Trout and redfin
	Other	Cold water pollution; snag & woody debris removal; flow modification; decreased water quality

References: 4, 5, 33, 38, 39, 40, 41, 153

Trout cod (<i>Maccullochella macquariensis</i>) Family: Percichthyidae		
Life history	Abundance and distribution across MDB	Three small populations remaining primarily in Murray River
	Adult Habitat	Associated with deeper water (pools) and large woody debris
	Adult micro-habitat association	Instream cover such as logs and boulders
	Home Range	Home range of 500 m around a home snag; sometimes undertake exploratory movements of 20-60 km
	Longevity	> 10 years
	Reproductive age	3-5 years
	Duration of spawning	Short
	Spawning style and timing	Single spawning, same time each year, Oct-Dec
	Spawning cues and habitat requirements	Circannual and min temp > 20°
	Spawning migration	No
	Spawning site	Eggs probably deposited on hard substrates such as logs and rocks
	Courtship display	Not known
	Number of eggs	~1200-11,000 eggs
	Size and type of egg	2.5 - 3.6 mm diameter; demersal & adhesive
	Egg Laying site	Probably deposited on hard substrates such as logs and rocks
	Time to hatching	5 - 10 days
	Parental Care	Yes
	Dispersal ability	Generally < than 10km
	Larvae Size	6-9 mm length
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		Fish, yabbies, mudeyes, aquatic insect larvae, shrimps and freshwater prawns
Adult size		Maximum length 850 mm
Schooling behaviour		Not known
Tolerance to cease-to-flow periods		Low- Medium
Temperature		Medium (25-30°C)
Conductivity		Medium
Dissolved Oxygen		Medium (down to 4 mg L ⁻¹)
Turbidity		Medium
Threats		Predators
	Competitors	Redfin, mosquitofish
	Other	Desnagging; sedimentation; clearing of riparian vegetation; cold-water pollution; over-fishing

References: 5, 43, 44, 45, 46, 47, 48, 153

Murray cod (<i>Maccullochella peelii</i>) Family: Percichthyidae		
Life history	Abundance and distribution across MDB	Limited abundance and patchy distribution in low-mid altitudes of Basin
	Adult Habitat	Associated with deep holes in rivers, wetlands, large woody debris
	Adult micro-habitat association	Instream cover such as rocks, stumps, fallen trees and undercut banks
	Home Range	Acute (home snag)
	Longevity	48+ years
	Reproductive age	4-5 years
	Duration of spawning	Short
	Spawning style and timing	Single spawning, same time each year, Oct-Dec
	Spawning cues and habitat requirements	Daylength. Circannual and min temp > 14°
	Spawning migration	Upstream migrations observed but not facultative
	Spawning site	Woody debris in faster flowing water
	Courtship display	Yes
	Number of eggs	10,000 - 200,000 eggs
	Size and type of egg	3 – 3.5 mm demersal adhesive
	Egg Laying site	Usually deposited onto a hard surface such as logs, rocks or clay banks
	Time to hatching	4.5 – 13 days
	Parental Care	Yes
	Dispersal ability	High, generally < than 10km
	Larvae Size	5 - 8 mm (have large yolk sac)
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		'Sit and wait' predator, its' diet contains fish, crayfish and frogs, birds, eggs
Adult size		Mass: up to 113 kg; 1.8 m total length (>450mm)
Schooling behaviour		Not known
Tolerance to cease-to-flow periods		High
Temperature		Medium (25-30°C; lower T _{critical} = 10°C; upper T _{critical} = 37°C)
Conductivity		Medium (observed 3000 µS.cm ⁻¹)
Dissolved Oxygen		Medium (down to 4 mg L ⁻¹)
Turbidity		High
Threats		Predators
	Competitors	Other Overfishing (especially in breeding season); sedimentation causing habitat loss; altered flows; snag removal; cold-water pollution

References: 46, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 153

Golden Perch (<i>Macquaria ambigua</i>) Family: Percichthyidae		
Life history	Abundance and distribution across MDB	Abundant in lower-mid Basin
	Adult Habitat	Found in the lowland, warmer, turbid, slow flowing rivers
	Adult micro-habitat association	Large woody debris, macrophyte beds
	Home Range	~ 100 m for weeks or months before relocating to establish new site
	Longevity	40+ years
	Reproductive age	2-3 in males; 4 years in females
	Duration of spawning	Variable in timing otherwise short.
	Spawning style and timing	Single spawning, can delay timing, Oct-March
	Spawning cues and habitat requirements	Rising water level more important than temperature, flowing water
	Spawning migration	Extensive upstream migration/larvae downstream drift
	Spawning site	Slow flowing backwaters of main rivers
	Courtship display	Yes
	Number of eggs	300,000 - 500,000 eggs
	Size and type of egg	3-4 mm diameter; semi-buoyant or planktonic
	Egg Laying site	Open water
	Time to hatching	1-2 days
	Parental Care	No
	Dispersal ability	High
	Larvae Size	3-5 mm length
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		Opportunistic carnivore: shrimps, yabbies, small fish and benthic aquatic insect larvae
Adult size		Maximum length = 760 mm (>450mm)
Schooling behaviour		Yes
Tolerance to cease-to-flow periods		High
Temperature		High (upper $T_{crit} = 37^{\circ}\text{C}$)
Conductivity		High (LC 50 = 38, 000 mg L ⁻¹)
Dissolved Oxygen		High (~13% saturation for 2+hr)
Turbidity		High (up to 400 NTU)
Threats		Predators
	Competitors	Barriers to spawning and larval dispersal
	Other	Cold water pollution, flow regulation

References: 16, 28, 30, 46, 48, 57, 58, 59, 60, 61, 62, 63, 64, 65, 66, 67, 68, 69, 153

Macquarie Perch (<i>Macquaria australasica</i>) Family: Percichthyidae		
Life history	Abundance and distribution across MDB	At times locally abundant, but isolated, small populations in cool, upper reaches of MDB
	Adult Habitat	Coastal and inland rivers
	Adult micro-habitat association	Woody debris, undercut banks
	Home Range	Occupy well-defined home-sites during the day
	Longevity	10+ years
	Reproductive age	Males 2 years; Females 3 years
	Duration of spawning	Short
	Spawning style and timing	Single? October - December
	Spawning cues and habitat requirements	Increase in daylength and temperature, cobbles/gravel riffles
	Spawning migration	Frequently upstream
	Spawning site	Located at the foot of pools and the eggs drift
	Courtship display	Yes
	Number of eggs	50,000-110,000 eggs
	Size and type of egg	1.0- 2.0 mm diameter; adhesive demersal
	Egg Laying site	Downstream and lodge amongst gravel and cobble in riffles
	Time to hatching	7 - 10 days
	Parental Care	No
	Dispersal ability	Generally < than 10km
	Larvae Size	7 mm length
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		Carnivorous: shrimps, small benthic aquatic insect larva & lake cladocerans
Adult size		Maximum length = 465 mm; usually 350 mm
Schooling behaviour		Yes
Tolerance to cease-to-flow periods		Medium
Temperature		Unknown (possibly medium)
Conductivity		Unknown (possibly medium)
Dissolved Oxygen		Unknown (possibly low)
Turbidity		Unknown (possibly medium)
Threats		Predators
	Competitors	Trout, redfin
	Other	Sedimentation; cold-water pollution; vegetation loss; migration barriers; exposure to epizootic <i>Haematopoietic necrosis Virus</i> (carried by Redfin perch)

References: 5, 14, 16, 30, 46, 62, 66, 70, 71, 72, 73, 74, 75, 76, 153

Estuary Perch (<i>Macquaria colonorum</i>) Family: Percichthyidae		
Life history	Abundance and distribution across MDB	Small, rare populations primarily Lower Murray & Lower Lakes
	Adult Habitat	Predominantly in tidal or estuarine waters, but will travel large distances upstream into fresh waters
	Adult micro-habitat association	Woody debris, rock bars
	Home Range	Yes
	Longevity	20+
	Reproductive age	Males at 220 mm; females 280 mm
	Duration of spawning	Short
	Spawning style and timing	Pelagic mid water, increasing freshwater flows
	Spawning cues and habitat requirements	When temperatures >19°C
	Spawning migration	Yes (downstream into Estuaries)
	Spawning site	Entrance of estuaries in winter
	Courtship display	Not known
	Number of eggs	Average 180, 000 eggs (increases with length)
	Size and type of egg	1.3 - 2.4 mm diameter; semi-buoyant, adhesive
	Egg Laying site	Open water
	Time to hatching	2-3 days
	Parental Care	No
	Dispersal ability	High
	Larvae Size	2.2 mm length
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		In estuaries: opportunistic carnivore of shrimp & fish; freshwater: mostly caddisfly larvae & shrimp
Adult size		Maximum length = 750 mm
Schooling behaviour		Yes
Tolerance to cease-to-flow periods		Medium
Temperature		Unknown (possibly medium)
Conductivity		High (tolerate fresh and saline environments)
Dissolved Oxygen		Unknown (possibly medium)
Turbidity		Unknown (possibly medium)
Threats		Predators
	Competitors	Trout, redbfin
	Other	River regulation

References: 14, 30, 46, 62, 76, 77, 153

Silver Perch (<i>Bidyanus bidyanus</i>) Family: Terapontidae		
Life history	Abundance and distribution across MDB	Patchy abundance mid-Murray
	Adult Habitat	Lowland, turbid and slow-flowing rivers
	Adult micro-habitat association	Woody debris, vegetation beds
	Home Range	Not known
	Longevity	26+ years
	Reproductive age	3 - 5 years (males earlier females)
	Duration of spawning	Short but variable
	Spawning style and timing	In spring and summer after an upstream migration
	Spawning cues and habitat requirements	Increase in water level
	Spawning migration	Upstream migration to spawn
	Spawning site	In backwaters
	Courtship display	Not known
	Number of eggs	500,000 (>10,000) eggs
	Size and type of egg	1.2-2.8 mm diameter; Buoyant and planktonic
	Egg Laying site	Open water
	Time to hatching	1-2days
	Parental Care	No
	Dispersal ability	High (drift)
	Larvae Size	3.5-3.7 mm length
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		Omnivorous: contains aquatic plants, snails, shrimps and aquatic insect larvae
Adult size		Maximum length 500 mm
Schooling behaviour		Form large schools during spawning
Tolerance to cease-to-flow periods		High
Temperature		High (upper $T_{crit} = 38^{\circ}\text{C}$)
Conductivity		Medium ($\text{LC}_{50} 16,000 \text{ mg L}^{-1}$)
Dissolved Oxygen		Medium ($>2 \text{ mg L}^{-1}$)
Turbidity		High
Threats		Predators
	Competitors	Redfin, carp
	Other	River regulation - disrupt migration and reproduction behaviour; thermal regulation

References: 13, 14, 16, 30, 62, 63, 66, 68, 77, 78, 79, 80, 81, 153

Spangled perch (<i>Leiopotherapon unicolour</i>) Family: Terapontidae		
Life history	Abundance and distribution across MDB	Widespread across NW Basin; can be especially abundant following flooding
	Adult Habitat	Rivers, billabongs, lakes, isolated dams, bore-drains, wells and waterholes in intermittent streams
	Adult micro-habitat association	Widespread
	Home Range	Not known
	Longevity	4-5 years
	Reproductive age	3-6 months
	Duration of spawning	Short
	Spawning style and timing	November to February
	Spawning cues and habitat requirements	Flooding maximises recruitment
	Spawning migration	Lateral, upstream and downstream migration
	Spawning site	In shallow areas such as backwaters or still pools and eggs are spread randomly over the bottom
	Courtship display	Yes
	Number of eggs	24,000-100,000 (>10,000) eggs
	Size and type of egg	0.6-0.7 mm diameter
	Egg Laying site	Eggs are spread randomly over the bottom
	Time to hatching	45-55 hours
	Parental Care	No
	Dispersal ability	High (after heavy rain can swim across paddocks and ruts in tracks)
	Larvae Size	1.7-2.5 mm length
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		Omnivore, primarily carnivorous
Adult size		150-450 mm
Schooling behaviour		Yes, form large aggregations
Tolerance to cease-to-flow periods		High
Temperature		High (upper $T_{crit} = 40^{\circ}\text{C}$; lethal at lower $T_{crit} = 4.1^{\circ}\text{C}$)
Conductivity		High ($55,000 \text{ mg L}^{-1}$)
Dissolved Oxygen		High (0.9 mg L^{-1})
Turbidity		High (>300 NTU)
Threats		Predators
	Competitors	
	Other	Cold water pollution; barriers to movement; reduced flooding; reduced lateral connectivity with floodplains

References: 14, 27, 28, 78, 82, 83, 153

Olive perchlet/Chanda Perch (<i>Ambassis agassizii</i>) Family: Ambassidae		
Life history	Abundance and distribution across MDB	Widespread northern NSW and Qld; extinct Vic; naturally extinct SA, but one translocated population
	Adult Habitat	Low to zero-flow habitats of lakes, creeks, swamps, wetlands and rivers
	Adult micro-habitat association	Woody habitat and aquatic vegetation
	Home Range	Not known
	Longevity	1-2 years
	Reproductive age	0-12months
	Duration of spawning	Medium
	Spawning style and timing	Oct - Dec; water temperatures 20-24°C
	Spawning cues and habitat requirements	Increase in temperature, vegetation
	Spawning migration	Not known
	Spawning site	Attach to aquatic plants, rocks and substrate
	Courtship display	Not known
	Number of eggs	200 - 2,350 eggs
	Size and type of egg	0.7 mm diameter; adhesive
	Egg Laying site	Attach to aquatic plants and rocks on the streambed
	Time to hatching	5-7 days
	Parental Care	No
	Dispersal ability	Low
	Larvae Size	3.0 mm length
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		Carnivorous: microcrustaceans (copepods and cladocera), aquatic/terrestrial insects & rarely small fish
Adult size		<150 mm
Schooling behaviour		Forms almost stationary, small schools during day close to in-stream cover; disperse during darkness
Tolerance to cease-to-flow periods		Low
Temperature		Possibly High
Conductivity		Medium (15102 $\mu\text{S}\cdot\text{cm}^{-1}$)
Dissolved Oxygen		Possibly High
Turbidity		Medium - High (144 NTU)
Threats		Predators
	Competitors	
	Other	Cold-water pollution that restricts spawning; habitat degradation; river regulation; vegetation loss

References: 5, 16, 27, 28, 84, 153

Congolli (<i>Pseudaphritis urvillii</i>) Family: Pseudaphritidae		
Life history	Abundance and distribution across MDB	Limited abundance; restricted to Lower-Murray drainage
	Adult Habitat	Primarily an estuarine species, but can live in freshwater and/or sea; wetlands and a few lowland streams
	Adult micro-habitat association	Partially buried leaf litter or sand; habitat cover such as logs, rocks or overhanging rocks
	Home Range	Not known
	Longevity	Not known
	Reproductive age	4-6 years
	Duration of spawning	Short
	Spawning style and timing	Autumn- winter
	Spawning cues and habitat requirements	High flows (downstream migration of females to estuaries)
	Spawning migration	Upstream migration
	Spawning site	Estuaries
	Courtship display	Not known
	Number of eggs	400,000 eggs
	Size and type of egg	Not known
	Egg Laying site	Not known
	Time to hatching	Not known
	Parental Care	Not known
	Dispersal ability	Not known
	Larvae Size	Not known
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		Predominantly an opportunistic benthic carnivore; ambush predator on small fish
Adult size		Maximum length = ~330 mm; commonly 150-200 mm
Schooling behaviour		Not known
Tolerance to cease-to-flow periods		Low
Temperature		Low (upper $T_{crit} = 20^{\circ}\text{C}$)
Conductivity		High (35, 000 mg L^{-1} ; $\text{LC50} = 17, 000 \text{ mg L}^{-1}$)
Dissolved Oxygen		
Turbidity		
Threats		Predators
	Competitors	
	Other	Loss of connectivity; reduced flows; desiccation of lowland habitats

References: 4, 5, 9, 16, 25, 85, 86, 153

Hyrtl's tandan (<i>Neosilurus hyrtlii</i>) Family: Plotosidae		
Life history	Abundance and distribution across MDB	Occurs only in northern region of MDB, locally abundant
	Adult Habitat	Flowing waters or still areas such as billabongs and lagoons
	Adult micro-habitat association	Soft substrates
	Home Range	Yes
	Longevity	Up to 5 years
	Reproductive age	12 months
	Duration of spawning	October - December
	Spawning style and timing	Spring-summer
	Spawning cues and habitat requirements	Possibly triggered by rising water levels and temperature
	Spawning migration	Upstream migration
	Spawning site	Gravel beds
	Courtship display	Not known
	Number of eggs	3,630 eggs
	Size and type of egg	1.3 mm, but 2.6 mm when water hardened
	Egg Laying site	Gravel beds
	Time to hatching	3 days
	Parental Care	No
	Dispersal ability	Medium
	Larvae Size	5.7-6.0 mm length
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		Nocturnal, benthic carnivore: chironomids, caddisflies, mayflies, microcrustaceans, molluscs & detritus
Adult size		454 mm (150 - 450 mm)
Schooling behaviour		Yes
Tolerance to cease-to-flow periods		Medium
Temperature		Possibly intolerant of low temperatures (lower $T_{crit} = 8 - 12^{\circ}\text{C}$)
Conductivity		Low ($1855 \mu\text{S.cm}^{-1}$)
Dissolved Oxygen		Possibly Low
Turbidity		High
Threats		Predators
	Competitors	
	Other	Barriers to movement

Reference: 5, 28, 29, 87, 88, 89, 153

Rendahl's tandan (<i>Porochilus rendahli</i>) Family: Plotosidae		
Life history	Abundance and distribution across MDB	Limited, rare distribution in southern Qld
	Adult Habitat	Turbid rivers and lagoons
	Adult micro-habitat association	Not known
	Home Range	Not known
	Longevity	Not known
	Reproductive age	Males: 100 mm total length; Females: 110mm total length (0-12 months?)
	Duration of spawning	October - December
	Spawning style and timing	
	Spawning cues and habitat requirements	Temperature exceeding 28°C
	Spawning migration	Not known
	Spawning site	Muddy lagoons
	Courtship display	Not known
	Number of eggs	900 eggs, but up to 3465 eggs have been recorded
	Size and type of egg	1.3 mm diameter
	Egg Laying site	
	Time to hatching	
	Parental Care	
	Dispersal ability	
	Larvae Size	
	Larvae/Juvenile functional feeding group	Not known
Adult Functional Feeding group	Benthic carnivore: aquatic insect larvae (e.g. chironomids and mayflies), microcrustaceans & detritus	
Adult size	240mm (150 - 450 mm) length	
Schooling behaviour	Not known	
Tolerance	Tolerance to cease-to-flow periods	Medium
	Temperature	High (found in temperatures ranging 26-38°C)
	Conductivity	Low – Medium (258 $\mu\text{S}\cdot\text{cm}^{-1}$)
	Dissolved Oxygen	High (2.0 mg L ⁻¹)
Threats	Turbidity	Medium – High (170 NTU)
	Predators	Large piscivorous fish, birds
	Competitors	
	Other	

References: 5, 28, 29, 88, 89, 153

Freshwater catfish (<i>Tandanus tandanus</i>) Family: Plotosidae		
Life history	Abundance and distribution across MDB	Widespread across Basin, but declining abundance in low, slow-flowing rivers
	Adult Habitat	Lowland rivers, lake and wetland habitats
	Adult micro-habitat association	Macrophytes, gravel substrates
	Home Range	Relatively sedentary, most individuals move < 5 km
	Longevity	8+ years
	Reproductive age	3-5 years
	Duration of spawning	Short
	Spawning style and timing	Single spawning, same time each year (Oct - Dec)
	Spawning cues and habitat requirements	Circannual and min temp > 24°C, nest builder
	Spawning migration	No
	Spawning site	Nests
	Courtship display	Elaborate
	Number of eggs	26,000+ eggs
	Size and type of egg	3mm diameter; demersal
	Egg Laying site	Build nests constructed from pebbles and gravel, with coarser material in the centre
	Time to hatching	Up to 7 days
	Parental Care	Yes - but abandons nest if low flows expose it
	Dispersal ability	Low
	Larvae Size	7 mm length
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		Opportunistic carnivore: shrimps, Yabbies, aquatic insects, snails and small fishes (eat carp gudgeons)
Adult size		Maximum length - 900 mm; usually < 200 mm
Schooling behaviour		
Tolerance to cease-to-flow periods		High
Temperature		High (prefer high temperatures)
Conductivity		High (juveniles have lower tolerance than adults)
Dissolved Oxygen		High (0.3 mg L ⁻¹)
Turbidity		High (>250 NTU)
Threats		Predators
	Competitors	Carp and redfin
	Other	Cold water pollution ; barriers to movement; loss of habitat

References: 28, 29, 68, 89, 90, 91, 92, 153

Lagoon goby (<i>Tasmanogobius lasti</i>) Family: Gobiidae		
Life history	Abundance and distribution across MDB	Only found in Lower Lakes and Coorong, where it is widespread but abundance is poor
	Adult Habitat	Estuaries, but found in areas of freshwater discharge. Completes lifecycle in freshwater streams/lakes
	Adult micro-habitat association	Estuaries
	Home Range	Not known
	Longevity	Not known, likely to be 1 – 2 years
	Reproductive age	Not known likely to be <12 months
	Duration of spawning	Not known
	Spawning style and timing	Not known
	Spawning cues and habitat requirements	Not known
	Spawning migration	Not known
	Spawning site	Not known
	Courtship display	Not known
	Number of eggs	Not known; likely to be <2,000 eggs
	Size and type of egg	Not known
	Egg Laying site	Not known
	Time to hatching	Not known
	Parental Care	Not known
	Dispersal ability	Not known
	Larvae Size	Not known
	Larvae/Juvenile functional feeding group	Not known
Adult Functional Feeding group	Benthic, burrowing species	
Adult size	Maximum length 55 mm	
Schooling behaviour	Not known	
Tolerance	Tolerance to cease-to-flow periods	Medium
	Temperature	Not known
	Conductivity	High (55,000 $\mu\text{S.cm}^{-1}$)
	Dissolved Oxygen	Not known
Threats	Turbidity	Not known
	Predators	Picivorous fish, birds
	Competitors	
	Other	

References: 2, 9, 153

Tamar goby (<i>Afurcagobius tamarensis</i>) Family: Gobiidae		
Life history	Abundance and distribution across MDB	Only found in Lower Lakes & Coorong, where it is widespread but abundance is poor
	Adult Habitat	Estuarine species, but also found in adjacent freshwater streams and lakes
	Adult micro-habitat association	Mud substrates, rocks, burrowing
	Home Range	Not known
	Longevity	Not known, likely to be 1 – 2 years
	Reproductive age	Not known likely to be <12 months
	Duration of spawning	Spring
	Spawning style and timing	Not known
	Spawning cues and habitat requirements	Not known
	Spawning migration	Not known
	Spawning site	Not known
	Courtship display	Elaborate
	Number of eggs	Not known
	Size and type of egg	Not known
	Egg Laying site	Not known
	Time to hatching	Not known
	Parental Care	Not known
	Dispersal ability	Not known
	Larvae Size	Not known
	Larvae/Juvenile functional feeding group	Benthic, burrowing species
Adult Functional Feeding group	Not known	
Adult size	Maximum length = ~110 mm; commonly 80 mm	
Schooling behaviour		
Tolerance	Tolerance to cease-to-flow periods	Medium
	Temperature	Medium
	Conductivity	High (55,000 $\mu\text{S.cm}^{-1}$)
	Dissolved Oxygen	Medium to high
	Turbidity	Medium
Threats	Predators	
	Competitors	
	Other	

References: 2, 9, 16, 93, 153

Western blue-spot goby (<i>Pseudogobius olorum</i>) Family: Gobiidae		
Life history	Abundance and distribution across MDB	Only found in Lower Lakes & Coorong, but locally abundant
	Adult Habitat	Marginal freshwater/estuarine species: brackish estuaries and associated freshwater streams and lakes
	Adult micro-habitat association	Aquatic vegetation, mud or rock substrates
	Home Range	Not known
	Longevity	Not known likely to be 1 – 2 years
	Reproductive age	Not known likely to be 0 – 12 months
	Duration of spawning	Not known
	Spawning style and timing	Early to late spring
	Spawning cues and habitat requirements	Aquatic vegetation,
	Spawning migration	Not known
	Spawning site	Aquatic vegetation
	Courtship display	Not known
	Number of eggs	Not known; likely to be < 2000 eggs
	Size and type of egg	Not known
	Egg Laying site	Dense aquatic vegetation in spring in the upper reaches of estuaries
	Time to hatching	Not known
	Parental Care	Yes
	Dispersal ability	Not known
	Larvae Size	Not known
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		Benthic and burrowing - in Western Australia, the species consumed benthic crustaceans and algae
Adult size		60mm (<150 mm)
Schooling behaviour		Not known
Tolerance to cease-to-flow periods		Medium
Temperature		Medium
Conductivity		High
Dissolved Oxygen		Medium
Turbidity		Medium
Threats		Predators
	Competitors	Not known
	Other	Not known

References: 2, 9, 16, 93, 94, 153

Climbing galaxias (<i>Galaxias brevipinnis</i>) Family: Galaxiidae		
Life history	Abundance and distribution across MDB	Largely restricted to upper Murray
	Adult Habitat	Prefer flowing rocky or silt based pools and riffles
	Adult micro-habitat association	Abundant vegetation and canopy
	Home Range	Not known
	Longevity	5 years
	Reproductive age	12 months
	Duration of spawning	April - May
	Spawning style and timing	In coastal streams and landlocked populations- spawn in autumn-winter
	Spawning cues and habitat requirements	Rise in water level, water level higher than normal level
	Spawning migration	No
	Spawning site	Adult habitats
	Courtship display	Not known
	Number of eggs	3,000 -7, 000 eggs
	Size and type of egg	1.8-2.1 mm diameter; round and adhesive
	Egg Laying site	Presumably scatters eggs amongst vegetation at stream edge
	Time to hatching	Hatch in next flood
	Parental Care	No
	Dispersal ability	High (larvae drift downstream to sea (5-6 months) before migrating upstream (freshwater and/or estuaries)
	Larvae Size	5.7 - 7.0 mm length
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		Aquatic invertebrates: mayflies, caddisflies dipterans and small crustaceans.
Adult size		Maximum size - 270 mm, usually 150 - 180 mm
Schooling behaviour		Yes; For spawning aggregations
Tolerance to cease-to-flow periods		Low
Temperature		Low (upper $T_{critical} = 23^{\circ}C$)
Conductivity		High (35, 000 $mg L^{-1}$)
Dissolved Oxygen		Medium
Turbidity		Medium
Threats		Predators
	Competitors	Competes with other galaxiids
	Other	Vegetation loss

References: 16, 38, 77, 95, 96, 97, 153

Barred galaxias (<i>Galaxias fuscous</i>) Family: Galaxiidae		
Life history	Abundance and distribution across MDB	~20 populations in headwaters of Goulburn catchment
	Adult Habitat	Cool, clear, upland streams
	Adult micro-habitat association	Stony or sandy substrates
	Home Range	Not known but likely
	Longevity	Not known but likely 1-2 years
	Reproductive age	Not known but likely 0 – 12 months
	Duration of spawning	Single spawning? late winter to early spring
	Spawning style and timing	Aerated flowing water
	Spawning cues and habitat requirements	Rising water level, aerated water
	Spawning migration	Streambed or aquatic vegetation
	Spawning site	Same as adult habitat
	Courtship display	Not known
	Number of eggs	500 (<2,000) eggs
	Size and type of egg	2.2mm demersal, adhesive
	Egg Laying site	Laid under large boulders
	Time to hatching	Days to weeks
	Parental Care	Not known
	Dispersal ability	Low
	Larvae Size	Not known
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		Drifting and benthic aquatic invertebrates
Adult size		Maximum size -160 mm, usually 70-90 mm
Schooling behaviour		Not known
Tolerance to cease-to-flow periods		Low
Temperature		Low
Conductivity		Low
Dissolved Oxygen		Low
Turbidity		Low
Threats		Predators
	Competitors	Trout
	Other	

References: 16, 38, 77, 95, 98, 99, 100, 101, 153

Common galaxias (<i>Galaxias maculatus</i>) Family: Galaxiidae			
Life history	Abundance and distribution across MDB	Common in Lower Lakes and in lowland regions of Lower Murray region	
	Adult Habitat	Permanent pools, spring fed, Lakes, lower Murray River	
	Adult micro-habitat association	Habitat generalists: abundant vegetation cover	
	Home Range	Not known	
	Longevity	Mostly up to 3 years	
	Reproductive age	~ 12 months (some at 2 years)	
	Duration of spawning	Short	
	Spawning style and timing	Coastal populations in autumn; landlocked late winter - early spring	
	Spawning cues and habitat requirements	Rising water levels	
	Spawning migration	Coastal: downstream migration to brackish areas; landlocked: short migration into tributaries (high flows)	
	Spawning site	Coastal: above normal tideline in estuaries; landlocked: terrestrial vegetation above normal water line	
	Courtship display	Not known	
	Number of eggs	Up to 13, 500 eggs	
	Size and type of egg	1 mm diameter; adhesive	
	Egg Laying site	Exposed vegetation in first flood/high tide; require 2nd inundation	
	Time to hatching	10-31 days, eggs hatch 2hrs post re-immersion	
	Parental Care	No	
	Dispersal ability	High, drift	
	Tolerance	Larvae Size	7 mm length
		Larvae/Juvenile functional feeding group	Cease feeding during inland migration
Adult Functional Feeding group		Coastal - carnivorous; landlocked - mainly amphipods, chironomid larvae and microcrustaceans	
Adult size		Maximum size 190 mm; usually < 100 mm	
Schooling behaviour		Yes, forms dense aggregations at both larval and adult phase	
Tolerance to cease-to-flow periods		Medium	
Temperature		Low (upper T _{critical} = 24.5°C)	
Conductivity		High (30, 000 mg L ⁻¹ ; LC50 = 62, 000 mg L ⁻¹)	
Dissolved Oxygen		Unknown (possibly medium)	
Turbidity		Medium (migrating juveniles avoid high turbidity)	
Threats	Predators	Trout, redfin, other piscivorous fish, birds	
	Competitors		
	Other	Reduced flows may limit recruitment and migration ; desiccation of refuge riffles	

9, 16,25,77,95,102,103,104,105,153

Mountain galaxias (<i>Galaxias olidus</i>) Family: Galaxiidae		
Life history	Abundance and distribution across MDB	Widespread throughout southeast of Basin, but populations declining
	Adult Habitat	Generally shallow, flowing areas at higher elevations
	Adult micro-habitat association	High instream structural integrity and heterogeneity
	Home Range	Yes (<20m)
	Longevity	Up to 5 years
	Reproductive age	12 months – 2 years
	Duration of spawning	Short
	Spawning style and timing	Single spawning - Late Winter or Summer
	Spawning cues and habitat requirements	None known
	Spawning migration	No
	Spawning site	Same as adult habitat
	Courtship display	Not known
	Number of eggs	50-400 eggs
	Size and type of egg	1.2-2.0mm, demersal, adhesive
	Egg Laying site	Under stones in riffles
	Time to hatching	9-21 days
	Parental Care	No
	Dispersal ability	High
	Larvae Size	10 mm length
	Thre Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		Aquatic and terrestrial insects
Adult size		140 mm: commonly 70-80mm
Schooling behaviour		Yes
Tolerance to cease-to-flow periods		Low
Temperature		Medium (upper $T_{critical} = 32^{\circ}C$)
Conductivity		Low (1, 500 mg L ⁻¹)
Dissolved Oxygen		Medium
Turbidity		High
Predators		Trout, other picivorous fish, birds
	Competitors	Trout
	Other	

References: 16, 77, 95,106,107,108,153

Flathead galaxias (<i>Galaxias rostratus</i>) Family: Galaxiidae		
Life history	Abundance and distribution across MDB	Patchy, limited distribution in southern Basin
	Adult Habitat	Found in billabongs, lakes, swamps and rivers
	Adult micro-habitat association	Main channel of rivers, wetlands, lakes
	Home Range	Not known
	Longevity	Not known likely up to 3 years
	Reproductive age	Probably 12 months, when 80 mm long
	Duration of spawning	Short
	Spawning style and timing	Single spawning - Late Winter or Summer
	Spawning cues and habitat requirements	None known (when temperature > 10.5 deg C)
	Spawning migration	Not known
	Spawning site	Mid-open water
	Courtship display	Not known
	Number of eggs	3,000 -7,000 eggs; laid several times over a period of 4 weeks
	Size and type of egg	1.3 - 1.6 mm diameter: planktonic and demersal
	Egg Laying site	Open water, eggs settle to benthos
	Time to hatching	Up to 9 days
	Parental Care	No
	Dispersal ability	Medium
	Larvae Size	5.7 - 8.1 mm length
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		Predominantly aquatic insects with some microcrustaceans
Adult size		146 mm; commonly <100mm
Schooling behaviour		Yes, congregate in mid-water
Tolerance to cease-to-flow periods		Medium
Temperature		High (prefers high temperatures)
Conductivity		Medium
Dissolved Oxygen		Unknown (possibly medium)
Turbidity		Medium
Threats		Predators
	Competitors	Possibly redfin and mosquitofish
	Other	Cold water pollution

References: 5, 16, 77, 95, 109, 153

Spotted galaxias (<i>Galaxias truttaceus</i>) Family: Galaxiidae		
Life history	Abundance and distribution across MDB	Small populations present in the upper Campaspe and Loddon drainages
	Adult Habitat	Tributaries
	Adult micro-habitat association	Woody debris, boulders, under-cut banks, pool edges
	Home Range	Not known but likely
	Longevity	Not known
	Reproductive age	Not known but 0-12 months likely
	Duration of spawning	Short
	Spawning style and timing	Single spawning - autumn to winter
	Spawning cues and habitat requirements	Not known
	Spawning migration	Upstream into headwater tributaries
	Spawning site	Not known
	Courtship display	Not known
	Number of eggs	1, 000 - 16, 000 eggs
	Size and type of egg	1.3 - 1.6 mm diameter
	Egg Laying site	Deposited amongst instream aquatic vegetation
	Time to hatching	28 days
	Parental Care	No
	Dispersal ability	High
	Larvae Size	6.5 - 9.0 mm length
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		Carnivorous: aquatic insect larvae, terrestrial insects& food drift mid-water (caddisflies and mayflies)
Adult size		maximum length = > 200 mm; usually 120-140 mm
Schooling behaviour		Not known
Tolerance to cease-to-flow periods		Unknown (possibly medium)
Temperature		Unknown (possibly medium)
Conductivity		High (larval marine phase)
Dissolved Oxygen		Unknown (possibly medium)
Turbidity		Unknown (possibly medium)
Threats		Predators
	Competitors	When translocated, spotted galaxias may outcompete other native species
	Other	Habitat loss

References: 16, 77, 95, 110, 111, 112, 153

Carp gudgeon complex (<i>Hypseleotris</i> spp.) Family: Eleotridae		
Life history	Abundance and distribution across MDB	Highly abundant & widespread in lowland reaches of Basin (7 morpho-species found; difficult to distinguish)
	Adult Habitat	In turbid, slow flowing rivers, adults littoral, larvae pelagic
	Adult micro-habitat association	Cover from boulders and aquatic vegetation
	Home Range	Not known
	Longevity	2-3 years
	Reproductive age	0-12 months
	Duration of spawning	Short
	Spawning style and timing	Protracted from Late winter to Autumn in the lower Murray River
	Spawning cues and habitat requirements	Not known
	Spawning migration	None known, low flow
	Spawning site	Hard substrates, logs, debris
	Courtship display	Yes
	Number of eggs	1,000-2,000 eggs: mean ~1350 eggs
	Size and type of egg	Attached demersal
	Egg Laying site	Shallow flooded backwaters amongst macrophytes & woody debris
	Time to hatching	2-4 days
	Tolerance	Parental Care
Dispersal ability		High
Larvae Size		1.7-2.1 mm length
Larvae/Juvenile functional feeding group		Obligate planktivore
Adult Functional Feeding group		Zooplankton, microinvertebrates, terrestrial invertebrates
Adult size		60 mm, commonly 30 – 40 mm
Schooling behaviour		Schools in moderately flowing water
Tolerance to cease-to-flow periods		High
Temperature		Medium to High
Conductivity		High (~26, 000 mg L ⁻¹ ; LC50 = 50, 000 mg L ⁻¹)
Threats	Dissolved Oxygen	High (tolerant < 1 mg L ⁻¹ ; for short periods; instigate ASR; eggs vulnerable)
	Turbidity	High
	Predators	Redfin
	Competitors	Mosquitofish
	Other	Vegetation loss; infestation of introduced tapeworm, <i>Bothriocephalus acheilognathi</i>

References: 16, 28, 77, 113, 114, 115, 116, 117, 118, 119, 153

Purple-spotted Gudgeon (<i>Mogurnda adspersa</i>) Family: Eleotridae		
Life history	Abundance and distribution across MDB	Locally abundant in Qld reaches; patchy & rare in NSW; extinct Vic; translocated population in SA
	Adult Habitat	Benthic species
	Adult micro-habitat association	Cobble and rock cover in Qld range, aquatic vegetation in southern range
	Home Range	Not known, likely
	Longevity	3 + years
	Reproductive age	6 months
	Duration of spawning	Short
	Spawning style and timing	Multiple spawning, Hard surfaces, spring and summer
	Spawning cues and habitat requirements	Increase in temperature
	Spawning migration	No
	Spawning site	Hard surfaces, adult habitat
	Courtship display	Yes
	Number of eggs	100-1,300 eggs (mean ~500 eggs)
	Size and type of egg	1.3 mm -3.8 mm; adhesive
	Egg Laying site	Deposit in single batch on a rock, log or aquatic plants.
	Time to hatching	3-9 days
	Parental Care	Yes
	Dispersal ability	Low
	Larvae Size	4 mm length
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		Slow-moving ambush predator: small fish and aquatic macroinvertebrates and also worms and tadpoles
Adult size		Maximum length = 152 mm; commonly 60-120 mm
Schooling behaviour		Not known
Tolerance to cease-to-flow periods		High
Temperature		High (upper T _{critical} 34°C; appear inactive in winter)
Conductivity		Medium to High (southern sp. ~35, 000; LC50 = 17, 100 mg L ⁻¹)
Dissolved Oxygen		High
Turbidity		High
Threats		Predators
	Competitors	Compete with other native fish species
	Other	Possibly fluctuations in water levels as result of river regulation

References: 5, 16, 28, 77, 120, 121, 153

Flathead gudgeon (<i>Philypnodon grandiceps</i>) Family: Eleotridae			
Life history	Abundance and distribution across MDB	Largely absent in upland areas of Basin; patchy in mid-regions, locally abundant in southern reaches	
	Adult Habitat	Found in lowland streams or lakes and dams	
	Adult micro-habitat association	Weedy/muddy areas with abundant cover in the form of rocks or logs, slow flow	
	Home Range	Not known	
	Longevity	Not known	
	Reproductive age	Not known likely <12 months	
	Duration of spawning	Protracted from Late winter - Autumn	
	Spawning style and timing	Protracted, serial or repeat	
	Spawning cues and habitat requirements	None known, low flow, when temperature between 18 - 27°C	
	Spawning migration	Not known	
	Spawning site	Hard surfaces: wood, debris	
	Courtship display	Yes	
	Number of eggs	1,400-2,300 eggs	
	Size and type of egg	1.5-2.2 mm, demersal, adhesive	
	Egg Laying site	Attach to solid objects such as rocks and wood and	
	Time to hatching	4 - 6 days	
	Parental Care	Yes	
	Dispersal ability	Low	
	Larvae Size	3.8 mm length	
	Thre	Larvae/Juvenile functional feeding group	Not known
Adult Functional Feeding group		Sit and wait predator - carnivorous ambush predator of aquatic insects, molluscs, tadpoles, crustaceans and small fish	
Adult size		Maximum length = 115 mm; usually 80 mm	
Schooling behaviour		Not known	
Tolerance		Tolerance to cease-to-flow periods	Unknown (possibly high)
		Temperature	High
		Conductivity	High (24, 600 mg L ⁻¹ ; LC50 = 23,700 mg L ⁻¹ at fast acclimation; 40, 000 mg L ⁻¹ slow acclimation)
		Dissolved Oxygen	High (tolerant below 1 mg L ⁻¹ for short periods, instigate ASR)
		Turbidity	Unknown (possibly high)
Other		Predators	Redfin
	Competitors	Mosquito fish	
	Other	Vegetation loss	

References: 2, 4, 16, 28, 77, 117, 122, 123, 153

Dwarf flathead gudgeon (<i>Philypnodon macrostomus</i>) Family: Eleotridae		
Life history	Abundance and distribution across MDB	Regionally common in coastal streams in Qld, Vic & SA; patchy distribution inland regions of MDB
	Adult Habitat	Reportedly prefer calm waters;
	Adult micro-habitat association	Over mud and rock substrates or in weedy cover
	Home Range	Not known
	Longevity	Not known
	Reproductive age	Not known likely <12 months
	Duration of spawning	Not known
	Spawning style and timing	Not known
	Spawning cues and habitat requirements	In aquaria breed at temperatures of 19-22°C.
	Spawning migration	Not known
	Spawning site	Hard surfaces, wood, debris
	Courtship display	Yes
	Number of eggs	Not known
	Size and type of egg	Not known, likely demersal, adhesive
	Egg Laying site	Hard surfaces, wood, debris
	Time to hatching	4 -5 days in aquaria
	Parental Care	Yes
	Dispersal ability	Low?
	Larvae Size	Not known
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		Benthic carnivore, feeding mainly on aquatic insects and their larvae such as chironomids, mayflies and caddisflies
Adult size		Maximum length = 65 mm; rarely more than 40 mm.
Schooling behaviour		Not known
Tolerance to cease-to-flow periods		Unknown (possibly medium)
Temperature		Unknown (possibly medium - high)
Conductivity		Unknown (possibly medium - high)
Dissolved Oxygen		Unknown (possibly medium - high)
Turbidity		Unknown (possibly medium - high)
Threats		Predators
	Competitors	
	Other	

References: 2, 4, 9, 16, 28, 38, 77, 117, 153

Australian smelt (<i>Retropinna semoni</i>) Family: Retropinnidae		
Life history	Abundance and distribution across MDB	Highly abundant in low to mid altitudes SE Australia
	Adult Habitat	Billabongs, wetlands and main river channels, pelagic
	Adult micro-habitat association	Habitat generalists
	Home Range	Not known but unlikely
	Longevity	3+ years
	Reproductive age	6-9 months
	Duration of spawning	September - March
	Spawning style and timing	Protracted, serial or repeat, Sept-Mar (when temp 15 - 18°C)
	Spawning cues and habitat requirements	None known, most conditions
	Spawning migration	Not known, likely?
	Spawning site	Broadcast over substrate and/or aquatic vegetation
	Courtship display	Yes
	Number of eggs	100-1,200 eggs; mean ~500 eggs
	Size and type of egg	1 mm diameter; demersal adhesive
	Egg Laying site	Sink and adhere to aquatic vegetation, sediment or debris
	Time to hatching	9 - 10 days
	Parental Care	No
	Dispersal ability	High
	Larvae Size	4.6 – 5mm length
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		Zooplankton (especially cladocerans)
Adult size		Maximum length 100 mm; usually 40 – 60 mm
Schooling behaviour		Large pelagic schools (1000's individuals) in open water
Tolerance to cease-to-flow periods		High
Temperature		High (upper $T_{critical} = 28^{\circ}C$)
Conductivity		High (LC50 = 59, 000 mg L-1)
Dissolved Oxygen		Moderate (<2 mg L ⁻¹ , ASR poor)
Turbidity		High
Threats		Predators
	Competitors	
	Other	Migration barriers – might be fragmenting populations

References: 2, 4, 9, 16, 28, 77, 84, 122, 123, 124, 125, 153

Murray River Rainbowfish (<i>Melanotaenia fluviatilis</i>) Family: Melanotaeniidae		
Life history	Abundance and distribution across MDB	Patchy distribution across MDB; disappeared from Lower reaches of Murray
	Adult Habitat	Prefer backwaters, billabongs and wetlands
	Adult micro-habitat association	Aquatic vegetation and woody debris
	Home Range	Not known
	Longevity	3 years
	Reproductive age	10 -12 months
	Duration of spawning	Short
	Spawning style and timing	Single spawning, late winter or summer
	Spawning cues and habitat requirements	None known
	Spawning migration	Not known
	Spawning site	Adult habitat: aquatic vegetation
	Courtship display	Yes
	Number of eggs	130 eggs, range 35-333 eggs
	Size and type of egg	1.3 - 1.8 mm demersal, adhesive
	Egg Laying site	Eggs sink and lodge amongst aquatic plants, where they attach via adhesive threads
	Time to hatching	After 7 days
	Parental Care	No
	Dispersal ability	low
	Larvae Size	~2.0-3.7 mm length
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		Carnivorous: aquatic invertebrates, terrestrial invertebrates that fall on the water surface and some filamentous algae
Adult size		Maximum length = 90 mm, usually < 70 mm
Schooling behaviour		Schools of 30 or more are commonly seen swimming just below the water surface.
Tolerance to cease-to-flow periods		Medium
Temperature		Medium (upper $T_{critical} = 28^{\circ}C$ and prolonged periods $<7^{\circ}C$ decrease fitness)
Conductivity		High (30, 000 $mg L^{-1}$)
Dissolved Oxygen		Medium (down to 4 $mg L^{-1}$)
Turbidity		High (up to 300 NTU)
Threats		Predators
	Competitors	
	Other	Loss of vegetation cover ; coldwater pollution

References: 2, 4, 9, 16, 77, 122, 123, 126, 153

Desert Rainbowfish (<i>Melanotaenia splendida tatei</i>) Family: Melanotaeniidae		
Life history	Abundance and distribution across MDB	Recently identified lower Warrego & Paroo Rivers,
	Adult Habitat	Ephemeral water bodies, swim just below water surface
	Adult micro-habitat association	Slow flowing rivers, lakes, bores, waterholes
	Home Range	Not known
	Longevity	Not known, likely 2-3 years
	Reproductive age	At 30 – 35 mm length
	Duration of spawning	October - March
	Spawning style and timing	Batch spawner, onto vegetation
	Spawning cues and habitat requirements	Temperature >20°C
	Spawning migration	Not known
	Spawning site	Aquatic vegetation
	Courtship display	Yes
	Number of eggs	In aquaria: 80 - 100 eggs; usually in daily batches
	Size and type of egg	0.8 - 0.95 mm diameter, demersal, adhesive
	Egg Laying site	Laid amongst aquatic plants or on the exposed roots of riparian vegetation
	Time to hatching	In aquaria after 7 days at 24°C
	Parental Care	No
	Dispersal ability	High
	Larvae Size	4.0 - 4.5 mm length
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		Omnivorous: small aquatic invertebrates and filamentous algae
Adult size		Maximum length = 90 mm
Schooling behaviour		Yes
Tolerance to cease-to-flow periods		High
Temperature		High
Conductivity		Unknown (possibly medium)
Dissolved Oxygen		Unknown (possibly high)
Turbidity		Unknown (possibly high)
Threats		Predators
	Competitors	Mosquitofish
	Other	

References: 28, 127, 153

Long-finned eel (<i>Anguilla reinhardtii</i>) Family: Anguillidae		
Life history	Abundance and distribution across MDB	Low abundance in Condamine-Balonne drainage in southern Qld and Lower Lakes of Murray River
	Adult Habitat	Flowing water also lagoons and swamps
	Adult micro-habitat association	Preferred habitats include undercut banks and areas with snags
	Home Range	Restricted home range of 300 m or less (unless migrating to ocean to spawn)
	Longevity	50+ years
	Reproductive age	Males migrate at 44-62 cm; females at 74 - 142 cm
	Duration of spawning	Short
	Spawning style and timing	Long migration, marine
	Spawning cues and habitat requirements	Flood, then Geomagnetic cues for orientation
	Spawning migration	Downstream into ocean, up to 5,000km to spawning ground
	Spawning site	Coral sea, Fiji, Tahiti, Solomon Islands
	Courtship display	Not known
	Number of eggs	Several million (>10,000) eggs
	Size and type of egg	Not known
	Egg Laying site	Not known
	Time to hatching	Not known
	Parental Care	Not known
	Dispersal ability	High
	Larvae Size	~58 mm length
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		Nocturnal predator of fish, crustaceans, molluscs and insects, and the occasional juvenile waterfowl
Adult size		Maximum length = 1650 mm, usually 1000 mm
Schooling behaviour		Not known (adults), Yes (leptocephali)
Tolerance to cease-to-flow periods		High
Temperature		Not known
Conductivity		High
Dissolved Oxygen		High
Turbidity		High
Thre		Predators
	Competitors	
	Other	Barriers to migration; overharvesting

9, 16, 25, 28, 77,128,129, 153

Short-finned eel (<i>Anguilla australis</i>) Family: Anguillidae		
Life history	Abundance and distribution across MDB	Predominantly coastal streams outside Basin, rare inland: upper Murrumbidgee River & Lower Murray
	Adult Habitat	In a variety of habitats including rivers, lakes and swamps
	Adult micro-habitat association	Still water
	Home Range	Occupy a well-defined home range of about 400 m
	Longevity	>32 years
	Reproductive age	Males at 14 years; female 18-24 years
	Duration of spawning	Not known
	Spawning style and timing	June - September
	Spawning cues and habitat requirements	Flood, then Geomagnetic cues for orientation to spawning ground
	Spawning migration	Downstream migration ocean, then up to 5000km to Coral Sea
	Spawning site	Adults may remain in fresh waters for 20 years or more before migrating to the sea to breed and then die
	Courtship display	Not known
	Number of eggs	1.5-3 million eggs
	Size and type of egg	1.5 mm
	Egg Laying site	Coral sea, marine
	Time to hatching	Not known
	Parental Care	Not known
	Dispersal ability	High
	Tolerance	Larvae Size
Larvae/Juvenile functional feeding group		Zooplankton, may absorb nutrients from water
Adult Functional Feeding group		Nocturnal predator, the Short-finned eel eats a variety of fish, crustaceans, molluscs and insects
Adult size		Maximum length = 1100 mm; usually < 700 mm long
Schooling behaviour		Not known (adults), Yes (leptocephali) and elver
Tolerance to cease-to-flow periods		High
Temperature		High (wide-ranging)
Conductivity		Moderate (13, 400 mg L ⁻¹)
Dissolved Oxygen		Medium-High
Turbidity		High
Threats	Predators	Picivorous fish, birds
	Competitors	
	Other	Barriers to migration; overharvesting

References: 9, 16, 28, 77, 128, 129, 153

Pouched lamprey (<i>Geotria australis</i>) Family: Petromyzontidae		
Life history	Abundance and distribution across MDB	Restricted to Lower Murray River; cryptic species, rarely seen
	Adult Habitat	Most of adult life spent at sea
	Adult micro-habitat association	Not known
	Home Range	Not known
	Longevity	Not known
	Reproductive age	Not known
	Duration of spawning	October - December
	Spawning style and timing	Not known
	Spawning cues and habitat requirements	Not known
	Spawning migration	Upstream migration (adults), downstream migration (juveniles)
	Spawning site	Probably occurs in headwater streams and adults probably die after spawning
	Courtship display	Not known
	Number of eggs	58,000 eggs
	Size and type of egg	1.1 mm diameter
	Egg Laying site	Not known
	Time to hatching	Not known
	Parental Care	Not known
	Dispersal ability	High
	Larvae Size	< 120 mm length
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		After metamorphosis to adulthood, become parasitic on other fish, rasping a hole in the side and feeding on blood and/or muscle (hosts unknown)
Adult size		Maximum length = 500-700 mm long
Schooling behaviour		Not known
Tolerance to cease-to-flow periods		High
Temperature		Medium (upper $T_{critical} = 28.3^{\circ}C$)
Conductivity		High
Dissolved Oxygen		High
Turbidity		High
Threats		Predators
	Competitors	
	Other	Loss of burrowing habitats; reduced organic inputs; increased temperatures around burrowing sites; migration barriers

References: 9, 16, 25, 77, 130, 153

Shortheaded lamprey (<i>Mordacia mordax</i>) Family: Petromyzontidae		
Life history	Abundance and distribution across MDB	Generally restricted lower - mid Murray River; adult abundance declining
	Adult Habitat	Most of the adult life is spent at sea or in estuaries
	Adult micro-habitat association	Not known
	Home Range	Not known
	Longevity	Not known
	Reproductive age	Not known
	Duration of spawning	October - December
	Spawning style and timing	Not known
	Spawning cues and habitat requirements	Not known
	Spawning migration	Upstream migration (adults), downstream migration (juveniles)
	Spawning site	Probably occurs in headwater streams and adults probably die after spawning
	Courtship display	Not known
	Number of eggs	3,800-13,400 eggs
	Size and type of egg	0.3 -0.5 mm diameter
	Egg Laying site	Deposited in a shallow nest (small depression) in the substrate
	Time to hatching	Not known
	Parental Care	Not known
	Dispersal ability	High
	Larvae Size	Ammocetes metamorphose at 100-140 mm length and migrating to the sea
	Larvae/Juvenile functional feeding group	Ammocetes are toothless, feeding on algae, detritus and micro-organisms filtered from the water
Adult Functional Feeding group	Parasitic on other fish, rasping a hole in the side and feeding on blood and/or muscle	
Adult size	500mm, commonly 300 – 400mm	
Schooling behaviour	Not known	
Tolerance	Tolerance to cease-to-flow periods	High
	Temperature	Medium (upper T _{critical} = 30°C)
	Conductivity	High
	Dissolved Oxygen	Unknown (possibly high)
Threats	Turbidity	Unknown (possibly high)
	Predators	Birds, piscivorous fish
	Competitors	
	Other	Barriers to migration; reduced stock of marine hosts;

References: 4, 9, 16, 77, 153

EXOTIC: Rainbow Trout (<i>Oncorhynchus mykiss</i>) Family: Salmonidae		
Life history	Abundance and distribution across MDB	Widely distributed in upland streams in Vic, NSW and ACT
	Adult Habitat	Streams, wetland with permanent flow, deep pools and cool, oxygenated waters
	Adult micro-habitat association	Vegetation beds, pools of rivers
	Home Range	Yes
	Longevity	5+ years
	Reproductive age	2-3 years
	Duration of spawning	July - October
	Spawning style and timing	Decreasing temperature and daylength
	Spawning cues and habitat requirements	Aerated flowing water
	Spawning migration	Frequently upstream
	Spawning site	Gravel riffle beds
	Courtship display	Yes
	Number of eggs	500-3,000 eggs
	Size and type of egg	4-5 mm diameter; slightly adhesive, demersal
	Egg Laying site	Constructs a nest (a 'redd') in gravel
	Time to hatching	3- 12 weeks
	Parental Care	Yes
	Dispersal ability	High
	Larvae Size	
	Larvae/Juvenile functional feeding group	
Adult Functional Feeding group	Insects, terrestrial insects, molluscs, crustaceans	
Adult size	850mm commonly 300 – 600mm	
Schooling behaviour	Yes	
Tolerance	Tolerance to cease-to-flow periods	Low
	Temperature	Low (<25°C; mortality induced at 27°C)
	Conductivity	High (LC50 = 35, 000 mg L ⁻¹)
	Dissolved Oxygen	Low (not found in hypoxic environments; but overseas adults found in selected habitats as low as 2.9 mg L ⁻¹)
Threats	Turbidity	Low
	Predators	Competitive displacement (i.e. native frogs & galaxiids)
	Competitors	Native galaxiids
	Other	Often found with the parasitic copepod <i>Lernaea</i> sp. attached, particularly around the fins

References: 131, 132, 133, 134, 153

EXOTIC: Atlantic Salmon (<i>Salmo salar</i>) Family: Salmonidae		
Life history	Abundance and distribution across MDB	Rare; not generally established significant populations in Australia
	Adult Habitat	Prefers deep pools with cool, oxygenated waters
	Adult micro-habitat association	Open water, woody debris
	Home Range	Yes
	Longevity	>10 years
	Reproductive age	1-3 years
	Duration of spawning	June - August
	Spawning style and timing	Multiple/serial
	Spawning cues and habitat requirements	?, gravel bed/aerated flowing water
	Spawning migration	Upstream movement into headwaters
	Spawning site	Gravel riffles
	Courtship display	Yes
	Number of eggs	10,000–20,000 eggs
	Size and type of egg	5 – 7 mm diameter
	Egg Laying site	Laid in a 'redd' excavated on gravel riffled bottom
	Time to hatching	6-20 weeks
	Parental Care	Yes
	Dispersal ability	High
	Larvae Size	
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		Carnivore: insect larvae, snails and wind-blown terrestrial arthropods, aquatic crustaceans, small fish
Adult size		Commonly 1-3 kg in Australia
Schooling behaviour		Yes
Tolerance to cease-to-flow periods		Low
Temperature		Low
Conductivity		High
Dissolved Oxygen		Low
Turbidity		Low
Threats		Predators
	Competitors	
	Other	

References: 131, 133, 135, 153

EXOTIC: Brown trout (<i>Salmo trutta</i>) Family: Salmonidae		
Life history	Abundance and distribution across MDB	Widespread distribution in upland reaches in Vic, NSW and ACT, low numbers in SA streams
	Adult Habitat	Streams, prefer permanent flow and deep pools with cool, oxygenated water
	Adult micro-habitat association	Pools and riffles, overhanging vegetation
	Home Range	Yes
	Longevity	6 + years
	Reproductive age	2-3 years
	Duration of spawning	Short
	Spawning style and timing	April - August
	Spawning cues and habitat requirements	Aerated flowing water
	Spawning migration	Frequently upstream
	Spawning site	Gravel riffles
	Courtship display	Yes
	Number of eggs	500-3,000 eggs
	Size and type of egg	4- 5 mm diameter;
	Egg Laying site	In a gravel nest ('redd') constructed
	Time to hatching	6 – 20 weeks (temperature dependent)
	Parental Care	Yes
	Dispersal ability	High
Larvae Size		
Larvae/Juvenile functional feeding group	Carnivore: Insect larvae, snails and wind-blown terrestrial arthropods, aquatic crustaceans, small fish	
Adult Functional Feeding group	Carnivore: insect larvae, snails and wind-blown terrestrial arthropods, aquatic crustaceans, small fish	
Adult size	20kg, commonly 1-5kg	
Schooling behaviour	Yes at spawning	
Tolerance	Tolerance to cease-to-flow periods	Low
	Temperature	Low (<25°C)
	Conductivity	High (LC50 = 35, 000 mg L ⁻¹)
	Dissolved Oxygen	Low (MDB - not found in hypoxic environments)/(overseas – select habitats as low as 4.5 mg L ⁻¹)
Threats	Turbidity	Low
	Predators	Competitive displacement of native fauna
	Competitors	Native galaxiids, trout cod, Macquarie perch, native frogs
	Other	Often found with the parasitic copepod <i>Lernaea</i> sp. attached, particularly around the fins

References: 131, 132, 135, 153

EXOTIC: Goldfish (<i>Carassius auratus</i>) Family: Cyprinidae		
Life history	Abundance and distribution across MDB	Typically abundant in areas following impoundment
	Adult Habitat	Generalist: slow flowing or stagnant habitat
	Adult micro-habitat association	Vegetation cover: submerged and emergent vegetation
	Home Range	No
	Longevity	10 + years
	Reproductive age	12 months
	Duration of spawning	October - December
	Spawning style and timing	Spawns at temperatures between 17-23°C
	Spawning cues and habitat requirements	Increasing temperature, vegetation
	Spawning migration	No
	Spawning site	Same as adult habitat
	Courtship display	Yes
	Number of eggs	2,000 – 10,000 eggs
	Size and type of egg	
	Egg Laying site	Amongst freshwater plants
	Time to hatching	>7 days
	Parental Care	No
	Dispersal ability	Medium-high
	Larvae Size	4.0-6 mm length
	Larvae/Juvenile functional feeding group	Algae, detritus
Adult Functional Feeding group	Omnivore: small crustaceans, freshwater insect larvae, plant material and detritus	
Adult size	Maximum size 400 mm; usually less than 200 mm	
Schooling behaviour		
Tolerance	Tolerance to cease-to-flow periods	High
	Temperature	High
	Conductivity	Medium (LC50 = 19176 mg L ⁻¹)
	Dissolved Oxygen	High (tolerant of 1 mg L ⁻¹ (for short periods) ; instigates ASR
Threats	Turbidity	High
	Predators	Believed to be responsible for introducing to Australia the disease 'Goldfish ulcer'
	Competitors	Generally considered 'benign' introduction
	Other	Often heavily infested with the parasitic copepod Anchorworm (<i>Lernaea</i> sp.) and goldfish ulcer disease

References: 136, 137, 153

EXOTIC: Common carp (<i>Cyprinus carpio</i>) Family: Cyprinidae		
Life history	Abundance and distribution across MDB	Highly abundant and widespread in lowland rivers and creeks and upland streams as well
	Adult Habitat	Generalist: often slow flowing and stagnant habitat
	Adult micro-habitat association	Woody debris, soft substrates
	Home Range	Yes
	Longevity	10+ years
	Reproductive age	Males 1 year; females 2 years
	Duration of spawning	Medium (spring – summer)
	Spawning style and timing	Multiple/ temperature 17 - 25°C
	Spawning cues and habitat requirements	Congregate in shallow waters
	Spawning migration	Lateral, upstream
	Spawning site	Inundated littoral, floodplain
	Courtship display	Yes
	Number of eggs	1, 500, 000 eggs
	Size and type of egg	0.5 mm diameter; adhesive
	Egg Laying site	Laid in clumps on freshwater vegetation, logs and submerged grass
	Time to hatching	2 – 6 days (temperature dependent)
	Parental Care	No
	Dispersal ability	High
	Larvae Size	3.5-4.6 mm length
	Larvae/Juvenile functional feeding group	Detritivore, algae,
Adult Functional Feeding group	Detritus, algae, zooplankton, annelids, freshwater insect larvae, crustaceans, molluscs some plant material	
Adult size	Maximum 1200 mm and 60 kg; usually up to 4–5 kg	
Schooling behaviour	Yes	
Tolerance	Tolerance to cease-to-flow periods	High
	Temperature	High
	Conductivity	Medium (LC50 = 12 800 mg L ⁻¹)
	Dissolved Oxygen	High (tolerant below 1 mg L ⁻¹ for short periods; capable of aerobic surface respiration (ASR))
Threats	Turbidity	High
	Predators	Feeding behaviour increases turbidity, alter zooplankton levels increasing risk of algal blooms
	Competitors	Compete with native species for food and space
	Other	Carry the parasitic copepod Anchorworm (<i>Lernaea</i> sp.),

References: 14, 136, 137, 138, 139, 140, 141, 142, 153

EXOTIC: Tench (<i>Tinca tinca</i>) Family: Cyprinidae		
Life history	Abundance and distribution across MDB	Primarily restricted to Vic, populations declining in NSW
	Adult Habitat	Streams, deep pools; avoids fast-flowing water
	Adult micro-habitat association	Habitats with muddy bottom and abundant aquatic plants
	Home Range	Not known
	Longevity	10+ years (typically 20 – 30)
	Reproductive age	3-4 years
	Duration of spawning	Medium (spring – summer)
	Spawning style and timing	Multiple
	Spawning cues and habitat requirements	Increasing temperature and daylength
	Spawning migration	No
	Spawning site	Not known
	Courtship display	Yes
	Number of eggs	300,000 to 900,000 eggs / several batches at 2 week intervals
	Size and type of egg	0.8–1.0 mm diameter; adhesive
	Egg Laying site	Shallow waters, on weeds
	Time to hatching	3-6 days
	Parental Care	No
	Dispersal ability	High
	Larvae Size	4 -5 mm length
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		Benthic carnivores: aquatic insects, microcrustaceans, some molluscs, worms and plant material.
Adult size		Maximum 700 mm; usually 100–300 mm
Schooling behaviour		Yes
Tolerance to cease-to-flow periods		High
Temperature		Medium
Conductivity		Low (11, 600 mg L ⁻¹ for 2 hours)
Dissolved Oxygen		High (5 – 13% saturation for 2 hours)
Turbidity		High
Threats		Predators
	Competitors	
	Other	

References: 16, 137, 153

EXOTIC: Roach (<i>Rutilus rutilus</i>) Family: Cyprinidae		
Life history	Abundance and distribution across MDB	Limited abundance in Vic, rarely in NSW in MDB
	Adult Habitat	Associated with lakes, ponds & slow-flowing rivers
	Adult micro-habitat association	Abundant vegetation
	Home Range	Not known
	Longevity	Up to 12 years
	Reproductive age	Males 1-2 years; females 2-3 years
	Duration of spawning	Short (spring – early summer)
	Spawning style and timing	Broadcast onto vegetation, October - December
	Spawning cues and habitat requirements	Increasing Temperature
	Spawning migration	Upstream and downstream movements recorded
	Spawning site	Shallow water amongst vegetation or stony bottom
	Courtship display	Yes
	Number of eggs	5, 000 to 200, 000 eggs
	Size and type of egg	~ 1 – 1.5 mm diameter: adhesive and transparent
	Egg Laying site	Vegetation, broadcast over substrate
	Time to hatching	4 -10 days (temperature dependent)
	Parental Care	No
	Dispersal ability	Medium
	Larvae Size	5 – 6 mm length
	Larvae/Juvenile functional feeding group	Plankton
Adult Functional Feeding group	Omnivores	
Adult size	Maximum size is 450 mm; usually much smaller at 150-200 mm	
Schooling behaviour	Yes	
Tolerance	Tolerance to cease-to-flow periods	Unknown (possibly medium)
	Temperature	Unknown (possibly medium)
	Conductivity	Unknown (possibly low)
	Dissolved Oxygen	Unknown (possibly medium)
	Turbidity	Unknown (possibly medium)
Threats	Predators	Very little known
	Competitors	
	Other	Often eaten by native cod and perch species

References: 16, 137, 143, 153

EXOTIC: Mosquitofish (<i>Gambusia holbrooki</i>) Family: Poeciliidae		
Life history	Abundance and distribution across MDB	Widely distributed across Basin
	Adult Habitat	Generalist: streams and wetlands with low flow
	Adult micro-habitat association	Often close to surface or at shallow edges or amongst vegetation
	Home Range	No
	Longevity	Up to 4 years?
	Reproductive age	2-6 months old
	Duration of spawning	October - May
	Spawning style and timing	Protracted, serial or repeat (September to March)
	Spawning cues and habitat requirements	None known
	Spawning migration	No
	Spawning site	Anywhere
	Courtship display	Yes
	Number of eggs	50 – 300 live young, several times per year
	Size and type of egg	viviparous
	Egg Laying site	Not applicable
	Time to hatching	Not applicable
	Parental Care	Yes
	Dispersal ability	Medium to high
	Larvae Size	Not applicable (no larval stage)
	Tolerance	Larvae/Juvenile functional feeding group
Adult Functional Feeding group		Carnivores: range of small freshwater invertebrates and wind-blown terrestrial insects
Adult size		Maximum length 60 mm
Schooling behaviour		Yes
Tolerance to cease-to-flow periods		High
Temperature		High (upper $T_{critical} = 40^{\circ}C$)
Conductivity		High (59, 000 mg L ⁻¹ for 30 days; LC50 = 15, 000 mg L ⁻¹)
Dissolved Oxygen		High (tolerant of 1 mg L ⁻¹ ; efficient use of aerobic surface respiration)
Turbidity		High
Threats		Predators
	Competitors	Compete with small native fish
	Other	

References: 115, 145, 146, 153

EXOTIC: Oriental weatherloach (<i>Misgurnus anguillicaudatus</i>) Family: Cobitidae		
Life history	Abundance and distribution across MDB	Moderate abundance, but widely distributed across basin, although absent from SA
	Adult Habitat	Slow or still-flowing water
	Adult micro-habitat association	Sand, mud or detritus substrates
	Home Range	Capable of burrowing into substrate to avoid predation or to aestivate
	Longevity	13+ years
	Reproductive age	~100 mm total length
	Duration of spawning	Short (summer)
	Spawning style and timing	Multiple spawner
	Spawning cues and habitat requirements	Not known in Australia
	Spawning migration	No
	Spawning site	Vegetation or substrate
	Courtship display	Yes
	Number of eggs	4, 000 to 8, 000 eggs
	Size and type of egg	1.5 mm diameter;
	Egg Laying site	Laid on freshwater plants and/or mud
	Time to hatching	>2- 3 days
	Parental Care	No
	Dispersal ability	Medium to high
	Larvae Size	
	Larvae/Juvenile functional feeding group	
Adult Functional Feeding group	Benthic omnivore: insect larvae, rotifers, algae, gastropods, molluscs, micro-crustaceans and detritus	
Adult size	Maximum length 250 mm; usually < 190 mm	
Schooling behaviour	No	
Tolerance	Tolerance to cease-to-flow periods	High
	Temperature	High (typically range 2 - 30°C; found up to 45°C)
	Conductivity	High
	Dissolved Oxygen	High (anoxia air-breathing)
	Turbidity	High
Threats	Predators	May increase turbidity and nitrogen levels, introduce parasites, prey on eggs of native species
	Competitors	Significant diet overlap with mountain galaxias
	Other	

References: 147, 148, 153

EXOTIC: Redfin perch (<i>Perca fluviatilis</i>) Family: Percidae		
Life history	Abundance and distribution across MDB	Widely distributed throughout temperate regions of Basin
	Adult Habitat	Low flow generalist; lakes, billabongs and swamps
	Adult micro-habitat association	Often near structure & abundant vegetation; but also open areas
	Home Range	No
	Longevity	10+ years
	Reproductive age	1-3 years
	Duration of spawning	Short (spring)
	Spawning style and timing	Benthic gelatinous egg mass
	Spawning cues and habitat requirements	When temperatures >12°C
	Spawning migration	No
	Spawning site	Vegetation
	Courtship display	Yes
	Number of eggs	Up to 300, 000 eggs
	Size and type of egg	2-3 mm diameter; adhesive
	Egg Laying site	Laid as gelatinous ribbons amongst freshwater plants
	Time to hatching	7 – 14 days
	Parental Care	No
	Dispersal ability	High
	Larvae Size	4 mm length
	Larvae/Juvenile functional feeding group	Zooplankton
Adult Functional Feeding group	Carnivore	
Adult size	Maximum length 600 mm; commonly 400 mm	
Schooling behaviour	Juveniles swim in large schools	
Tolerance	Tolerance to cease-to-flow periods	Moderate
	Temperature	Moderate to high
	Conductivity	Moderate (17, 500 mg L ⁻¹ ; LC50 = 15, 000 mg L ⁻¹)
	Dissolved Oxygen	Moderate (<2 mg L ⁻¹ , ASR poor)
	Turbidity	High
Threats	Predators	Eat small native fish (e.g. carp gudgeon, galaxiids) and exotics (mosquitofish and trout).
	Competitors	Macquarie perch, Silver perch, trout and Mountain galaxias susceptible to virus
	Other	Main host for Epizootic Haematopoietic Necrosis Virus (EHNV) which natives (e.g. Macquarie perch, mountain galaxias) and exotics (e. g. trout) susceptible to

References: 149, 150, 151, 152, 153

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10.0 Appendices

Appendix 1. Regression analysis outputs – Total Resistance and Resilience scores

<i>Regression Statistics</i>	
Multiple R	0.740619
R Square	0.548517
Adjusted R Square	0.532392
Standard Error	6.755239
Observations	30

ANOVA					
	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>Significance F</i>
Regression	1	1552.344	1552.344	34.01782	0.000
Residual	28	1277.731	45.63325		
Total	29	2830.075			

Appendix 2. PERMANOVA analysis outputs

PERMANOVA						
Source	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>Pseudo-F</i>	<i>P (perm)</i>	Unique perms.
Cl	2	196.96	98.478	11.17	0.001	998
Res	27	238.04	8.8164			
Total	29	435				

Appendix 3. Principal Components analysis outputs

Eigenvalues		% Variation	Cum. %Variation
PCA 1	6.27	41.8	41.8
PCA 2	3.46	23.1	64.9

Eigenvectors	PCA 1	PCA 2
Abundance	-0.234	-0.021
Distribution	-0.321	0.167
Patchiness	-0.335	0.182
Low Flow Tolerance	-0.302	-0.064
Temperature Tolerance	-0.339	0.001
DO Tolerance	-0.312	-0.111
Salinity tolerance	-0.294	-0.149
Predator Susceptibility	0.014	0.362
Feeding specificity	-0.115	0.357
Longevity	0.013	0.484
Age to maturity	0.138	0.358
No flow spawning	-0.236	-0.308
Dispersal Ability	-0.302	0.16
Fecundity	-0.22	0.369
Spawning constraints	-0.335	-0.146

Appendix 4. SIMPER analysis outputs

Average squared distance = 102.06 **Group 1** **Group 2**

Variable	Av. Value	Av. Value	Av. Sq. Dist	Sq. Dist/SD	Contrib%	Cum. %
Patchiness	1.32	5	15.1	1.68	14.8	14.8
Distribution	1.71	4.6	11.2	1.17	10.95	25.75
Dispersal Ability	1.76	4.5	10.3	1.28	10.07	35.82
Predator Susceptibility	2.56	4.2	9.39	1.02	9.2	45.02
Age to maturity	2.03	3.5	7.95	0.94	7.79	52.81
Fecundity	2.24	4.8	7.82	1.3	7.66	60.47
Longevity	2.65	5	7.65	1.07	7.5	67.97
No flow spawning	3	1.6	6.48	0.75	6.35	74.32
Temperature Tolerance	3.18	5.2	6.28	0.87	6.16	80.48
Low Flow Tolerance	3.56	4.9	4.93	0.74	4.83	85.31
Abundance	3.29	4	3.99	0.77	3.91	89.22
Feeding specificity	4.29	5.8	3.93	0.67	3.85	93.07

Average squared distance = 130.07 **Group 1** **Group 3**

Variable	Av. Value	Av. Value	Av. Sq. Dist	Sq. Dist/SD	Contrib%	Cum. %
Patchiness	1.32	5.63	19.8	2.25	15.21	15.21
Distribution	1.71	5.5	16.3	1.75	12.49	27.7
Dispersal Ability	1.76	5.19	14.3	1.43	10.96	38.66
Spawning constraints	2.06	5.38	11.9	1.85	9.13	47.79
No flow spawning	3	5.56	10.8	1.2	8.29	56.09
Low Flow Tolerance	3.56	5.69	7.76	0.86	5.96	62.05
DO Tolerance	3.18	5.19	7.53	0.97	5.79	67.84
Temperature Tolerance	3.18	5.38	7.35	0.9	5.65	73.49
Abundance	3.29	5.38	7.11	0.97	5.47	78.95
Salinity tolerance	3.41	5.56	6.97	1.15	5.36	84.31
Predator Susceptibility	2.56	2.81	5.87	0.85	4.52	88.83
Fecundity	2.24	3.69	4.85	1.06	3.73	92.55

Average squared distance = 85.14 **Group 2** **Group 3**

Variable	Av. Value	Av. Value	Av. Sq. Dist	Sq. Dist/SD	Contrib%	Cum. %
No flow spawning	1.6	5.56	16.7	2.24	19.59	19.59
Spawning constraints	2	5.38	12	2.16	14.12	33.72
Age to maturity	3.5	1.13	9.74	1	11.44	45.15
Predator Susceptibility	4.2	2.81	8.56	0.95	10.05	55.2
Longevity	5	2.63	7.49	1.25	8.79	64
Salinity tolerance	3.4	5.56	5.66	1.59	6.64	70.64
DO Tolerance	3.9	5.19	4.77	0.94	5.6	76.24
Dispersal Ability	4.5	5.19	4.22	0.73	4.96	81.2
Fecundity	4.8	3.69	3.86	0.67	4.53	85.73
Abundance	4	5.38	3.58	1.13	4.2	89.93
Distribution	4.6	5.5	2.75	0.94	3.23	93.16

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