

Refugial Waterholes Project

Research Highlights



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Glossary

Assignment testing: any of several related statistical methods that use genetic information to ascertain population membership of individuals or groups of individuals (see Manel et al. 2005)

Condition, fish: a determination, using any of a number of potential indices e.g. body tissue lipid content, of fish robustness. The assumption is that the higher the condition of the individual, the greater its energy reserves (Paukert and Rogers, 2004).

Ecological values: A broad range of environmental parameters, which may include particular species (rare & threatened, EFAP ecological asset species), biophysical processes, food webs or habitats, that are required to support natural systems and which may be targeted for management or restoration.

IQQM – Integrated Quantity-Quality Model (DLWC 2006)

Population, local: individuals of a species that reside within a single refuge when it is hydrologically isolated

Population, regional: individuals of a species that are present in a catchment, and have opportunities to mix during flow events

Population, global: The entire distribution of individuals of a species, this may be a single location, across a number of catchments or worldwide

Quality, waterhole: a measure of how well a waterhole is able to support biota, recognising that not all refugia are created equal. This may include any number of attributes (e.g. primary productivity, microhabitat availability) and often requires identification of the needs of a particular species of interest.

Resistance: Traits in dryland aquatic organisms that allow them to survive disturbance, in this case, unfavourable conditions during dry spells e.g. adaptive feeding strategies

Resilience: Traits in dryland aquatic organisms that allow them to take advantage of hydrological connectivity during flows to recolonise habitat and increase regional population size.

Waterhole refugia: Wetted environments that provide suitable habitat for aquatic biota during a dry spell. The size and attributes that define it as a refugium are dependant on the requirements of the organism in question. A large-bodied fish has different refuge requirements to an aquatic invertebrate. (see Magoulick & Kobza 2003)

Abstract

Waterhole refugia play a vital role in many river systems, allowing aquatic taxa to survive periods when there is no flow and surface water availability is limited. An understanding of the role and function of refugial waterholes is necessary to best manage these habitats, and ensure that risk to waterhole-dwelling biota is minimised. In order to maintain viable regional populations of biota, refugia must be able to support both the resistance and resilience of local populations. This requires the persistence of good-quality waterhole habitats for the duration of dry spells, as well as connectivity between them during flows. We undertook a number of investigations on the themes of persistence, quality and connectivity, to provide knowledge for decision-making.

The modelled persistence time for Moonie waterholes in the absence of flow and rainfall was up to 820 days, and only a small number of the studied sites had persistence times longer than the IQQM modelled maximum no-flow spell of 700 days, indicating that during severe droughts, loss of available habitat may pose a risk to aquatic biota. We were able to use the models to develop a simple predictive relationship between depth and persistence for the Moonie, and apply this to a reach of river to map temporal habitat availability, however the relationship could not be extended to other catchments. The effect of two pressures on waterhole persistence, water resource development and sedimentation, were assessed. Using a tool developed to identify the likelihood of waterholes drying, the effect of water resource development scenarios was compared, and in the Moonie and Fitzroy examples, there was little increase in risk between natural and development cases. However, sedimentation rates were high in the Moonie, at up to 2.8m of sediment accumulation since the 1950s, reducing waterhole depth and persistence time. Waterhole quality, in terms of primary production, was spatially and temporally variable, but fish were able to switch feeding preferences in order to cope with changing conditions. Lastly, longitudinal connectivity in the Moonie was high, with tagged fish able to migrate up to 70km during periods of flow in order to select optimal habitat, and genetic mixing apparent at the whole-catchment scale.

Introduction

In Australia's semi-arid and arid zones, and in headwater streams in many coastal catchments, perennial flow is rare and waterholes are often the primary source of surface water. These systems are widespread and characterised by low or patchy localised precipitation, variable flows, and intermittent hydrological connectivity among habitat patches (Walker et al. 1995, Puckridge et al. 2000). During dry spells, waterholes provide refuge for both aquatic and terrestrial biota (Davis et al. 2002). For obligate aquatic species - those restricted to freshwater for their entire life cycle - these refugia are crucial for survival, as individuals are unable to persist without functioning waterhole habitats (Nekola 1999, Humphries and Baldwin 2003, Magoulick and Kobza 2003).

Refugial waterholes enable resistance and resilience of aquatic populations in temporary systems, processes essential for vigour and long term viability, by providing habitat to ride out dry spells (Davis et al. 2002, Humphries and Baldwin 2003, Magoulick and Kobza 2003) and allowing dispersal during flow events (Puckridge et al. 1998, Balcombe et al. 2007). There are three major attributes of waterhole refugia which contribute to their ability to sustain biota: the length of time they retain water during no-flow events, or *persistence*; their *refuge quality* which encompasses factors such as water quality, habitat availability and intact food webs; and *connectivity* between waterholes, enabling recolonisation and gene flow (Puckridge et al. 1998, Humphries et al. 1999, Thoms and Sheldon 2000, Davis et al. 2002, Balcombe et al. 2007). Without a network of waterhole refugia within a catchment, each displaying all three of these attributes, aquatic biota are at risk of system-wide extinction (Fig. 1).

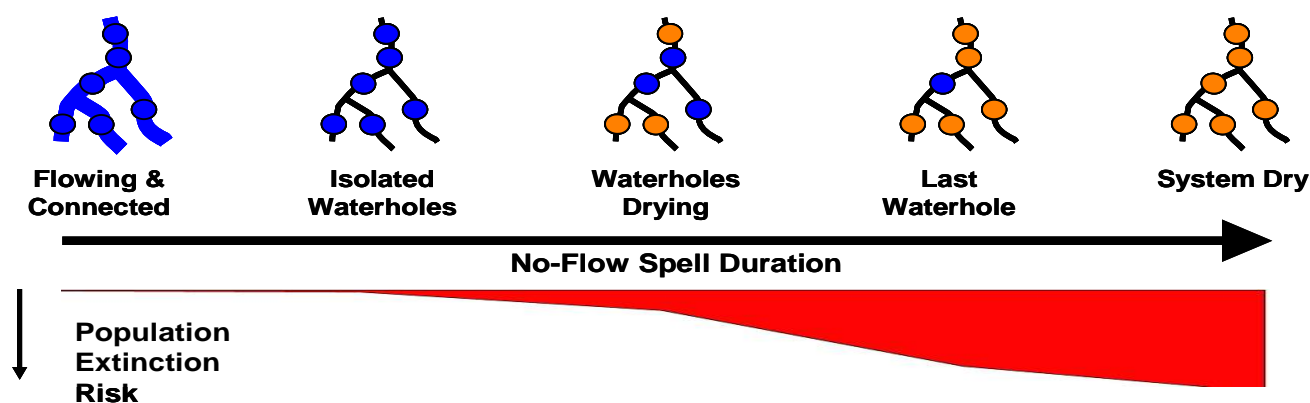


Figure 1: refuge waterhole availability and population extinction risk

As climatic and anthropogenic pressures create stress on available water resources in Australia, the maintenance of waterhole refugia is an increasingly hot topic. However, aside from a small number of studies (e.g., Costelloe et al. 2007, Roberts et al. 2008), waterhole persistence and habitat quality thresholds to protect refuge function have rarely been investigated, and the role of waterhole connectivity and spatial scale in population resilience is still poorly understood. This lack of information about the complex physical and ecological interactions at play has made it difficult for water managers to predict impacts and compare scenarios. There is, however, a compelling need for such assessments to help ensure water management maintains ecological values in systems with temporary flow.

In Queensland, the development and review of Water Resource Plans (WRPs), especially in terms of their ability to balance human water needs and those of the environment, has created the need for improved empirical understanding of flow-biota relationships. Through the process of selecting and ranking 'Ecological Assets', waterholes as refugia have been identified as high priority in a number of WRP areas across the State. In order to assess the risk posed by water management to the ecological function of refugia, specific information about the relationship between flow regime and the attributes of waterhole function is required.

This study, undertaken as part of DERM's Environmental Flows Assessment Program (EFAP) and in collaboration with eWater CRC, has gathered vital information about the processes acting upon in-channel waterholes and their ability to act as refugia (Fig. 2). Insights into the function of waterhole refugia from selected catchments (Moonie, Weir, Flinders, Mary and Mitchell Rivers) were used to develop generalisations and methods for investigating persistence, quality and connectivity applicable to temporary river systems throughout Queensland and elsewhere. An approach for quantifying risk to waterhole refugia from flow regime change has also been developed for use in WRP development and review.

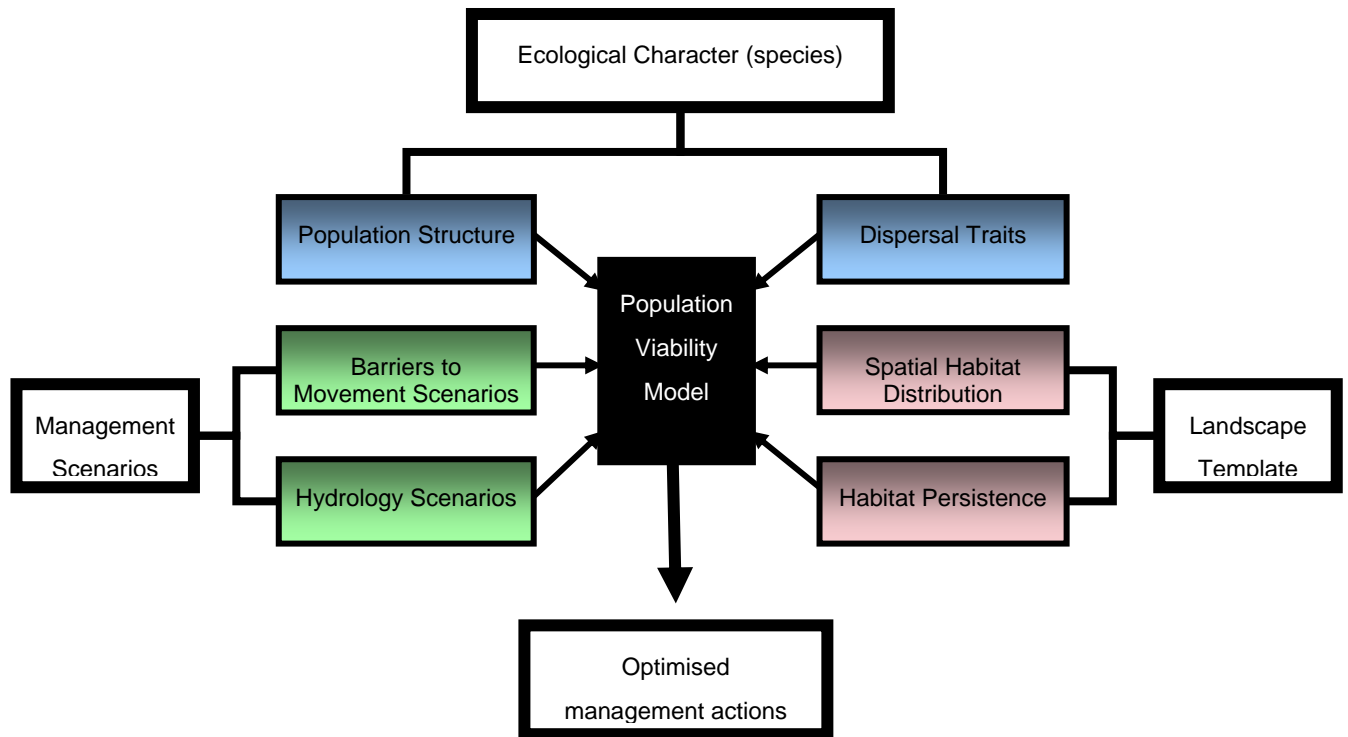


Figure 2: eWater Refugia Project structure

Study catchments

The focus catchment for the Refugial Waterholes Project is the Moonie River in southwest Queensland. The Moonie is a dryland system in the headwaters of the Murray-Darling, which experiences a semi-arid climate with low and variable annual rainfall and high evaporation rates. It is a rainfall-runoff dominated hydrology with very little base-flow contribution (Sternberg et al. 2008). During dry spells, a string of waterholes along the river channel provide refuge for aquatic biota, habitat for terrestrial plants and animals and water for human and agricultural consumption. There is only moderate water resource development with 4 surface water licenses and 32 unsupplemented water allocations, most of which are for water harvesting during flow events (NRM&W 2006), and some unlicensed waterhole extraction for stock and domestic use.

Along with the Moonie, several other catchments have been studied in order to understand the importance of local conditions on waterhole persistence and the transferability of relationships, and to collect catchment-specific data for WRP assessment (Fig. 3). The Weir River in southwest Queensland and The Flinders River in the southern gulf are both dryland systems and were selected to represent different geographical areas that are also dominated by rivers with temporary flow regimes. Conversely, the Mary River in the southeast and the Mitchell River on the Western Cape are more perennial systems but have tributaries or headwater streams which experience intermittent flow. These were selected to further test the transferability of our understanding of waterhole refugia.

Research in the Flinders and Mitchell was undertaken as part of the Tropical Rivers and Coastal Knowledge (TRaCK) program and further information from this study is available in the TRaCK Waterholes Project Report.

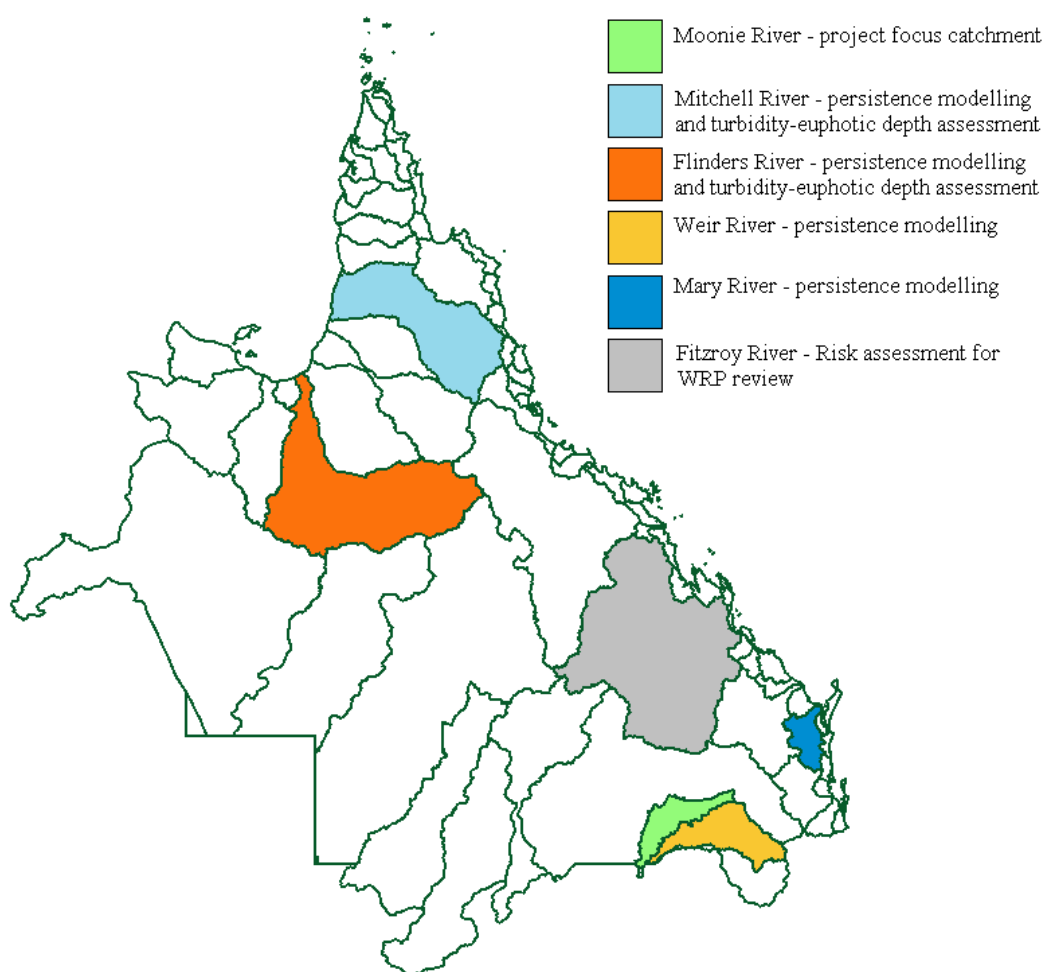


Figure 3: Study catchments

Research Highlights

Waterhole persistence

The persistence of a refugial waterhole (i.e. the length of time it contains water in the absence of flow) defines the maximum survival time of obligate aquatic biota that reside in it (e.g. fish, some invertebrates) (Balcombe et al. 2007). At the most basic level, whether or not a waterhole contains water provides an indication of habitat availability in a catchment. In order to conserve populations of aquatic biota, it is therefore important to understand the factors which affect waterhole persistence.

To more clearly understand the important variables determining the persistence time of a waterhole, we developed a conceptual model, identifying the key components (Fig. 4).

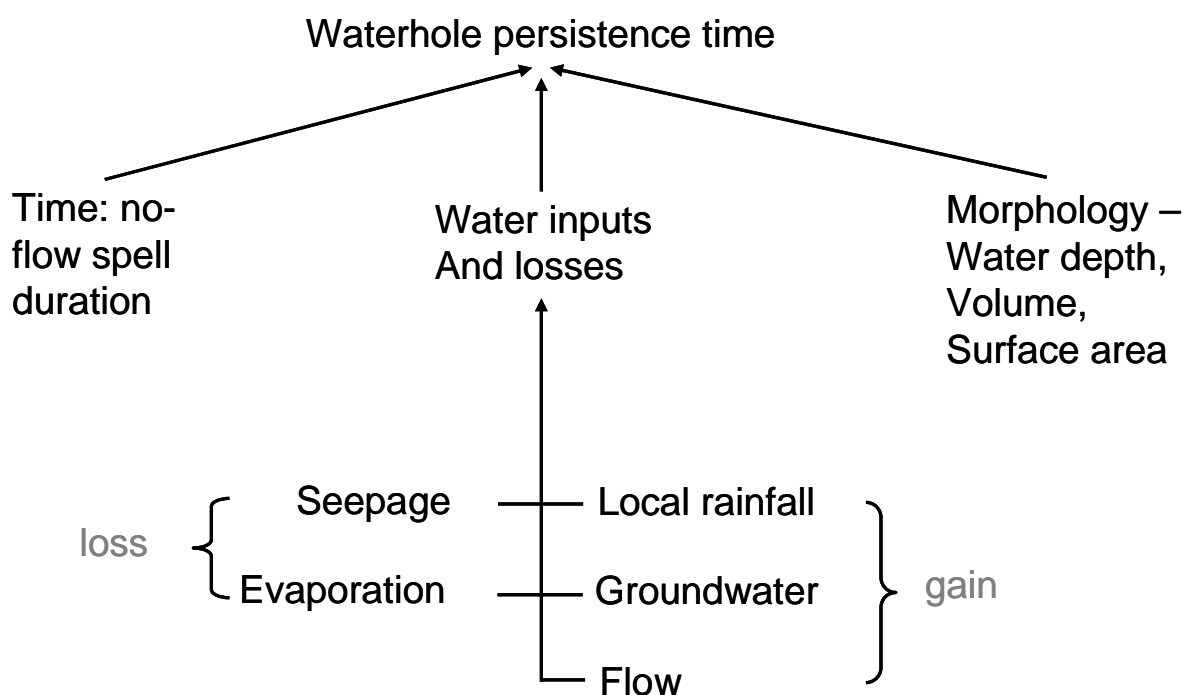


Figure 4: Conceptual model for waterhole persistence

We were able to simplify the model to three main attributes that determine the persistence of a waterhole, these being: how much water is in a pool, based on its size, shape and depth; the amount of time between flow events which is dictated by the flow regime; and local sources of water loss or gain such as rainfall and evaporation. By quantifying these parameters using actual or hypothetical values, waterhole persistence can be calculated or predicted.

The ability to predict the persistence of a waterhole has obvious benefits. For example, the most persistent waterholes in a stream network could be identified and targeted for conservation, or predicted changes in persistence under different flow or climate change scenarios could be compared to optimise management options. However, measuring and predicting persistence can be time-consuming and expensive, making it difficult to apply widely. At present, persistence is typically estimated on a site-specific basis using complicated modelling procedures requiring the inclusion of difficult-to-measure variables (e.g. Costelloe et al. 2007).

While highly detailed hydrological models are desirable, and may be necessary for specific places of interest, simple time- and cost-effective measures are required in order to make information about waterhole persistence widely accessible for decision-making. Ideally, key physical parameters that are easy to measure or estimate could be used as predictors for waterhole persistence at broad scales.

The key questions:

What is the persistence time of waterholes in the Moonie catchment?

Are there any simply-measured waterhole parameters that can be used to estimate persistence? If so, can these relationships be applied in systems outside the Moonie?

Does changing waterhole morphology due to sedimentation affect waterhole persistence? Over what time scale does this occur?

Persistence time

To determine waterhole persistence time, we constructed hydrologic models incorporating data on the aspects of persistence outlined in the conceptual model (Fig. 4). Fifteen waterhole sites were selected to represent the range of size, shape, permanence and connectivity present in the Moonie and to achieve balanced spatial distribution (Fig. 5).

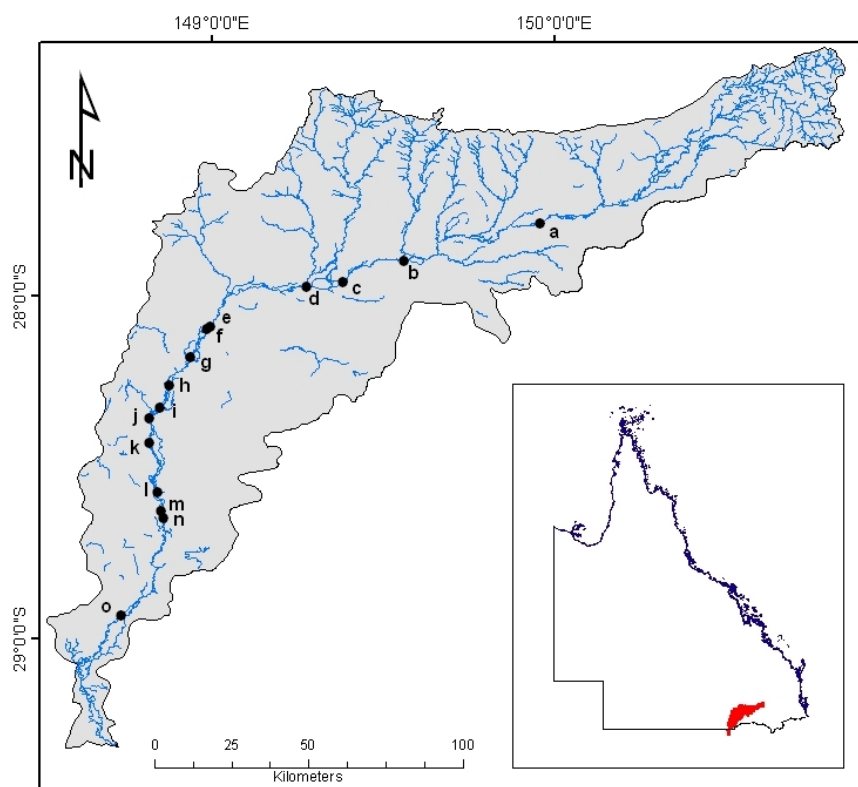


Figure 5: Moonie River site map

a=Kurmala, b=Verena, c=Kooroon, d=Altonvale, e=Warrie 1, f=Warrie 2, g=Carbeens, h=Kurrajong, i=Appletree, j=Nindigully Pub, k=Nindigully Gauge, l=Bullamon Plains, m=Broadwater, n=Nullera, o=Fenton

The bathymetry of each waterhole was surveyed (DERM method WMO015A) in February 2006 immediately after the cessation of a flow event, when they were full but not flowing. The coordinate-depth data collected were used to create digital elevation models (DEMs) for each waterhole in ArcGIS ver. 9 (ESRI) (e.g. Fig. 6). Using the 3D Analyst tool, size and volume statistics were calculated at 0.1m depth intervals to determine changes in waterhole morphology with drying (DERM method AEML013). Depth loggers were also installed at each location to monitor depth change at 20 minute intervals for up to 26 months (DERM method AEMF013), and interpolated Bureau of Meteorology (BOM) climate data were collated from SILO Data Drill.

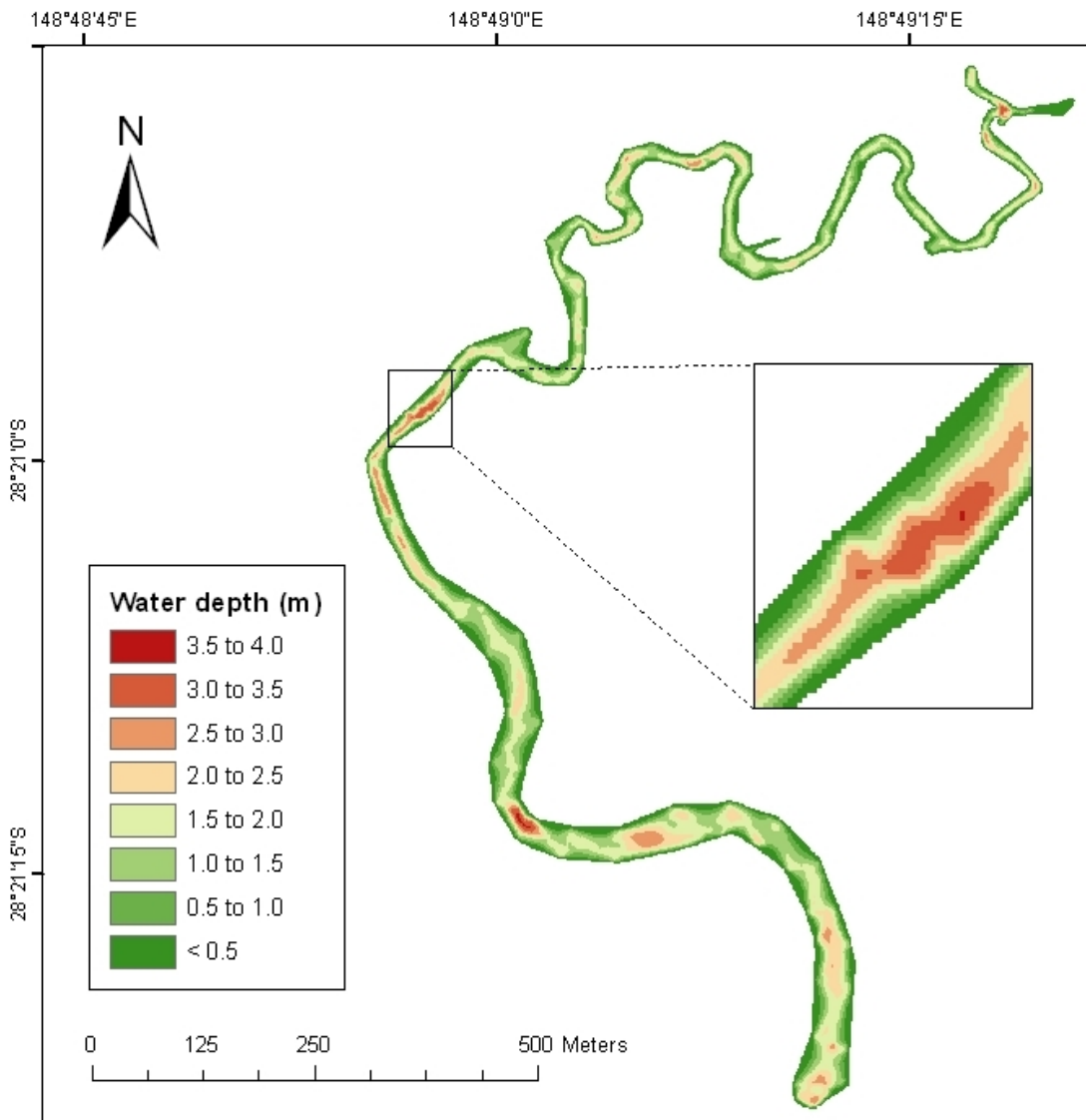


Figure 6: Waterhole digital elevation model, 417201A Moonie River at Nindigully Pub

Using this information, a hydrological model was developed for each of the 15 studied waterholes. The model is a water balance that tracks the volume in a waterhole subject to evaporation from the water surface, seepage, rainfall on the water surface, rainfall inflow (including a recession factor) and external inputs and outputs of water. The waterhole model is written in Visual Basic and is accessed using Excel macros. It is used in conjunction with stream flow data from either gauging stations or an Integrated Quantity-Quality Model (IQQM) (Simons et al. 1999, DLWC 2006) and is invoked when there is no flow in the stream. Uncertainty in the waterhole model increases with time since flow and is contributed to by uncertainty in the IQQM, especially for early simulation before the advent of stream gauges (pre-1950) where data were in-filled with a Sacramento Model (Burnash et al. 1973).

The waterhole models were calibrated (Fig. 7) to account for local variation in parameter values and inconsistencies in the data, such as rainfall events not recorded at weather stations and therefore absent from BOM data. The calibration was based on a least-squares fit with the measured logger data, with Excel Solver employed for the minimisation. A number of calibrations were performed, beginning with a couple of parameters, such as the seepage rate, local rainfall, and continuing until no significant improvement in the fit of the model was observed. Generally, a good match between measured and calibrated model depths was achieved.

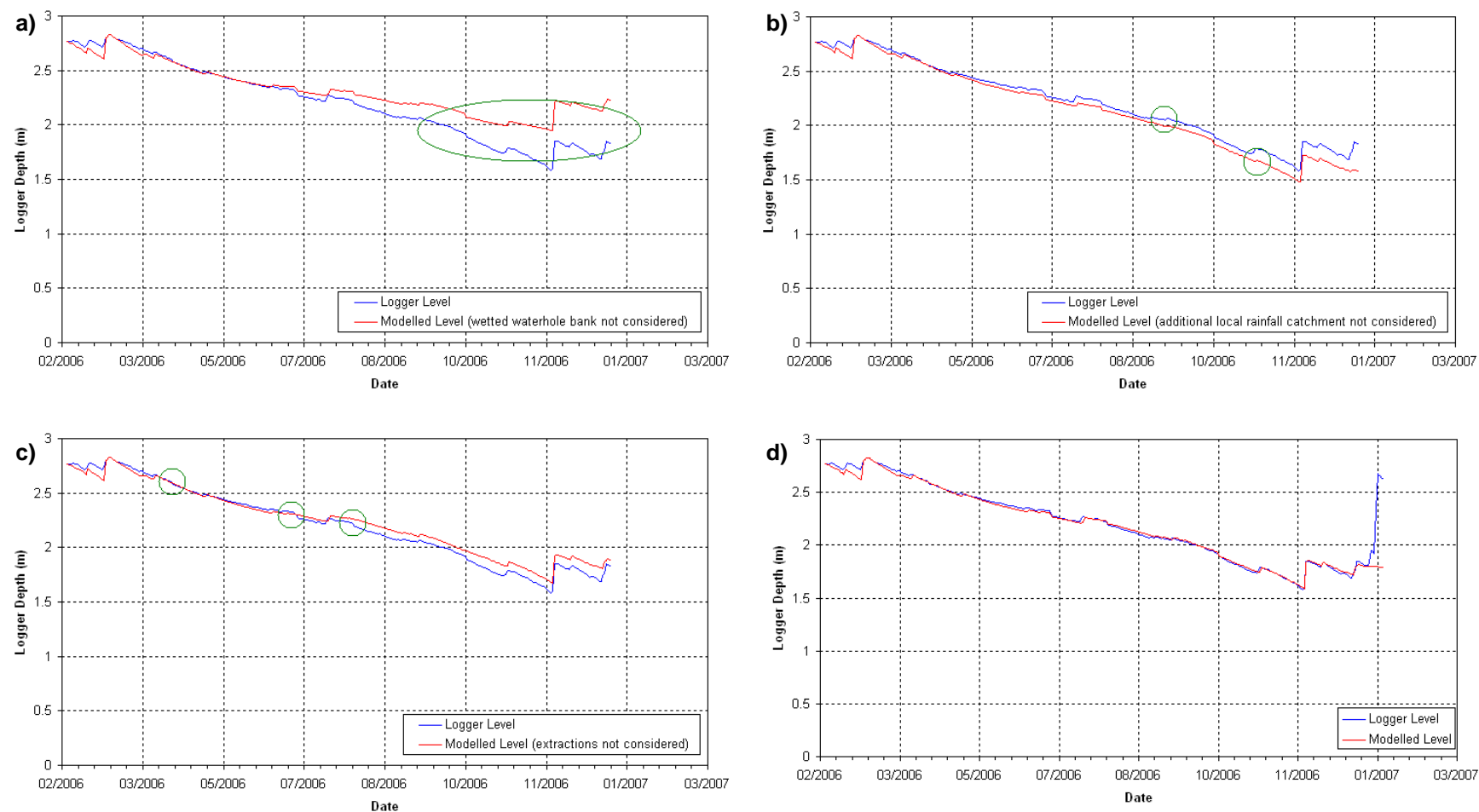


Figure 7: Modelled vs. measured depth change calibration results a) model result where extractions are not considered b) model result where evaporation from wetted perimeter is not considered c) model result where local catchment rainfall events are not included d) final model result showing good fit. Green circles indicate deviation in the model where calibration parameters were not included.

The waterhole models provide information about the hydrological character of individual waterholes, but in order to assess risk to populations of refuge-dwelling biota, we needed to examine patterns of persistence at the catchment scale. Risk in this instance is a function of the number of refugial waterholes remaining within a system over time (Fig. 1). When a system is flowing or recently disconnected, the large number of refugia available means that even in the event of some local population failures (e.g. if a pool is pumped dry to carry out road works, or a crash in dissolved oxygen causes a fish kill), the broader population is still healthy and viable (Davis and Thoms 2002). So, some local extinctions in a system with a large number of refugia is of little consequence to the population as a whole. Over the progression of a dry spell, as waterholes contract and the number of refugia becomes small, stochastic disturbances within the remaining refugia have serious consequences for populations at the whole-of-catchment scale. In the worst case, if all waterholes in a system dry up, extinction of aquatic biota occurs throughout the system.

Since risk to refugia is highest when few waterholes remain, we decided to assess the risk in terms of the occurrence of multiple waterhole failures (i.e. occasions when a number of refugia dried or ‘failed’ simultaneously). To do this, we developed a tool which combines flow data from the IQQM with the waterhole model and tracks water depth for the 100-year simulation period. Whenever flow ceases in the system, as determined by the IQQM, the waterhole model is activated and waterhole depth decreases at the rate determined by the model calibration. This continues until another flow event occurs, at which point waterholes return to full level until the next dry spell (Fig. 8a). Any refuge waterholes that dry up are identified, and the proportion of waterholes that fail simultaneously is calculated (Fig. 8b).

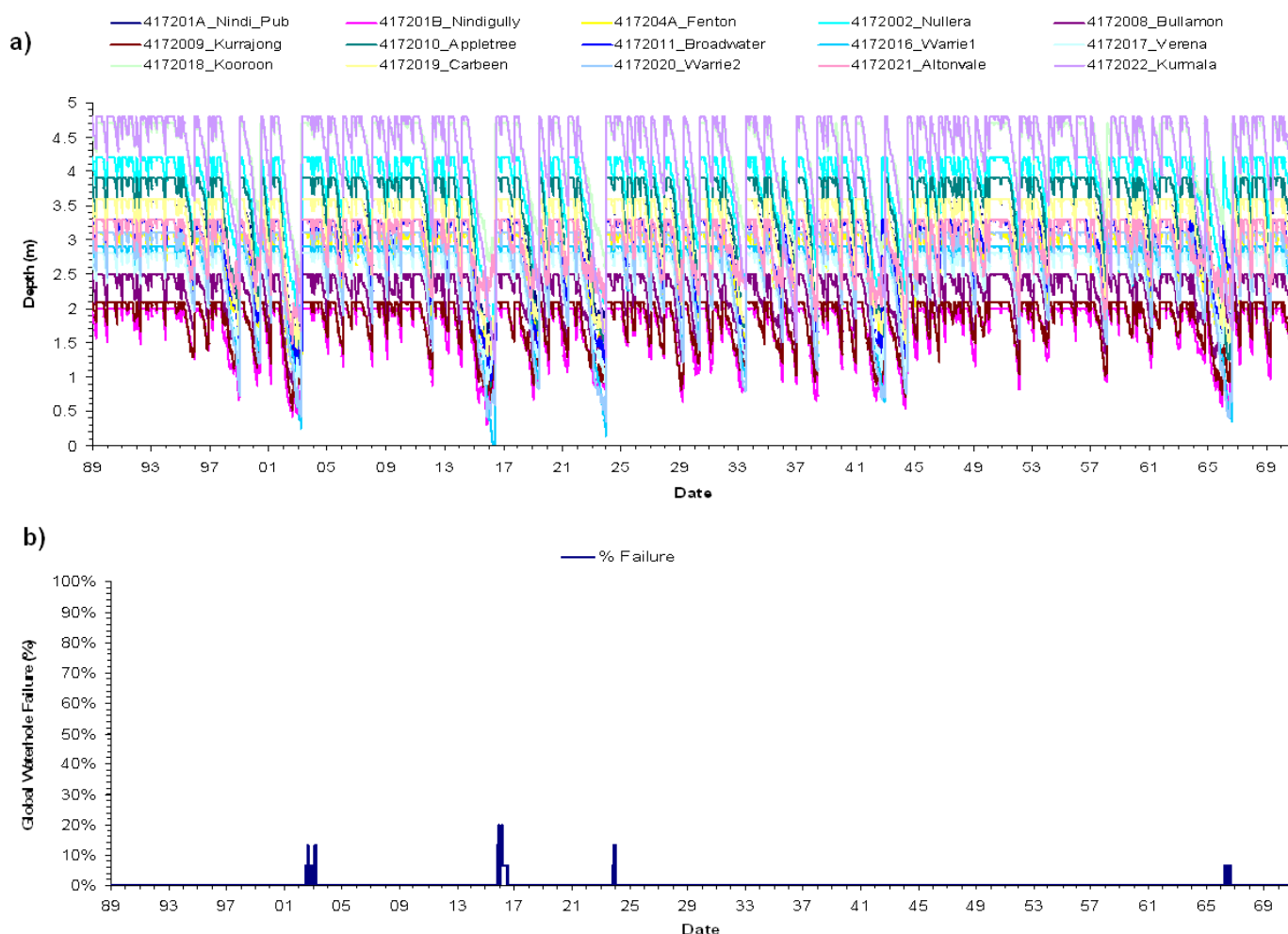


Figure 8: Output from Waterhole Multiple Failures tool for the Moonie showing a) waterhole depths for the simulation period and b) the proportion of waterholes failing simultaneously

The tool can be used with any IQQM scenario, so enables the comparison of pre-development and development cases, or climate change scenarios. Changes in the occurrence of multiple waterhole failures can be calculated, allowing the

identification of management scenarios that increase or decrease risk to aquatic biota. The multiple failures tool was used in the Fitzroy WRP review to identify whether refugia were at risk, and if this was increased under management or climate change scenarios (DERM 2009). In the Fitzroy example, risk to refuge waterholes was low in the pre-development case, and while some management scenarios did increase the incidence of failure in particular waterholes, widespread failures remained rare. The multiple failures tool also features a user-defined failure level, so where a habitat quality threshold exists (e.g. at least 50% of maximum waterhole depth is required for fish 'x' to access breeding habitat), the incidence of threshold breaches can be assessed, as well as the occurrence of complete drying.

To further assess the persistence of waterholes in extreme droughts, and to compare their water loss characteristics, we used the models to estimate persistence in a simulated severe drought scenario, where all water inputs were removed. It is a worst-case analysis with neither local rainfall nor inflow from the upstream catchment considered. Average daily historical evaporation rate was used for this work. Figure 9 shows the output, with all Moonie waterholes full at day zero, then water levels falling at the rate determined by the model parameters until they become dry. Some manual correction was required as the waterholes neared empty because the models weren't well calibrated at this depth.

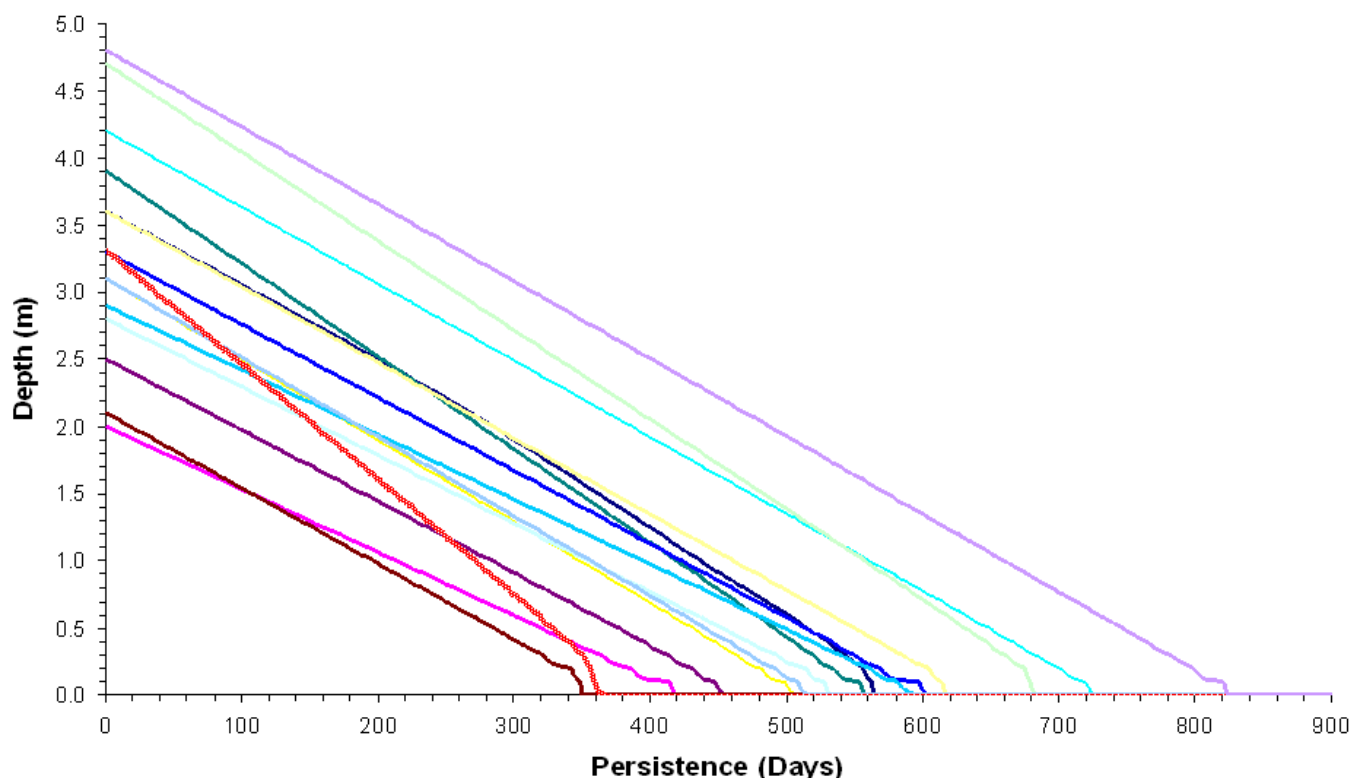


Figure 9: Waterhole persistence in the absence of flow or rainfall. Altonvale, the site with the faster water loss rate is highlighted in red.

In general, waterholes in the Moonie have similar water loss characteristics and depth change is driven by evaporation. In the absence of flow or rainfall, persistence time is between 350 and 820 days. The modelled maximum no-flow spell from the IQQM is just over 700 days, so without localised rainfall topping up levels, it's likely that severe droughts could cause nearly all the waterholes to dry up. Considering that reductions in local rainfall are predicted under some climate change predictions (CSIRO 2008), these events may become more of a real possibility over time.

One of the studied sites, Altonvale (the red line in Fig. 8), had a water loss rate markedly higher than that at other sites, due to loss to groundwater. The connection to groundwater at this site was determined based on radon levels (DERM method AEMF032). Radon is found in waters in contact with subsurface sediments and has a short half-life, so dissipates quickly when exposed to atmospheric gas exchange (Cook et al. 2003). Therefore it is a good indicator of recent local influx of groundwater to surface waters (Burnett et al. 2010). Altonvale had high radon levels compared to the rest of the sites, indicating that at some times, groundwater infiltrates to the surface. We had expected that groundwater-connected waterholes may be more persistent, however, they actually tend to lose water, especially when local groundwater levels are quite low (Creswell et al. 2008). In the case of Altonvale, its persistence time is approximately 40% less than expected if evaporation alone were responsible for depth

loss. This highlights the need to identify and account for seepage into groundwater when modelling waterhole persistence.

Predicting persistence

While the waterhole models provide excellent insight into the function of the 15 studied Moonie waterholes, in order to get a better understanding of temporal refuge distribution at the catchment scale, a simple method for estimating the persistence of other pools in the system is required. A set of morphological variables calculated from the DEMs - maximum depth, total volume, surface area, perimeter and average width - were used in a multiple linear regression analysis (STATISTICA ver. 6.0), to build a simple predictive model for the Moonie.

The data were tested for normality using the Shapiro-Wilk test and transformed where necessary, and the independence of the variables was tested using correlation analysis (table 1). Surface area, volume and perimeter were all highly correlated ($R^2 > 0.9$), so volume and perimeter were removed from the dataset, with surface area being retained owing to its conceptual link with evaporative loss and the relative ease of measurement.

Table 1: Correlation coefficients for Moonie waterhole morphological variables

	Max depth	Volume	Surface area	Perimeter	Av. width
Max depth	1				
Volume	0.56478477	1			
Surface area	0.48985977	0.931174	1		
Perimeter	0.54025549	0.94251977	0.99072079	1	
Av. width	0.21098235	0.51557433	0.62434148	0.5339806	1

With the remaining variables, a forward stepwise multiple regression was used to find the model with the best predictive ability, as judged by adjusted R^2 values. Using this variable set, the best model included maximum waterhole depth and average width (adjusted $R^2 = 0.76$).

Altonvale's unusual water loss characteristics, due to the high seepage rate, meant it showed up as an outlier in several assessments. For this reason, we chose to remove it from the dataset and repeat the analysis. This time, maximum waterhole depth alone produced the best model (adjusted $R^2 = 0.81$). This means that the persistence time can be rapidly estimated for waterholes in the Moonie based on a simple depth measurement, using the equation:

$$\text{Persistence time} = 169.57 \times \text{depth}$$

To take advantage of the depth-persistence relationship and get a clearer idea of the availability of refuge patches in the Moonie, and the nature of the river channel between waterholes, we surveyed a longitudinal profile. Using bathymetric profiling equipment attached to a kayak, we traversed approximately 150km of the river channel, collecting paired depth-location readings for the thalweg (Fig. 10). By applying the depth-persistence equation we were able to estimate the persistence time of each patch (Fig. 11). This work provides detailed information about the number and location of refugia in the Moonie, along with their temporal distribution over the progression of dry spells.

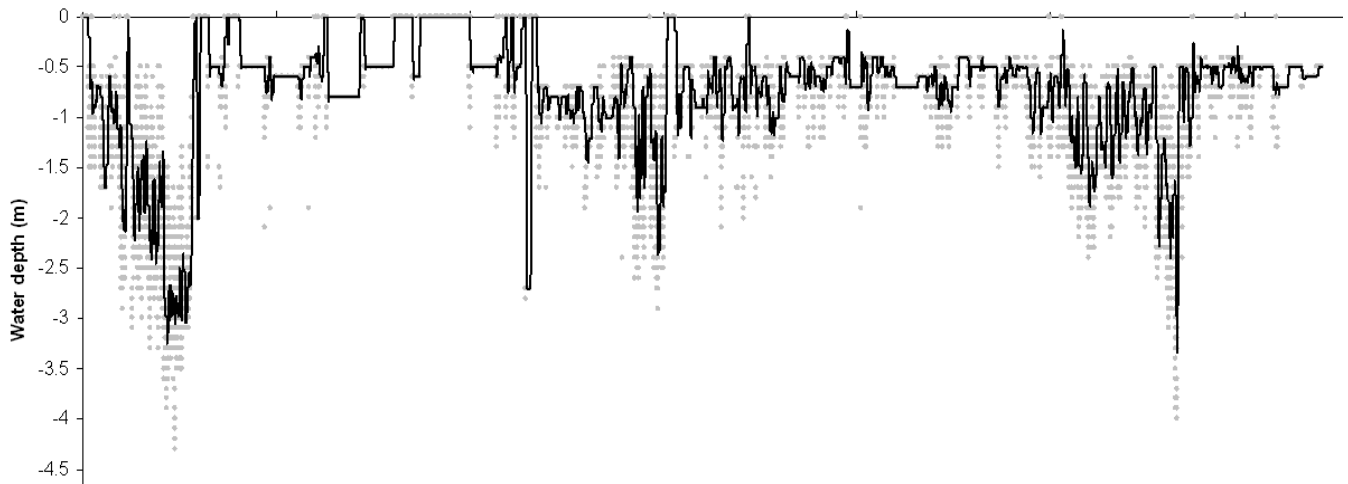


Figure 10: Longitudinal depth profile, as a moving average, for approximately 35km stream reach

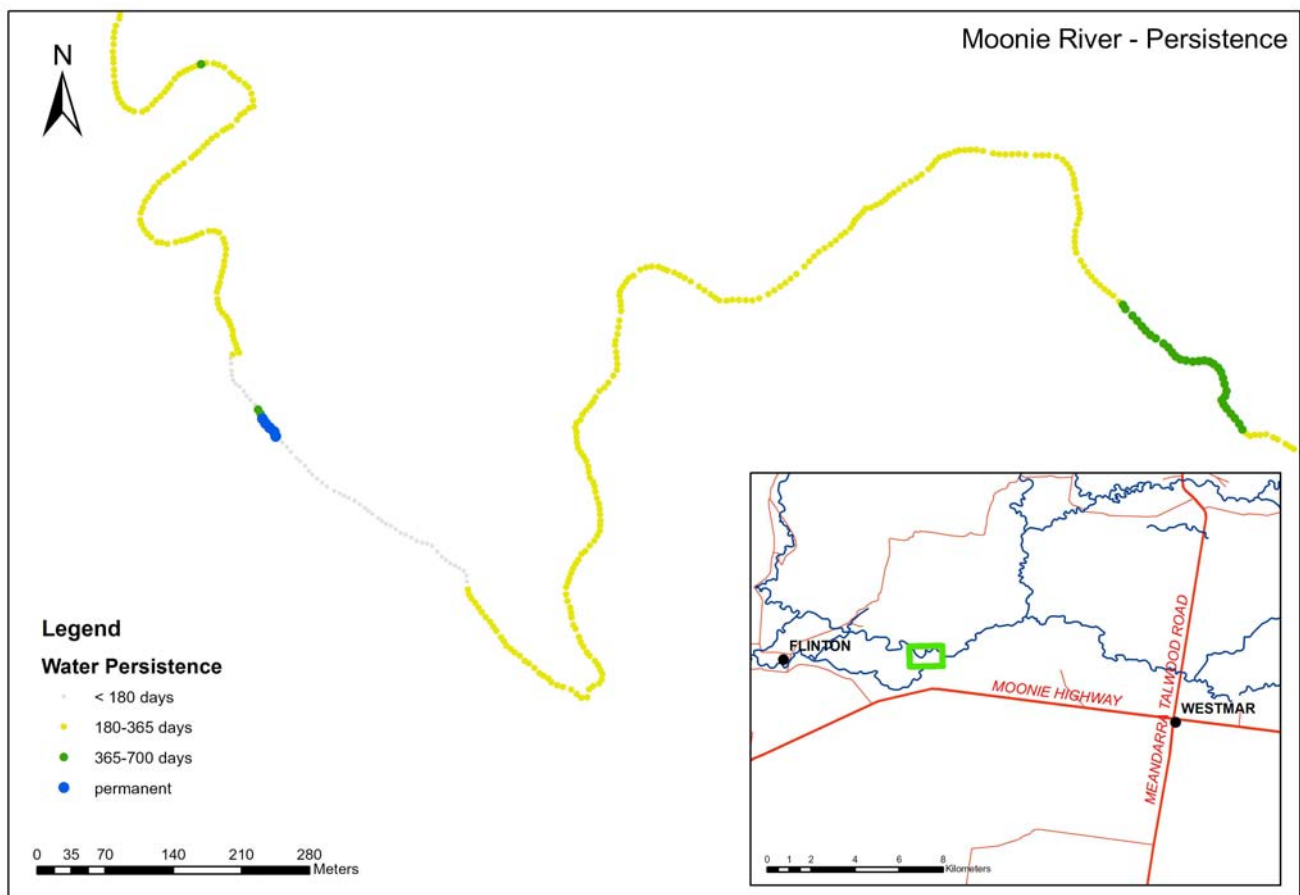


Figure 11: Section of long profiled reach, showing predicted persistence time

Transferability of models

In order to assess transferability of the depth-persistence correlation beyond the Moonie, we repeated the persistence modelling exercise in four other Queensland catchments, two dryland systems (the Weir and Flinders) and two perennial systems (the Mary and Mitchell). If maximum depth proved to be a good predictor of persistence time in each of the additional catchments,

then differences in slope and intercept could be identified and additional variables included, to develop broadly applicable predictive models. Fewer waterholes were modelled in these catchments due to operational limitations and equipment failures.

Six waterholes were selected for modelling in the unregulated upstream reaches of the Weir River. Depth change was recorded over 14 months, and a lengthy dry spell provided good data for thorough model calibration. Persistence time of the studied waterholes ranged from 160 to 600 days (Fig. 12a). According to the models, half of the sites experienced quite high rates of seepage, though field sampling for groundwater interaction was inconclusive.

Results of multiple regression analysis to determine which morphological variables might predict persistence were weak, compared to those from the Moonie. Average waterhole width alone provided the best model (Adjusted $R^2=0.52$) though this was not statistically significant. Because depth change, and therefore persistence, was not evaporation driven in half the sites, waterhole depth was a poor predictor of persistence time.

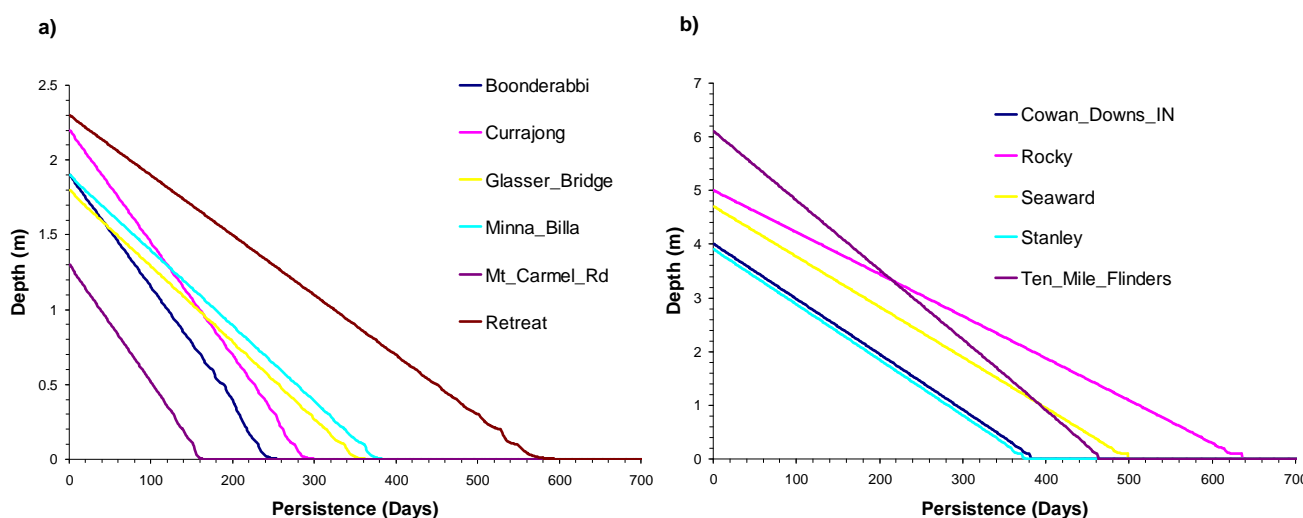


Figure 12: Waterhole persistence in additional dryland study catchments – a) the Weir River and b) the Flinders River

In the Flinders, where depth change data was recorded at five sites over a six month dry spell, modelled persistence time is between 380 and 640 days (Fig. 12b). Because of the small amount of data, statistical power was low and predictive models were not significant. Again, model calibration results suggest that most of the studied waterholes experience high rates of seepage loss at some times. This further suggests that the inclusion of an estimate of seepage rate, along with variables of waterhole morphology, may be required to best explain persistence.

In both the perennial systems, despite selecting sites in drier headwaters and tributaries, studied waterholes were only briefly isolated, and at most sites not enough water depth change was recorded to sufficiently calibrate water loss models. Persistence has been modelled for most waterholes in the Mary and Mitchell using interpolated evaporation values, however it is difficult to make confident assessments when other sources of local water loss and true variability is unaccounted for. Figure 13 shows persistence time as modelled for the eight studied sites in the Mary and five in the Mitchell. The longer persistence times predicted for waterholes in these catchments may be due to differences in climate and the selection of deeper pools as study sites, but more importantly, persistence was probably over-estimated because without calibration, not all sources of water loss can be correctly factored in.

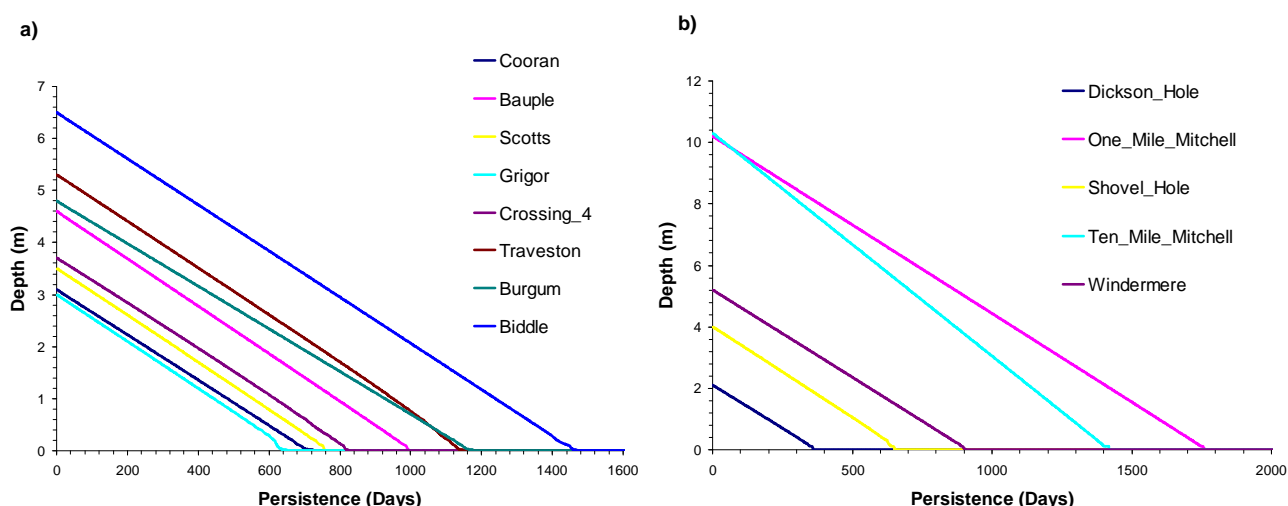


Figure 13: Waterhole persistence in additional dryland study catchments – a) the Mary River and b) the Mitchell River

In both the Mary and Mitchell, regression analysis suggested waterhole depth was a good predictor of waterhole persistence (Adjusted R^2 of 0.96 and 0.92 respectively). However, this is probably an artefact of the limited parameterisation of the models and is unlikely to represent real world refuge persistence in these catchments. Because evaporation was the only source of water loss included, and local variability hasn't been accounted for, it is not surprising that correlations between depth and modelled persistence were strong. Additional depth change data to better calibrate the models and include variability during periods of waterhole drying would enable improved assessments.

Work is ongoing to find appropriate statistical techniques and variables to develop predictive models that can be applied across broad geographic areas. For all four additional study catchments, field data and waterhole hydrologic models, along with a Multiple Failures tool similar to that described on page 13, are available for further analysis.

Sedimentation and persistence

It is important to keep in mind that waterholes are part of dynamic riverine environments, changing location and morphology over time. Along with water resource development, pressures that lead to changes in the physical shape, size and location of waterholes are most likely to have an effect on the persistence of refuge waterholes (Puckridge et al. 1998, Choy et al. 2002, Davies et al. 2009, Larned et al. 2010). One of the most common drivers of change in waterhole morphology is sediment infilling (Hooke 2007) (Fig. 14).

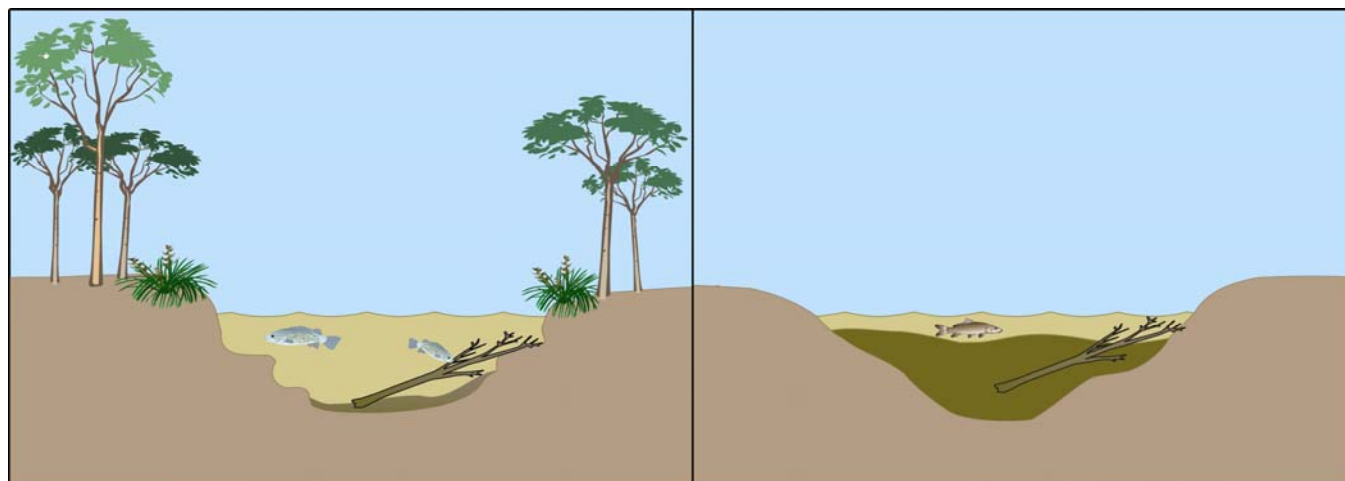


Figure 14: Effects of sedimentation on waterhole habitat and morphology

To investigate the effect of sedimentation on the morphology of waterholes and their persistence, sediment cores were collected from three waterholes in 2008 and 2010 and analysed to estimate the age of deposited layers. Sedimentation rates were established using a combination of ^{210}Pb , radiocarbon and optically stimulated luminescence (OSL) dating. Radiocarbon dating was also performed on layers of terrestrial leaf matter present in the cores. For detailed methods, see Myburgh 2008.

Preliminary results suggest that the entire length of the cores collected (up to 2.8m at Kooroon, 1.5m at Kurmala and 1.9m at Verena) has been deposited since the arrival of European settlers to the region. The presence of a nuclear signature from atomic field testing indicates that the sampled sediment has most likely been deposited in the last 50 years (Myburgh 2008). This corresponds with the commencement of broad-scale vegetation clearing for agriculture in the region in the 1950s and 60s (Biggs et al. 2005). Further sampling is required to verify the sedimentation rate and the extent of sediment deposits, but these preliminary results suggest that waterhole depth reduction due to sedimentation may be affecting waterhole persistence.

Given that depth has been identified as a major driver of persistence time, processes such as sedimentation which reduce waterhole depth have the potential to markedly reduce persistence. Figure 15 shows the possible impact of sedimentation on waterhole persistence. The long dashed lines demonstrate the depth and persistence of the three pools we cored as they may have been 50 years ago, prior to observed sedimentation. Persistence times under these conditions are up to 1000 days, long enough to survive even very severe droughts. The short dashed lines represent the persistence of pools in the future if observed rates of sedimentation continue. Under this scenario, these waterholes, currently some of the most permanent in the catchment, have persistence times much shorter than the maximum no-flow spell for the system, meaning they dry more frequently and risk to aquatic biota is increased. Based on these results, in the Moonie River, reduced waterhole depth due to sedimentation poses a much greater threat to refuge function than does current water resource management. The processes driving morphological change therefore need to be considered along with hydrology when managing refuge waterholes.

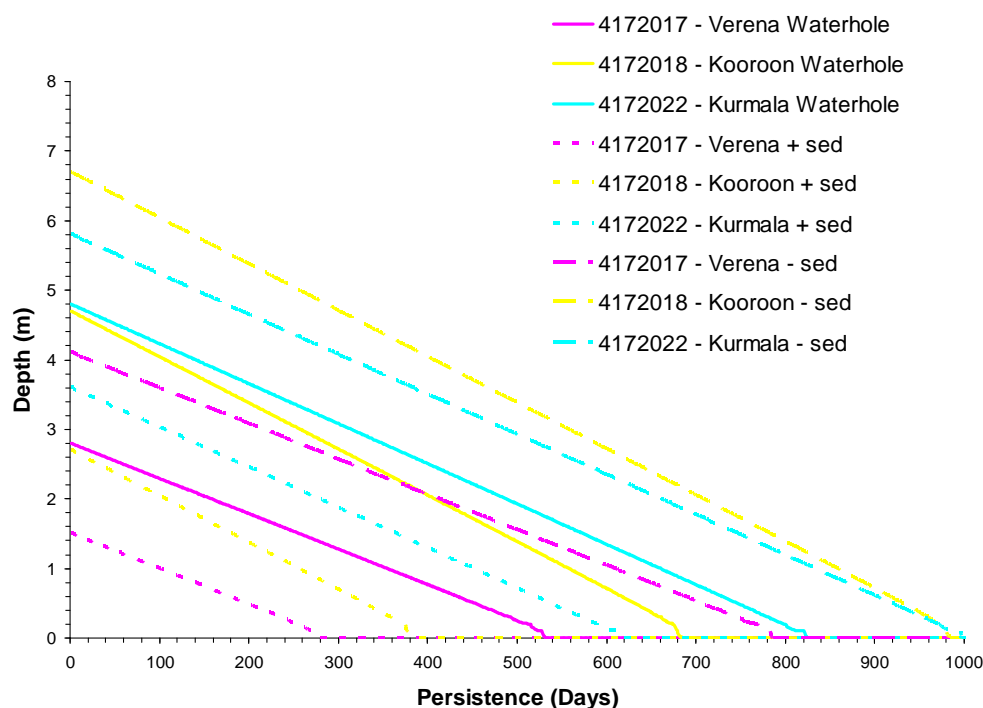


Figure 15: Waterhole persistence plot demonstrating possible effect of sedimentation. Solid lines are current day persistence times for three waterholes; long dashed lines show persistence in the absence of sediment, as it may have been in the past; short dashed lines show persistence as it may be in the future if current rates of sediment deposition continue.

Habitat Quality

The persistence time of a refuge waterhole indicates the maximum survival time for obligate aquatic biota. However, some persistent waterholes may provide higher quality habitat than others, and therefore be better able to support biota. Habitat conditions within a waterhole may also decline as water level recedes, meaning that it could become unsuitable as a habitat for some species long before it dries completely. As water level drops, changes can occur in water quality (e.g. reduction of dissolved oxygen, concentration of ions), water temperature, and availability of food and complex habitat features, and the effect of disturbance, e.g. trampling by livestock, becomes more pronounced (Seehausen & Bouton 1997, Bouvy et al. 2003, Lake 2003, Magoulick & Kobza 2003, Bond et al. 2008, Beesley & Prince 2010) (Fig. 16).

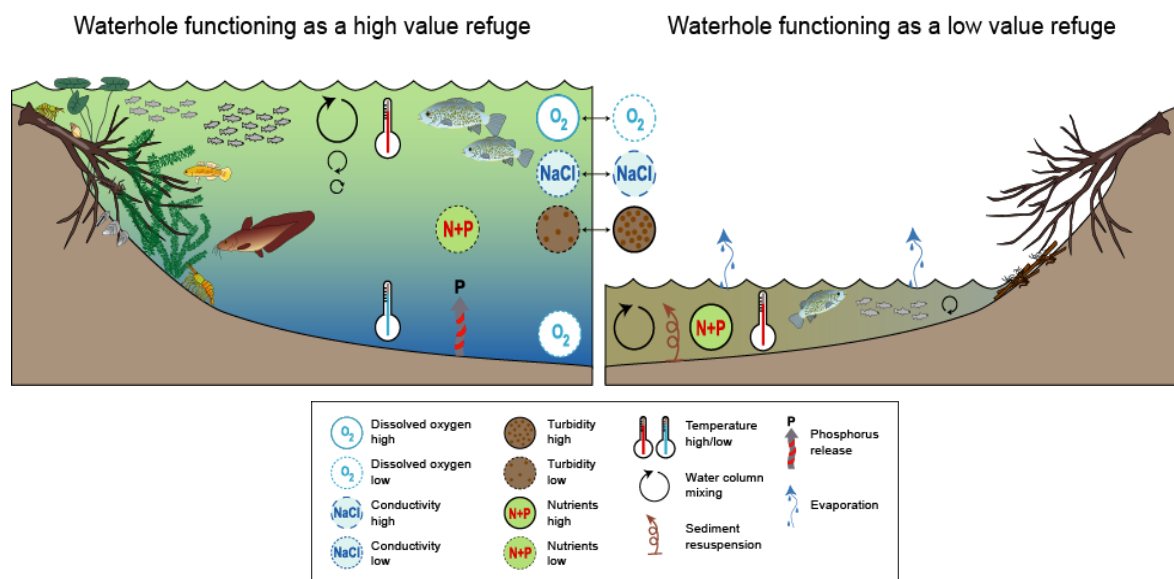


Figure 16: Conceptual change in waterhole habitat quality with reduced depth

Changes in these parameters may breach survival thresholds for some species or affect population and community processes (Closs & Lake 1996, Lake 2003, Magoulick & Kobza 2003, Beesley & Prince 2010). For example, many species of *Ambassis* require macrophyte beds for breeding (Pusey et al. 2004) so if low water levels restrict access to breeding sites, adults could still survive but they would be unable to recruit, reducing population resilience and threatening population viability.

Also, as habitat changes and species disappear or become rare, waterhole food webs are likely to change (Balcombe & Arthington 2009, Ludlam & Magoulick 2009, Ludlam & Magoulick 2010). Herbivores may need to feed more exclusively on one food source, and higher order predators may shift towards omnivorous foraging strategies. Such alternative food sources are often nutritionally poor (Balcombe & Humphries 2006). During periods of prolonged isolation, competition causes the progressive depletion of food resources to the extent that individuals lose body condition, reducing population resilience (Collins and Anderson 1995, Arthington et al. 2005, Balcombe et al. 2005, Balcombe et al. 2006).

Key questions:

Does changing food availability in waterholes alter the body condition of resident biota?

Do fish species that inhabit drying waterholes shift their feeding preferences?

Is there a depth threshold below which refuge habitat quality is reduced?

Waterhole quality and fish condition

To investigate the relationship between food availability and waterhole habitat quality we calculated the change in potential primary production and fish body condition over the dry season.

As waterholes in the Moonie are highly turbid (mean 688 NTU, DERM unpublished data) and major nutrients are readily available, light is likely to be the limiting factor controlling primary production. Light attenuates as it passes through water, and once it falls below 1% of its incident intensity, the rate of respiration in plants becomes greater than the rate of photosynthesis, so no net primary production can occur (Vadeboncoeur and Steinman 2002). We used an index of productivity potential, measured as the planktonic volume and benthic area of a waterhole within the euphotic zone (the region with >1% incident light), to determine changes in primary production over time. Waterhole-scale primary production is a function of euphotic area/volume and the rate of gross primary production. Using the productivity potential index is appropriate because while both aspects of waterhole-scale primary production vary in space and time, overall the influence of change in area/volume is far greater than that of variation in the rate of primary production (C. Fellows, pers comm. 2006).

We developed a turbidity-light attenuation relationship (Fig. 17) using replicated light profiles at each site (Method AEMF014), so that regular turbidity measurements could be converted into an estimate of light attenuation depth. To calculate the productivity potential index, water levels and converted light attenuation depths were applied to waterhole morphology from the DEMs to calculate volume and area within the euphotic zone at monthly intervals during the dry season. Productivity potential was then scaled against the relative fish population in each waterhole to give an indication of food resources per individual.

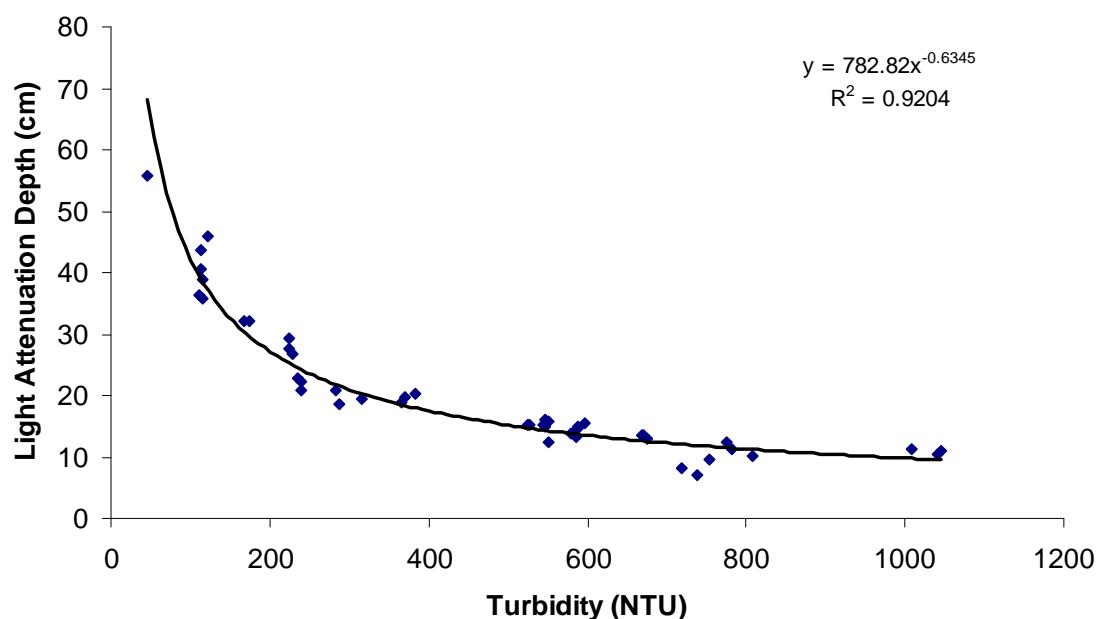


Figure 17: Turbidity and light attenuation in Moonie waterholes

We considered productivity potential to be indicative of waterhole quality in terms of food availability, so predicted that fish in waterholes with higher productivity potential would exhibit better condition. Fish condition is an indicator of robustness which assumes that the healthier a fish, the greater its energy reserves, measured as the proportion of lipids in its tissues (Paukert & Rogers 2004, Cunjak et al. 2007). We hypothesized that fish condition would change in response to the amount of primary production in a waterhole, and therefore be able to differentiate pools with better or worse habitat quality, or detect declines in quality occurring with waterhole drying (Fig. 18).

To test this, condition was estimated for 214 individuals of two common species, *Nematolosa erebi* and *Macquaria ambigua*, using lipid and water content analysis (Method AEML011) (Ly 2007) and compared against scaled productivity potential. This analysis was performed with productivity data collected at the same time as the fish, and also with productivity data from one and three months prior to fish collection to test for a lag in condition response.

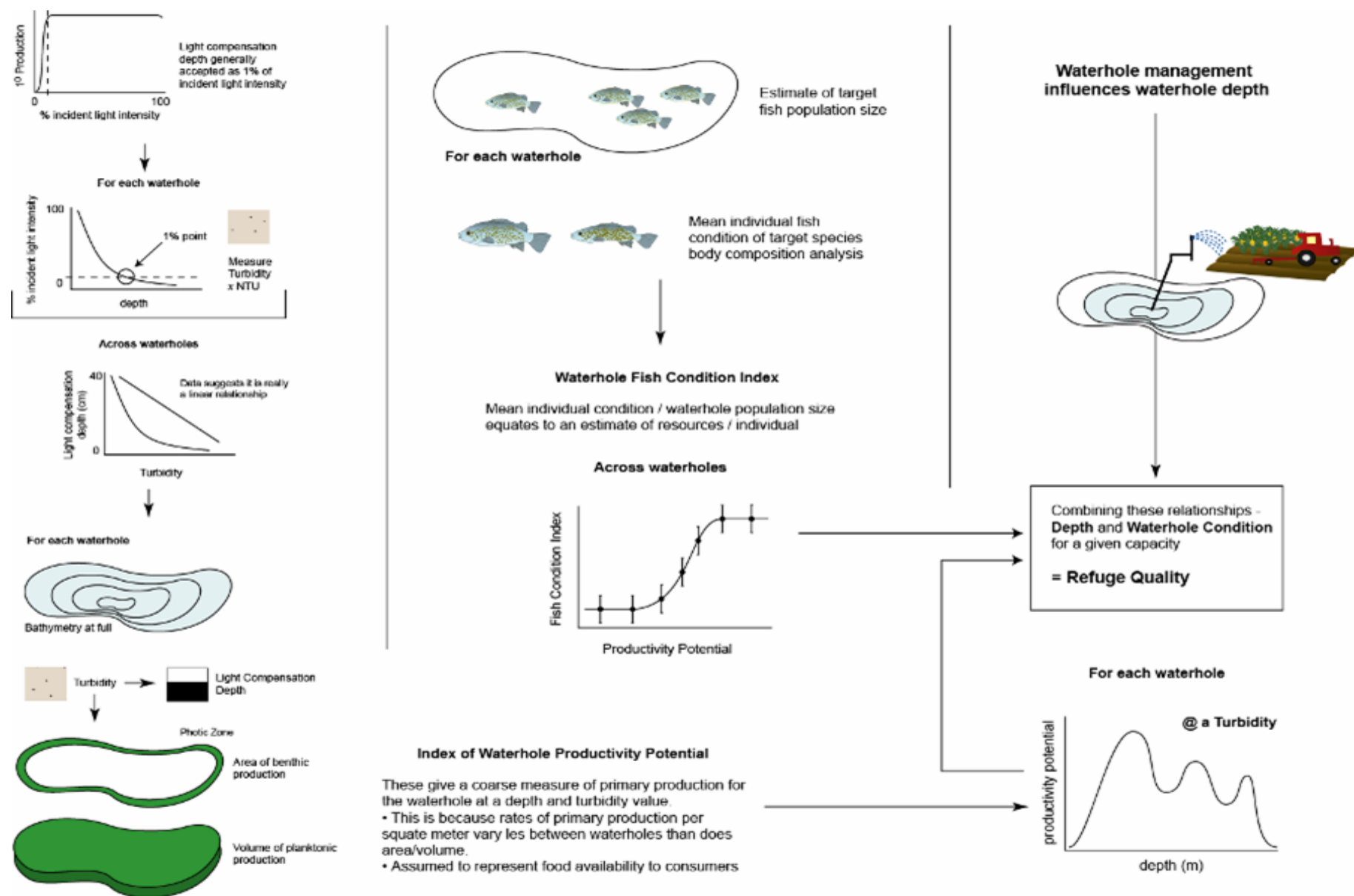


Figure 18: Conceptual model – productivity potential and fish production

It was expected that fish condition would decrease as waterholes dried and habitat quality worsened, however the results indicated that fish condition was extremely low compared to levels reported in the literature (Balcombe et al. 2005, Balcombe et al. 2006, Cunjak et al. 2007) and did not change significantly over time (Ly 2007), despite changes in productivity potential with varying water depth and turbidity. Because there was so significant change in condition results, we were not able to evaluate refuge quality responses. Why fish condition is so low and invariant remains unresolved. It is possible that with such low lipid levels, fish that do lose condition during dry spells are unable to survive and therefore aren't sampled and included in the analysis. Or, perhaps adaptive feeding strategies enable fish to maintain enough nutrition for body condition to remain stable. Another two years worth of fish condition samples have since been collected, so analysis of these may provide better results and allow for further investigation.

Food availability and fish diet preferences

Diet analysis was conducted on the same specimens of *N. erebi* and *M. ambigua* used for condition analysis, to determine whether food availability and fish feeding behaviour changed over time (Sternberg et al. 2008). The gut contents of 94 fish, collected in February, May and September 2006, were examined and the dietary components identified.

The analysis revealed that as waterholes dried, both species shifted to different food resources. Individuals of *N. erebi* fed predominantly upon non-filamentous algae in the period soon after the cessation of flow, and shifted to predominantly detritus and some filamentous algae as the dry season continued (Fig. 19 – Sternberg et al. 2008). This represented a shift from high quality (high energy content) to low quality food during prolonged isolation of waterholes. *M. ambigua* also exhibited a shift in food sources in response to time since flow, though the response was more variable.

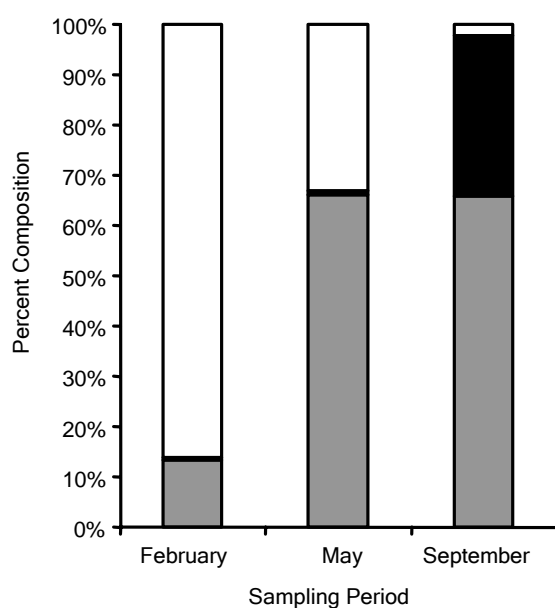


Figure 19: Percent diet contribution (■, detritus; ■, filamentous algae; and □, non-filamentous algae.) of *N. erebi* in the Moonie River for February (n=14), May (n=24), and September (n=23) in 2006. Figure reproduced from Sternberg et al. (2008)

These results demonstrate the resistance capacity of fish in the Moonie and their ability to cope with changing conditions within refuge waterholes. The generalist nature of fish species which are common in these systems allows them to take advantage of whatever resources are available to withstand disturbances such as drought (Poff & Allan 1995). While they are adapted for variability, it is possible that there are still limits in the amount of change they can survive (Bond et al. 2008).

Waterhole quality thresholds

The concept of ecological thresholds - “a point at which small changes in environmental conditions produce large or abrupt

changes in ecosystem state or function” (Groffman et al. 2006) - has been gaining popularity over the last 30 years as the basis for the development of tools to manage natural resources (Huggett 2005). A large number of ecological thresholds have been investigated in this time. The Resilience Alliance, an international research collective, maintains an online database of ecological thresholds which currently contains 102 demonstrated or proposed examples (Resilience Alliance 2004). Thresholds with the best confidence tend to relate to specific taxa, pressures and places or experimental or modelled interactions (e.g. Butler et al. 2004, Otten et al. 2004, van der Ree et al. 2004), since these are often the easiest to test. Although there is still some debate about whether stable, predictable, ecological thresholds really exist, and to what extent they apply to broader community assembly (Catalan et al. 2009), we attempted to identify a threshold of waterhole depth loss for pool habitat quality.

Despite an understandable desire from managers and policy makers to set waterhole drawdown levels for protection of ecological values, in our studies there were no obvious depth thresholds below which habitat quality worsened. The measures of productivity potential, fish catch, condition and diet preference, and zooplankton and phytoplankton abundance tended to either show no change, or fluctuate up and down over the course of a dry spell, suggesting a range of influences, not just depth. Patterns also varied from one site to the next, meaning no universal thresholds were identifiable.

These results fit with opinions reported in the literature that the complex interactions at play within ecosystems (Groffman et al. 2006, Huggett 2005), along with environmental stochasticity (Swift and Hannon 2009), especially inherent in temporary systems, make it difficult delineate meaningful thresholds for ecosystems as a whole. Further compounding this complexity is the varying responses of different species to the same pressures or environmental conditions (Ficetola and Denoël 2009, Lindenmayer et al. 2005, Catalan et al. 2009, Solheim et al. 2008). These difficulties, along with a lack of clear management objectives, mean that attempting to set drawdown limits based on thresholds of waterhole ecological function may not be the best approach.

Where specific, depth-related, habitat or response thresholds can be determined for waterhole-dwelling taxa (e.g. WRP asset species), the approaches we developed for waterhole modelling and risk assessment (p 9) are useful for assessing the occurrence of threshold breaches. However, where waterholes themselves are the ‘ecological asset’, rather than setting drawdown levels within pools, the best approach may be to manage for broad ecosystem resilience (Zimmer et al. 2009). In order to do this, catchment-scale thresholds should be set, maintaining enough waterhole habitats with appropriate spatial distribution, to enable ecosystems to ride out dry spells and bounce back. What is ‘enough’ will be largely determined by the management objectives and values (Samhouri et al. 2010) though population modelling, like that being undertaken as part of the eWater project, will assist with optimisation and threshold development.

Connectivity

While the presence of persistent waterhole refugia is critical for the resistance of aquatic biota during dry spells, longitudinal connectivity between refugia and lateral connectivity between river channels and inundated floodplains is also necessary for population viability at large geographic scales (Bunn & Arthington 2002, Jenkins and Boulton 2003). The extent of hydrologic connectivity, coupled with the dispersal traits of organisms, will determine their ability to recolonise waterhole habitats after drought, and maintain a wide spatial range (Bunn & Arthington 2002, Magoulick & Kobza 2003, Hughes 2007). Opportunities for connectivity between resistant populations also allow gene flow, improving the vigour of organisms over generations (Dunham & Minckley 1998, Whitlock et al. 2000). As long as connectivity is maintained, species that can widely disperse will remain common at a landscape scale despite local extinctions. This is a critical aspect of the resilience of populations in intermittent systems, though it can be diminished by barriers or poor dispersal ability of organisms (Bunn & Arthington 2002, Bond & Arthington 2008, Beesley & Prince 2010).

Connectivity and dispersal among populations is geographically and temporally variable. Changes in the availability and quality of refuge waterholes and fluctuations in hydrological regime will lead to variation in dispersal among populations and colonisation of new habitats. These processes also fluctuate through time based on changes in population demography (Dingle & Drake 2007, Hughes 2007). As such, it is important to understand both historical and contemporary connectivity and dispersal to assess the viability of a species at the landscape scale.

Key question:

What is the spatial extent of connectivity among populations of aquatic species in the Moonie?

Fish movement

We used both direct and indirect approaches to estimate contemporary and historical dispersal among fish and crustacean populations.

The direct technique involved tagging fish of four species (Bony Bream – *N. erebi*, Golden Perch – *M. ambigua*, Eel-tailed Catfish - *Tandanus tandanus* and Spangled Perch - *Leiopotherapon unicolor*) with acoustic tags (V7-4L-69KHz, Vemco Corporation). Catchability was an important consideration when selecting target species, as was body size, since the tags are physically too large to use on small-bodied species. Dispersal scale of the target species was also important since the technique is best at detecting between- rather than within-waterhole movements.

To determine the dispersal ability of the target species and the effect of flow on their behaviour, a network of 17 recorder stations was installed throughout a reach of approximately 85km (Fig. 20). Recorder stations were generally placed in refuge pools, with some also installed in anabranches and sections of stream channel that dry between flows. A total of 220 fish were caught, tagged and released into disconnected pools in the late dry season over three consecutive years (2007 – 09), and their movements during periods of flow were recorded. Fish were handled in accordance with animal ethics guidelines. So far, only data from years 1 and 2 have been analysed. The inclusion of the third year's data and interrogation of the entire dataset should provide a thorough understanding of fish response to flows in the Moonie.

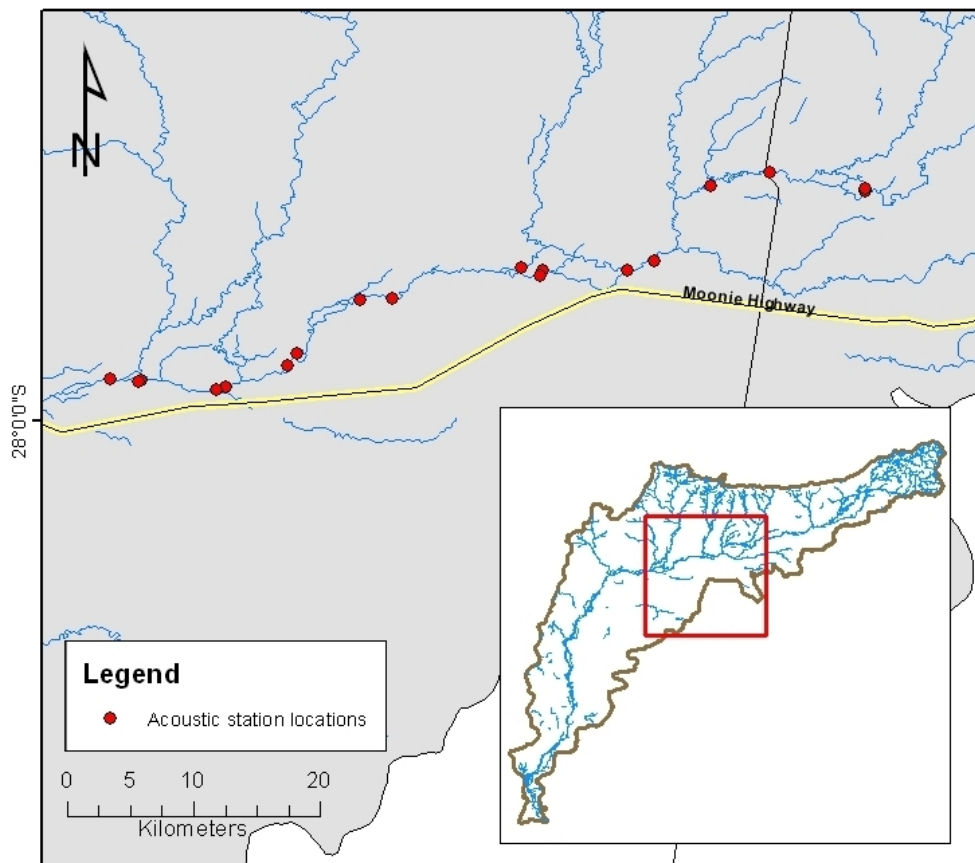


Figure 20: Acoustic recorder station network

Preliminary tagging results (2009/10 data yet to be analysed) reveal that the majority of fish move, though the response is species-specific (Fig. 21a). Most Golden and Spangled Perch moved between acoustic stations within a single flow season, while *Tandanus* and Bony Bream were more likely to remain in the waterhole where they were tagged. Of the fish that moved, most remained within a 20-30km reach of stream, though some ranged over more than 70km during a single flow season (Fig. 21b), with large movements often occurring over just a few days. This suggests that fish in this catchment could recolonise quite rapidly after a severe drought.

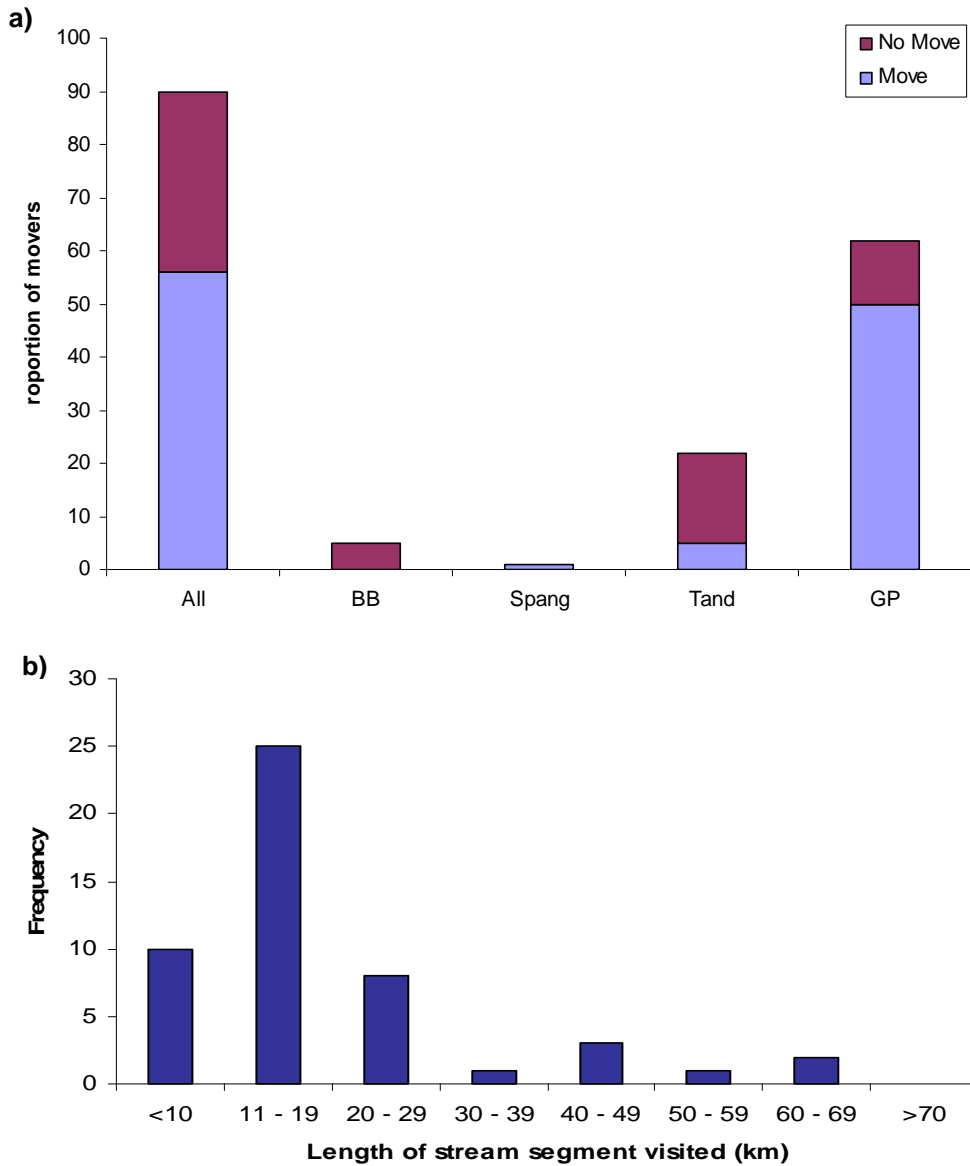


Figure 21: Fish movement a) the proportion of tagged fish that moved by species and in total b) of tagged fish that moved, the length of stream segment visited

BB=Bony Bream, Spang=Spangled Perch, Tand=Tandanus, GP=Golden Perch

Combining fish movement data with hydrology (Fig. 22) revealed that in the Moonie, the majority of fish move on the first post-winter flow, independent of the magnitude of the event, and that subsequent, larger flow events triggered a lesser response. This finding matches reports from the literature and results of similar studies, identifying the first post-winter flow as a critical cue for flow-spawning fish species (Lake 1967, Pusey et al. 2004, Balcombe et al. 2006, Roberts 2008). These results highlight the importance of the timing of environmental flows, not just their magnitude or frequency.

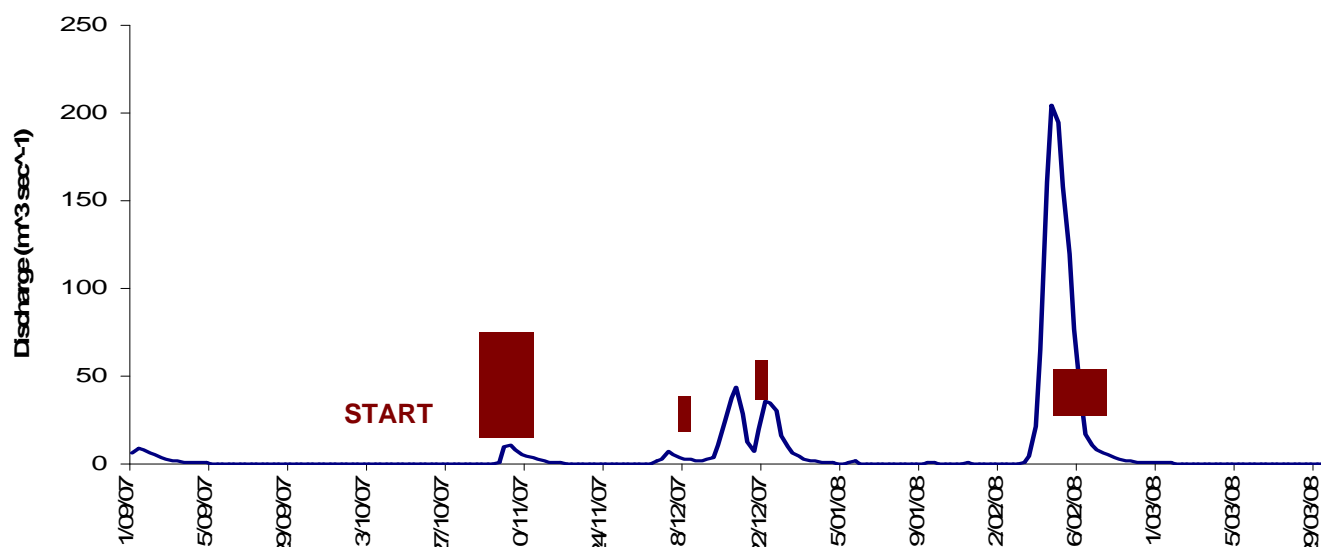


Figure 22: Fish movement in response to flow

Width of boxes indicates the length of time over which fish moved height represents relative number of tagged fish that moved in each event

Tagged fish in the Moonie showed no obvious upstream or downstream movement preference. Instead, they tended to move in both directions at different times and then return to their starting waterhole by the end of the flow season, suggesting an ability to home and a preference for deeper, more permanent refuge pools. This fits with theories from the literature suggesting that fish take opportunities to explore their home range and select optimum local habitats (Crook 2004a, Crook 2004b, Crook et al. 2010).

Population genetics

The indirect technique we used for assessing connectivity utilised population genetic and phylogeographic data to simultaneously estimate historical and contemporary gene flow among populations of *M. ambigua*, *T. tandanus* and *Macrobrachium australiensis*. This technique is useful as it can identify historical and rare processes that may be missed by direct assessment techniques (Wang 2005, Hughes 2007, Schwartz et al. 2007).

Estimates of dispersal from population genetics revealed comparable results to those of the fish tagging. Genetic structure was weak for all three species (Fig. 23), suggesting high levels of gene flow (analogous to dispersal) among populations in the Moonie catchment. Assignment testing, a technique used to detect recent movement of individuals between local populations (Manel et al. 2005), also identified small numbers of migrants in the populations at each waterhole. This suggests that despite waterholes being isolated much of the time, flow events are sufficient to allow dispersal. This is important, as dispersal and gene flow between populations makes them more robust and improves viability (Whitlock et al. 2000) by allowing advantageous alleles to disperse among populations and dry waterholes to be recolonised.

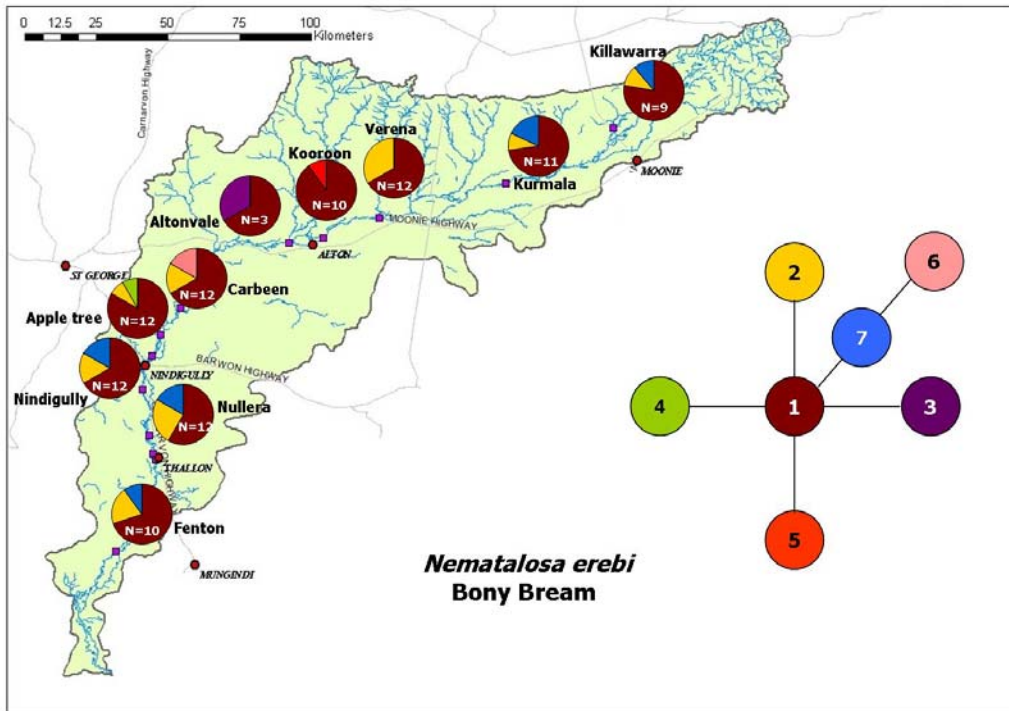


Figure 23: Distribution of Bony Bream genotypes in the Moonie, showing weak structure, suggesting high connectivity

The tagging and genetics studies in the Moonie highlight that fish in dryland systems use networks of waterholes, not just individual pools, so the population or catchment scale is most appropriate for management. To ensure healthy populations, the ability for fish to move between refuge pools to select prime habitat and to recolonise following droughts must be maintained. This requires a match between the migration ability and behaviour of fish species, the spatial distribution of refugia and the location and size of barriers along with the appropriate timing and magnitude of flows.

Conclusion

In systems that experience temporary flow, refuge waterholes provide critical habitat for obligate aquatic biota. These species have evolved traits for resistance and resilience which enable them to survive the often harsh conditions in dryland rivers, however they require catchment-wide networks of persistent, connected refugia to utilise these traits and maintain viable populations in the long term.

Climatic and anthropogenic pressures can affect the distribution of persistent refugia and the connectivity between them, increasing risk to aquatic biota. In order to effectively manage these habitats and to enable a balance of consumptive use and ecological protection, clear understanding of the processes and interactions which maintain refugia is necessary.

This project has begun filling knowledge gaps about the function of refugia in terms of their persistence, quality and connectivity, by addressing the following key questions:

1. What is the persistence time of waterholes in the Moonie catchment?
2. Are there any simply-measured waterhole parameters that can be used to estimate persistence? If so, can these relationships be applied in systems outside the Moonie?
3. Does changing waterhole morphology due to sedimentation affect waterhole persistence?
4. Does changing food availability in waterholes alter the body condition of resident biota?
5. Do fish species that inhabit drying waterholes shift their feeding preferences?
6. Is there a depth threshold below which refuge habitat quality is reduced?
7. What is the spatial extent of connectivity among populations of aquatic species in the Moonie?

By modelling persistence, we were able to develop a simple predictive relationship between depth and persistence time in the Moonie River, and apply this to a reach of river to map temporal availability of waterhole habitat. This relationship, however, was not transferrable to other catchments, and it appears that a number of parameters are generally needed to predict persistence. A tool was also developed to assess the likelihood of waterholes drying during no-flow spells and compare the effects of water resource management scenarios. The effect of sedimentation, another pressure on waterhole persistence, was also assessed. In the Moonie, sedimentation rates were high, reducing waterhole depth and persistence time. Waterhole quality, in terms of primary productivity, was variable in space and time, but the generalist nature of the fish species present enabled them to switch feeding preferences in order to maintain condition. Lastly, longitudinal connectivity was evident in the Moonie, with tagged large-bodied fish able to migrate over relatively large distances during periods of flow and genetic mixing apparent at the whole-catchment scale.

Overall, the findings of our research to date have reinforced the opinion that the best outcomes for refuge-dwelling biota can be achieved by utilising their inherent resistance and resilience traits. This means ensuring that enough waterhole habitats of sufficient quality are maintained within a catchment for local populations to survive dry spells, and that connectivity is ensured during flows to enable recolonisation, gene flow and viability of regional populations.

Specific information has been generated about the five study catchments, along with general approaches that can be broadly applied. In many cases, work to integrate results is ongoing. In order to best use the methods developed, management values for waterhole refugia must be clearly defined, along with the specific habitat requirements of refuge-dwelling assets. Finally, in many instances, this study has raised as many questions as it has answered and further research is needed to address the gaps in understanding that still exist.

Future directions

This project has provided information and insight into a number of the functions of refugial waterholes. Some studies are ongoing and work has begun on answering the follow-on questions that have arisen from the findings we already have. The project has also highlighted a number of other areas that would benefit from targeted research.

Persistence

- Seepage as a factor reducing persistence of some waterholes. Investigation of methods to detect and quantify this e.g. change in ionic concentration
- Determination of sediment sources and the pressures that lead to increased sedimentation
- Building multi-factor waterhole persistence models that can be applied broadly
- Population modelling to optimise the number and arrangement of persistent waterholes required for population viability

Quality

- Development of light-turbidity relationships for estimation of primary productivity. Currently under development and showing consistency between catchments.
- Investigation of the influence of waterhole productivity and light limitation on food-web structure, waterhole carrying capacity and the health/body condition of consumers at local (waterhole) and regional (river reach/valley) scales
- Identification of other habitat attributes that may be indicators of quality. In order to be broadly applicable and assessable, these must have a quantifiable relationship with changing waterhole depth/volume
- Determination of lethal thresholds in waterholes e.g. water quality parameters, body condition limits

Connectivity

- Genetic measures of recent changes in connectivity to better understand the effect of modern barriers
- Improved understanding of longitudinal connectivity for fish migration and examining the effect of weirs on fish movement
- Better understanding of the spatial scales of target populations (e.g. discrete metapopulations, multi-catchment panmictic populations) and the connectivity processes required to appropriately maintain them
- Lateral floodplain connectivity and inundation extent and its role in creating recruitment hot-spots
- Examination of carp recruitment patterns in the Moonie and inter-catchment connectivity using otolith micro-chemistry

Project outputs and collaborations

The nature of this project has been highly collaborative, spanning a number of disciplines, and involving input from many contributors and organisations. Results have been applied in several other projects, and there are a number of papers, theses and documents completed or in progress.

- TRaCK – collaboration on 6.1 Waterholes project, summary report in preparation
- MDBC Projects: “Ecosystem resilience and importance of refugia for native fish communities/populations (MD1086)”, collaboration with SARDI, Moonie selected as northern MDB focus catchment; and “The protection of drought refugia for native fish in the Murray-Darling Basin (MD1087)”
- Joint University of Adelaide-DERM project: determining sedimentation rates in waterholes of the Moonie River in South-West Queensland
- Fitzroy WRP Review – development of method for risk assessment for refugia
- AquaBAMM (Murray-Darling and Gulf) – Contribution of data for prioritising measures and scoring sub-regions
- Development of DERM methods documents
- Papers in prep:
 - Modelling waterhole persistence time in a dryland river
 - Turbidity and light limitation of primary productivity in waterholes
 - Determining sedimentation rates and sources in waterholes of the Moonie River
 - Fish migration behaviours in response to flows in a dryland system
 - Response of fish assemblages to variable hydrology: temporal patterns in abundance and body condition
 - Understanding population dynamics of stream fauna to inform restoration and conservation efforts
 - Spawning and dispersal behaviour of the common carp in the Moonie River
- Published papers
 - Sternberg, D., Balcombe, S., Marshall, J. & Lobegeiger, J 2008, 'Food resource variability in an Australian dryland river: evidence from the diet of two generalist native fish species', *Marine and Freshwater Research*, 59: 137-144.
 - Sternberg, D, Balcombe, SJ, Marshall, JC, Lobegeiger, JS & Arthington, AH 2010, 'Flooding in an Australian Dryland River: Relationships Between Antecedent Hydrology, Food Resources and *Macquaria ambigua* biomass and body condition', *Journal of Fish Biology*, in press.
 - Balcombe, S, Huey, J, Lobegeiger, J, Marshall, J, Arthington, A, Davis, L & Thoms, M 2010, 'Comparing fish biomass models based on biophysical factors in two northern Murray-Darling Basin Rivers: a cautionary tale', in *Ecosystem Response Modelling in the Murray-Darling Basin*, Eds N. Santilan and I. Overton, pp 67-83, CSIRO Press, Canberra, ACT.
- Complete honours theses
 - Ly, D 2007, Body condition of two native fish species, bony bream *Nematolosa erebi* and golden perch *Macquaria ambigua*, in waterholes of the Moonie River, Upper Murray Darling Basin. Honours Thesis, Australian School of Environmental Studies, Griffith University.
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