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Wetland connectivity: understanding the dispersal of organisms that occur in Victoria's wetlands

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Summary

Increasing recognition of the ecological significance of dispersal in maintaining species diversity has highlighted the need to consider connectivity in conservation planning. Such initiatives require an understanding of the processes that connect habitats. This report assesses the processes that biologically connect wetland habitats and will inform the development of landscape-scale maps of potential connectivity for wetland ecosystems. To achieve this objective, a synthesis of the dispersal biology of waterbirds, amphibians, fish, aquatic invertebrates and wetland plants are reported. Modelling approaches to assess connectivity are also appraised to identify a suitable approach for developing connectivity maps for wetland biota across Victoria.

An examination of the literature revealed that the dispersal characteristics of wetland biota are highly variable and will result in diverse temporal and spatial patterns of connectivity in the landscape Waterbirds are the most mobile group examined, capable of dispersing over large distances unconstrained by the nature of the landscape. However, the scale of movement varies among species and over time. Although some waterbirds move regularly over hundreds of kilometres, others do so only rarely. Even among the most mobile waterbirds, dispersal capacity becomes constrained during breeding and moulting. During these critical life stages the proximity of suitable foraging wetlands to breeding and moulting sites is likely to play an important role in the persistence of waterbird populations.

In contrast to waterbirds, amphibians have limited mobility, and the nature of the intervening landscape strongly influences movement patterns. Mobility ranges from species that are very sedentary and move less than 0.5 km to the most vagile that may move up to 3 km, although longer distances may be travelled under optimal conditions. Areas of the landscape that offer high resistance to amphibian movement include dry terrestrial areas, saline areas, urban areas and transport networks.

Fish differ in their movement abilities; large fish generally disperse farther than small fish. Water depth can constrain fish movement in different ways. Shallow water can limit movement in large fish that require deeper water to swim, whereas small fish may avoid deep water because the risk of predation is higher. Fish movement between rivers and floodplain wetlands can be influenced by hydroperiod, distance, elevation gradient and the presence of water control structures such as regulators, weirs, levees, and dams. Movement between river drainage systems can occur when flood waters provide temporary connections across the landscape, or when they produce plumes of freshwater in the sea that permit the temporary passage of freshwater species to other catchments.

Aquatic invertebrates are a large group with diverse dispersal abilities. They can be segregated into winged species that disperse by flight and wingless species that rely on vectors to disperse dormant life stages. Among the winged invertebrates, species can be further segregated into strong and weak flyers. Strong flyers may disperse hundreds of kilometres, some using high-altitude currents to increase the distance they disperse.

Wingless insects and plants rely on vectors to disperse dormant eggs, seeds or vegetative fragments. Wind, water and waterbirds are the most important natural dispersal vectors in aquatic systems. Each dispersal vector produces different spatial and temporal patterns of connectivity in the landscape. Wind-mediated dispersal is likely to be more effective in connecting wetlands when they are close together and aligned with the direction of the prevailing winds. Adaptations for dispersal by wind are common in plants seeds, but adaptations in invertebrate propagules, other than a small size, are lacking.

Water serves as a vector for the dispersal of plant and invertebrate propagules. In rivers, flow facilitates longitudinal connectivity by carrying propagules from upstream sites to downstream sites. Flooding facilitates lateral connectivity when floodwaters carry propagules between the river and

floodplain. Floods are particularly important for dispersal as they flush propagules that have accumulated in vegetation into streams, and they can fragment and uproot plants which may then be dispersed in floodwaters to distant sites. Buoyant propagules are usually dispersed farther than those that sink. River regulation has altered the timing, frequency and duration of hydrological connections between rivers and floodplains, disrupting dispersal processes and driving changes in community assemblages.

Waterbirds disperse propagules that become attached to the feet, feathers or bill, or are consumed and survive passage through the gut. Waterbirds are an important dispersal vector because they can disperse propagules over long distances and to sites not connected by water-mediated or wind-mediated dispersal. Differences in foraging behaviour or movement patterns between species of waterbirds can influence the types of propagules dispersed and the spatial patterns of connectivity across the landscape.

Assessing wetland connectivity requires a multispecies approach to represent the diverse biota of wetland systems. For such an approach to succeed, maps of connectivity are needed for key groups that share similar modes of dispersal. An appraisal of landscape connectivity models found that only a few are capable of incorporating rules for landscape permeability and the direction and scale of movement to produce maps of connectivity for the organism(s) of interest. Circuit theory accommodates most of these requirements but is computationally demanding, and this currently limits its application at a state-wide scale. Alternative techniques are available in a GIS framework, which can be carried out with more modest computing requirements and processing times, and currently provide the best option for modelling connectivity of Victoria's wetlands.

Integrating patterns of connectivity for different groups of aquatic taxa is desirable to guide strategic investment and planning, and to improve our understanding of how wetland systems interface with other ecosystems. Producing a map that represents patterns of connectivity for wetland biota could be achieved by combining models for individual groups. Although an integrated map of wetland connectivity will provide a useful tool for guiding policy, an understanding of the patterns of connectivity at a group or species level is needed to inform more targeted management interventions.

1 Overview and objectives

Biological connectivity broadly refers to the ability of plants and animals to move among habitat patches in the landscape (Hanski 1998, Tischendorf and Fahrig 2000). Understanding connectivity is of fundamental importance because it underlies landscape-scale ecological processes such as species invasion, immigration and metacommunity dynamics (Nathan and Muller-Landau 2000, Hubbell 2001, Wright et al. 2003, Leibold et al. 2004). Increasing recognition of the ecological significance of dispersal in maintaining species diversity has highlighted the need to consider connectivity in conservation planning. The conservation of biodiversity has been addressed in the past through a system of protected areas, but only 6–12% of land area, both in Australia and globally, is protected (Soulé et al. 2004, Mackey et al. 2007). The existing area of reserves is considered 5–10% too small and the biological connections among them inadequate to prevent species extinctions, the rate of which has been estimated to be 1000–10 000 times higher than natural (Soulé et al. 2004).

In response, there has been a shift towards developing conservation programs that interconnect core reserves, and that manage the intervening landscape in ways that assist the movement of organisms (Amezaga et al. 2002, Soulé et al. 2004, DSE 2010). Such initiatives require an understanding of the processes that connect habitats. Assessing biological connectivity requires a species-level approach that identifies how the spatial and temporal characteristics of the environment interact with an organism's dispersal biology to impede or facilitate movement among habitat patches (Taylor et al. 1993).

Our understanding of biological connectivity has been developed in terrestrial systems, particularly in fragmented forests and woodland habitats, and the processes that connect aquatic systems are less understood (Weins 2006, Doerr et al. 2010). The broad purpose of this report is to assess the processes that biologically connect wetland habitats. This information may be used to guide the development of landscape-scale maps of potential wetland connectivity for key groups of aquatic organisms in Victoria. Understanding the connectivity of Victoria's wetlands will assist the landscape-scale management of aquatic habitats by identifying:

- wetlands that are biologically linked and form functional mosaics
- bottlenecks in the movement of taxa among core habitats
- wetlands that act as stepping stones, permitting the exchange of plants and animals among many wetlands
- whether a loss in connectivity could be contributing to poor wetland condition
- sites for habitat restoration or creation that will have flow-on benefits because they allow dispersal to other habitats
- pathways for the invasion of introduced species.

This report provides a general background of landscape connectivity and its importance in understanding the spatial distribution of species. The significance of connectivity in aquatic habitats is then examined, and approaches to measuring dispersal are summarised. The dispersal of key groups of wetland organisms is then described, including invertebrates, amphibians, fish, plants and waterbirds. For each group the objective has been to identify, where possible:

- patterns of habitat utilisation
- the mode(s), scale, and pattern of dispersal in the landscape
- landscape barriers to dispersal
- evidence that supports the ecological significance of dispersal.

Finally, key modelling approaches to assess connectivity at a landscape-scale are described, which — along with the dispersal biology of the focal groups — can inform the development of maps that represent potential connectivity among wetlands.

2 Landscape connectivity

2.1 What is connectivity?

Connectivity broadly refers to the ability of plants and animals to move among habitat patches in the landscape (Hanski 1998, Tischendorf and Fahrig 2000). A distinction is often made between structural and biological connectivity. Structural connectivity describes the physical elements of the landscape that influence species distributions, including the size and configuration of habitat patches in the landscape, the distances among habitats, and sometimes the nature of the intervening landscape. Biological connectivity considers whether species can navigate the landscape to access suitable habitat patches. It does this by considering the mobility of an organism and the characteristic of the landscape that favour or limit movement. Species vary in their mobility and how they respond to the landscape, and this produces different rates, patterns and scales of biological connectivity in the landscape (Taylor et al. 1993).

Our ability to directly assess the movement of an organism between habitats — 'actual connectivity' — requires a study of movement or genetics. Such studies are uncommon, so 'potential connectivity' is usually inferred from knowledge of the species' mobility and the nature of the landscape. This approach requires and understanding of the processes that shape patterns of dispersal, including the following (Tischendorf and Fahrig 2000):

- species abundance, which influences the number of individuals dispersing
- the number, area and arrangement of habitat patches in the landscape
- mode(s) of dispersal (e.g. wind, water, animal vectors)
- spatial patterns of movement (e.g. prevailing winds that disperse seeds)
- scales of movement of the organisms being studied
- features of the landscape between habitats that may facilitate or impede dispersal
- temporal patterns in the availability and behaviour of dispersal vectors (e.g. floods), or in the movement behaviour of an organism (e.g. seasonal movements associated with breeding or moulting in waterbirds)
- mortality risks associated with movement.

2.2 The importance of biological connectivity

Understanding biological connectivity is fundamentally important because it underlies landscape-scale ecological processes (Nathan and Muller-Landau 2000, Hubbell 2001, Wright et al. 2003, Leibold et al. 2004). For example, dispersal provides opportunities for both native and introduced species to expand their range and migrate in response to local and regional changes in habitat conditions such as climate change. High rates of dispersal can allow species with narrow habitat requirements to reach suitable habitats in the landscape. Dispersal can also rescue populations in suboptimal habitats from extinction and, where disturbance events have caused local extinctions, dispersal can help species to recolonise these sites. Dispersal also promotes gene flow among populations and prevents populations becoming reproductively isolated. Maintaining gene flow among populations increases genetic diversity, which facilitates adaptations to the environment on ecological and evolutionary time scales (Whitlock and McCauley 1999).

Where dispersal links populations of multiple species across the landscape, they interact to form a 'metacommunity'. The concept of metacommunities forms the basis for all of the recognised models explaining community assembly — neutral, species sorting, source–sink, and patch dynamics (Leibold et al. 2004). These models consider how community assemblages are influenced by the frequency of dispersal, species habitat requirements, interaction among species, and trade-offs between traits that increase dispersal and those that confer a competitive advantage.

- **Neutral theory**

  The neutral model is based on the premise that species are ecologically equivalent; that is, they do not differ in fitness, niche specialisation or dispersal ability, and this renders the environment neutral. Under these conditions, species distribution patterns are not influenced by environmental heterogeneity in the landscape but by distances among habitats, which determine the probability of colonisation. The neutral model has sparked considerable debate in the ecological literature on the relative importance of environment and dispersal in determining species distribution patterns. A number of studies have shown that differences in environmental conditions among habitats explains as much, if not more, of the variation in community structure explained by distances among habitats (McGill 2003, Thompson and Townsend 2006). It is evident from these landscape-scale studies that in some systems both the environment and dispersal contribute to community structure.

- **Species sorting**

  The species sorting model incorporates the influence of both environmental heterogeneity and dispersal limitation. In this model, dispersal determines the probability of a species arriving at a site, but variation in environmental conditions among sites, coupled with species niche specialisation, acts as a filter on species distributions (Leibold et al. 2004). Under conditions where dispersal is not limiting, the structure of communities at a landscape-scale is shaped predominantly by environmental conditions, and species distributions are strongly correlated with environmental variables and not spatial elements. In contrast, where dispersal is limited, species reach only a small subset of suitable habitats and both spatial elements and environment variables explain patterns of distribution in the landscape.

- **Source–sink**

  The source–sink or mass effects model posits that high rates of dispersal from ‘source’ populations maintain species in ‘sink’ habitats, when they would otherwise be displaced by stronger competitors, suboptimal conditions or high levels of disturbance (Pulliam 1988, Leibold et al. 2004)

- **Patch dynamic**

  The patch dynamic model applies when habitats are considered to be identical. As habitats are identical in this model, species cannot coexist at a regional scale via niche separation, and instead coexist through trade-offs between competition and colonisation (Hanski 1998, Leibold et al. 2004). In this scenario a species that is a weak competitor for resources can persist among stronger competitors if it is a better colonist, and this is achieved by maintaining higher rates of dispersal or fecundity (Gardner and Engelhardt 2008).

These models illustrate the complexity of predicting the ecological outcomes of altered rates of dispersal. Changes in connectivity may favour some species, and at the same time exert negative effects on others. As pointed out by Taylor et al. (2006), connectivity is ‘inherently neither good nor bad’. Therefore the aim of management should not necessarily be to maximise connectivity, but to assess how changes in the landscape will alter patterns of connectivity, and how this will affect the persistence of species.

3 Connectivity of wetland habitats

3.1 Introduction

Wetland habitats are among the most modified ecosystems in the world (Pringle 2006). Globally more than half of the world's wetlands may have been destroyed (Ramsar Convention Bureau 1996). Similar losses have been incurred in Australia: Victoria has lost 30% of its natural wetlands and New South Wales up to 70% of some wetland types, and in Western Australia 70% of wetlands on the Swan Coastal Plain have been lost (Wasson et al. 1996).

Compounding the impact of habitat loss has been the over-abstraction of water for human use, which has degraded rivers and isolated wetlands. Humans have already acquired more than half of the Earth's accessible freshwater resources, a figure predicted to climb to 70% by 2025 (Postel 1996, Pringle 2006). In the USA almost all streams have been modified by dams or other water diversion schemes (Poff et al. 1997). In Australia river regulation has produced highly modified flow regimes and alienated floodplain wetlands (Kingsford 2000, Arthington and Pusey 2003).

These landscape changes have reduced populations of aquatic plants and animals directly through habitat loss, but also indirectly because they impinge on the ability of organisms to move among habitat patches. Reduced connectivity, coupled with multiple environmental threats such as eutrophication, salinisation and invasive species, have driven many aquatic systems into a perilous state. The World Wildlife Fund reported that, on a global scale, populations of 200 freshwater fauna have declined by 50% in just over 30 years (1977–1999). Master et al. (1998) reported that freshwater species in the USA are in greater peril than terrestrial species. In Australia, 14% of frog species and 9% of freshwater fish species are now endangered or threatened. A third of Australia's rivers have lost 20–100% of the aquatic invertebrate species that should be present, and 80% of River Red Gum trees in South Australia are stressed because of reduced flooding regimes and saline groundwater (Saunders et al. 1996, Wasson et al 1996).

Current threats to aquatic biodiversity are likely to be compounded as regions of Australia shift towards a more arid climate in response to climate change (Murphy and Timbal 2007). With increasing aridity it is likely that the number and size of wetlands will decline, and the duration, frequency and magnitude of flood events that periodically link aquatic habits in the landscape will be compromised. These changes are likely to profoundly affect the movement of organisms among habitat patches, limiting their ability to relocate to more favourable climate zones. For organisms that are intolerant of desiccation, recovery from periods of drought will depend on their ability to access refuges and to recolonise following these events.

Addressing threats to aquatic systems requires a landscape-scale management approach. Although the principles of landscape conservation have been applied for some time in terrestrial systems (e.g. forests and grasslands), such an approach has not been adopted in aquatic systems (Doerr et al. 2010). In Australian systems the focus has been largely on assessing habitat connectivity for native mammals and birds living in woodland and forest ecosystems; the processes that connect aquatic systems are less understood (Weins 2006, Doerr et al. 2010).

Developing a landscape-scale approach for the conservation of aquatic systems is a challenging task. Aquatic systems are diverse, and this necessitates a multi-species approach (Haig et al. 1998) that considers the processes that allow the exchange of plants, invertebrates, fish, amphibians and waterbirds among habitats. The dispersal potential of these organisms differs greatly, from waterbirds capable of moving vast distances to sessile organisms such as plants and many invertebrates that rely on vectors to disperse their propagules (e.g. seeds and vegetative fragments of plants, and resting eggs of invertebrates).

In the following chapters a conceptual framework for understanding how dispersal operates in wetland systems is outlined, followed by a synthesis of the dispersal biology of the main groups of wetland-dependent taxa, including invertebrates, plants, frogs and fish. For each group the objective has been to identify where possible:

- patterns of habitat utilisation;
- the mode(s), scale, and pattern of dispersal in the landscape
- features of the landscape that may represent barriers to dispersal
- evidence of the ecological significance of dispersal.

3.2 A conceptual model of dispersal

The processes that determine the dispersal of aquatic taxa across the landscape are represented schematically in Figure 1 (developed from Morris et al. 2009). The number, size and spatial arrangement of habitat patches in the landscape, the availability and behaviour of dispersal vectors, and the features of the landscape that impede or facilitate movement combine with species dispersal traits to produce unique patterns of connectivity in landscapes.

Population size — Population size can affect the strength of dispersal because more individuals are likely to disperse when the population is large, thus increasing the number of individuals that reach more distant sites.

Realised landscape permeability — For mobile species such as fish, frogs, waterbirds and winged insects, the distances individuals are able to move and their responses to the landscape determine the pattern and scale of dispersal (Figure 1). For sessile taxa such as plants and many invertebrates, patterns of dispersal result from interactions between propagule traits and the behaviour and availability of dispersal vectors (Figure 1).

Dispersal vectors: wind, water and waterbirds — Wind, water and waterbirds are considered the most important natural dispersal vectors in wetland systems (Amezaga et al. 2002). Propagules adapted for wind dispersal are very small and light, or have special adaptations that help them to stay in the air. Wind-mediated dispersal will connect wetlands that are close together and aligned with the direction of the prevailing wind.

Water connects habitats longitudinally, laterally and vertically. In rivers, flow facilitates longitudinal connectivity by carrying propagules from upstream sites to downstream sites. Flooding facilitates laterally connectivity when floodwaters carry propagules between the river and floodplain. Vertical connectivity occurs when organisms move between the riverbed and the hyporheic (subsurface) zone. Floods are particularly important for dispersal because they flush propagules that have accumulated among vegetation into streams, and they fragment and uproot plants which are then dispersed in floodwaters to distant sites. Buoyant propagules are usually dispersed farther than those that sink.

Propagules are dispersed by waterbirds when they become attached to the feet, feathers or bill, or when they are consumed but survive the passage through the gut. Waterbirds can disperse propagules to sites not connected by water and are important in dispersing propagules between catchments. In this way waterbirds play a critical role in connecting aquatic habitats.

Realised dispersal — Realised dispersals are dispersals that result in successful establishment or the exchange of genetic material (e.g. pollen transfer). Upon arrival at a site, the success of colonisation will depend on the habitat requirements of the species. If the conditions are unsuitable the dispersers will perish, although plants and invertebrates with dormant propagules may remain viable in the soil seed bank. The potential for plant and invertebrate propagules to establish later if conditions become suitable will depend on how long the propagules remain viable and how variable the local conditions are.

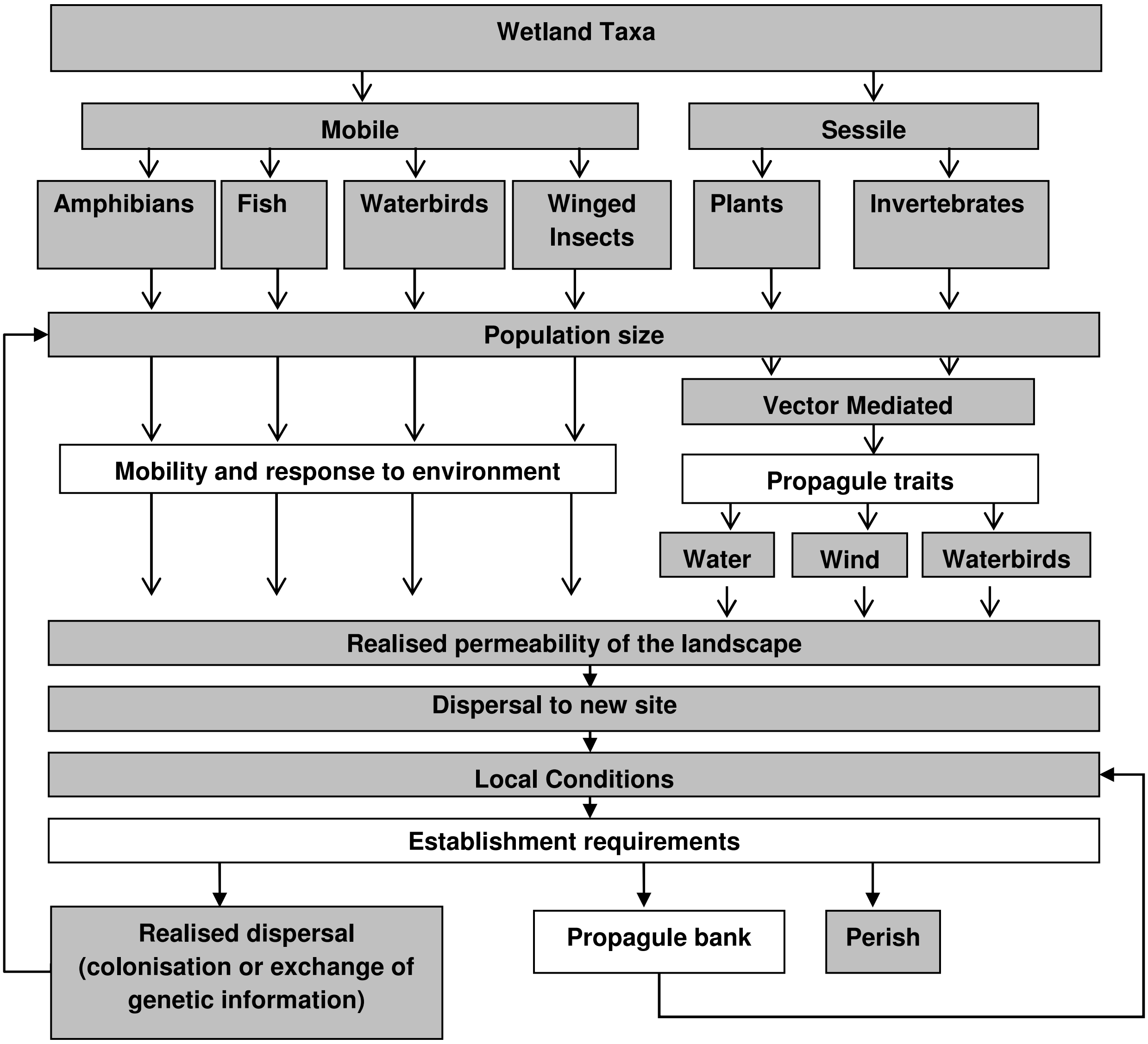

Figure 1. Conceptual model of dispersal processes for different groups of aquatic organisms. White boxes indicate species traits that will influence dispersal and establishment (developed from Morris et al. 2009).

Positive feed-back mechanisms — The establishment of new populations results in an increase in local species richness, with benefits that extend to the regional population (metapopulation). Increased population size increases the strength of dispersal regionally, and this in turn increases the likelihood of further colonisation and reduces the probability of extinction, creating a positive feedback effect.

Temporal variability — Wetland connectivity is a highly dynamic process. Wetting and drying cycles determine the frequency with which water connects habitats, and wetlands can alternate from high connectivity during floods to extreme fragmentation during droughts. Australian systems in particular are characterised by such extreme hydrologic variability (Arthington and Pusey 2003). Hydrology not only affects the structural elements that define the connectivity of the landscape — it also shapes the composition, abundance and fecundity of wetland taxa, and thus the type and abundance of organisms that disperse.

4 Measuring dispersal

Many methods have been developed to capture the movement of organisms among habitats, but most provide only a snapshot of dispersal. The following sections discuss five methods that differ greatly in cost, effort, level of accuracy and temporal and spatial resolution.

4.1 Mark–recapture studies

Mark–recapture studies are a traditional method of assessing the movement of large animals. Individuals are marked in some way (e.g. tags, leg bands, clipping or notching, paint or dye marks) and subsequently identified at other locations over time. This has been the key method for tracking migratory birds, but recovery rates of marked individuals can be low. For example, only about 18% of birds banded by Frith (1959) were recovered 15 months later, and of 5060 juveniles American Wood Frogs (*Rana sylvatica*) marked only 9% were recaptured (Berven and Grudzien 1990). Some organisms such as invertebrates may be too small to mark or may be easily damaged by this method, although dragonflies have been successfully tracked by marking wings. As individuals move farther away from the site where they were marked, the potential dispersal area may become too great to search efficiently, and low recapture rates limit the detection of long-distance dispersal using this approach (Whitlock and McCauley 1999).

4.2 Stable isotopes

Studies by Fry (1981) and others in the early 1980s pioneered the use of stable isotopes in studying animal movement. Stable isotopes are naturally occurring forms of an element that differ in the number of neutrons held in the nucleus, forming heavier and lighter forms of the element (Fry 2006). The use of stable isotopes in studying animal movement requires that the natural abundance of isotopes in dietary sources of a target animal varies geographically, and that these signatures are incorporated in animal tissues. If these prerequisites are fulfilled, stable isotopic analysis of potential dietary sources and animal tissues can reveal the location of major food sources, giving an indirect measure of movement (Hobson 1999, Fry 2006). In metabolically active tissues such as muscles the isotopic signatures may last only months, but in metabolically inert tissues such a fur and feathers the signature may be preserved until the tissue is shed, allowing movement over longer time frames to be detected (Hobson 1999).

In aquatic systems, stable isotopes have been employed to study animal movement among estuaries, lakes and rivers. Typically, multiple isotopes are analysed to develop a clear spatial signal; the most commonly used are $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$, δD and $\delta^{87}Sr$ (Hobson 1999). Many studies have used stable isotopes to assess patterns of animal movement between marine and freshwater systems, since dietary sources associated with these ecosystems have distinct isotopic signatures ($\delta^{13}C$ $\delta^{15}N$, $\delta^{34}S$). The taxa studied in these systems include fish, terns, cormorants, mink and rats. In fish otoliths, calcium carbonate structures of the inner ear, layers of inert tissue that are laid down each year store the isotopic signature of the water occupied by the fish. Fish otoliths therefore provide a persistent record of movement between rivers and estuaries over the life of diadromous fish (Nelson et al. 1989).

Fine-scale movement can be detected where the isotopic signatures of dietary sources are distinct over small spatial scales. Although isotopic differentiation at small spatial scales may not be common, one study in which this approach was informative was an Australian study by Cook et al. (2007). This study used isotopes ($\delta^{15}N$, $\delta^{13}C$) as well as other approaches to assess movement, both among and within stream habitats, of the threatened Southern Pigmy-perch (*Nannoperca australis*). In a stream where base flows ceased in summer, isotopic signatures from muscle tissues of fish caught at several sites in the stream closely matched dietary sources at the site of collection. This suggested that populations were isolated at small spatial scales. In contrast, in a stream where base-flows persisted in summer, isotopic signatures of fish were not as good a match to the dietary sources at collection sites, suggesting greater mobility.

Stable hydrogen isotope ratios have been used to study large-scale movements of birds (Rubenstein et al. 2002) and the Monarch butterfly (*Danaus plexippus*) (Hobson et al. 1999). Stable hydrogen isotope ratios of precipitation vary geographically because water vapour is rich in the lighter isotope of hydrogen whereas rainfall is rich in the heavier isotope. As moist air masses move from low to high latitudes and from low to high altitudes, rainfall becomes progressively depleted in the heaver isotope (Fry 2006). Rainfall with different ratios of isotopes is subsequently incorporated into food webs, producing strong signatures that change with latitude and altitude. Stable isotope methods have so far been applied only to track animal movements, but could prove useful in tracing the origins of seeds or seedlings, and hence dispersal distances (Wang and Smith 2002).

4.3 Genetic markers

When dispersal results in successful colonisation, or when pollen reaches plants from other habitats, genetic information is exchanged. The levels of genetic variation among populations can therefore be used to infer levels of connectivity among habitats (Sork et al. 1999, Wang and Smith 2002). Populations that are highly connected will have high levels of gene flow and will be genetically similar. Populations that are isolated experience genetic drift and have high levels of genetic differentiation. These assumptions underlie the use of genetics in identifying patterns of movement (Hughes 2007).

Genetic markers allow levels of genetic variation among populations to be assessed (Bilton et al. 2001). The fixation index (F_{ST}) provides a measure of gene flow among populations by comparing levels of genetic variation *within* populations with levels of variation *among* populations (Holsinger and Weir 2009). When the level of genetic variation within habitats approximates that found among populations, F_{ST} is small and the population is likely to be well connected to other populations in the landscape. Conversely, where the pattern of genetic variation within habitats differs substantially to that found among populations, F_{ST} is large and the population is likely to be isolated from other populations (Wang and Smith 2002). Genetic techniques can also be used to determine the probability that an individual is from a particular population and when juveniles are studied it can provide insights into recent patterns of dispersal, provided there is a high level of genetic variation among populations (Sork et al. 1999).

There are many instances when genetic markers fail to represent levels of dispersal. Firstly, both zooplankton and aquatic plants (via clonal growth) are capable of rapid population growth upon colonising new habitats. Therefore early colonists can dominate the genetic makeup of the population, giving a picture of lower connectivity even when propagule or pollen exchange is frequent (Boileau et al. 1992, Gómez et al. 2002, DeMeester et al. 2002). This 'founder effect' is reinforced when large resting propagule banks are produced by early colonists (De Meester et al. 2002). Secondly, in some habitats natural selection may produce a gene pool best suited to the local conditions, and new colonists will then be at a competitive disadvantage and be less successful at colonisation. As a result, high rates of immigration may exert little effect on the gene pool. Low levels of connectivity will be incorrectly inferred when cryptic species are not distinguished among populations, and if geographical barriers have existed in the past, it may take thousands of years for the gene pool to reach an equilibrium that reflects contemporary patterns of gene flow (Bohonak and Jenkins 2003, Balkenhol et al. 2009).

4.4 Radio-tracking

Radio-tracking monitors the entire dispersal event and provides information on the dispersal pathway not possible with other approaches. Although most studies using radio-tracking have been on vertebrates, miniature transmitters have enabled dispersal patterns of large invertebrates to be studied including butterflies and flying beetles (Rink and Sinsch 2007). Because this method is labour-intensive and expensive, the sample size is usually small.

4.5 Radar

Radar technology was first used to observe aerial insect migration in 1969, founding the discipline of radar entomology (Chapman et al. 2004). Specialised radars can now operate autonomously and gather data for extended periods of time on the intensity, direction, speed and height of insect migration up to 1 km from the radar unit (Chapman et al. 2004). Some radar also collect data on the size, shape and wing beat frequency of individual insects, which offers the possibility of identifying migratory insects (Dean and Drake 2005).

5 Dispersal of wetland taxa

5.1 Amphibians

Amphibians are fundamental components of aquatic food webs. As larvae they are predominately herbivores but as adults they are mostly carnivores, consuming invertebrates, small mammals, fish and other amphibians. Amphibians are themselves preyed upon, both as tadpoles and as adults. Tadpoles are consumed by fish, birds and diving beetles, and adults are preyed upon by birds, fish, snakes and foxes.

Thirty-seven amphibian species occur in Victoria. Many amphibian species depend on permanent or ephemeral wetlands to complete their life cycle. Although reproductive strategies are varied, with some species laying their eggs on land or in water-filled burrows, the majority (86%) of species that occur in Victoria are pond breeders, indicating a strong dependency on wetland habitats (Appendix 1). A few species, however, show a greater affinity for flowing waters, but even these will utilise adjacent wetlands as refuges, or as stepping stones to other habitats (Appendix 1). Amphibian populations are in decline throughout the world, and are at greater risk of extinction than any other vertebrate group, with one third of species under threat (Beebee and Griffiths 2005). Seventeen Victorian frog species (one third of the total) are listed as threatened in the state, excluding species for which data is insufficient to assess the extinction risk (DSE 2007). Seven of the 17 species listed as threatened have affinities with wetland habitats:

- Giant Bullfrog (*Limnodynastes interioris*)
- Alpine Tree Frog (*Litoria verreauxii alpina*)
- Baw Baw Frog (*Philoria frosti*)
- Growling Grass Frog or Southern Bell Frog (*Litoria raniformis*)
- Giant Burrowing Frog (*Heleioporus australiacus*)
- Green and Golden Bell Frog (*Litoria aurea*)
- Rugose Toadlet (*Uperoleia rugosa*).

5.1.1 Habitat preferences

Although their habitat is usually constrained by the availability of water for breeding and foraging, frogs often move hundreds of metres away from water onto land to forage, shelter and overwinter (Sinsch 1990, Semlitsch and Bodie 2003). The habitat boundary for some species may be 300–1000 m beyond the wetland perimeter (Richter et al. 2001, Semlitsch and Bodie 2003).

Studies of amphibian habitat preferences conducted overseas and in Australia have shown that high vegetation cover and the absence of fish correlates with a higher species diversity of frogs (Pavignano et al. 1990, Ficetola and Bernardi 2004, Hazell et al. 2004). In Australia, for example, Growling Grass Frogs favour sites with a high proportion of emergent vegetation (Clemann and Gillespie 2010), and Green and Golden Bell Frogs prefer habitats with certain plant species such as *Juncus kraussii* that are used for basking and foraging, as well as habitats that are adjacent to other waterbodies (Goldingay 2008). The extent of native canopy cover in the landscape is positively related to frog species richness in ponds in south-eastern Australia (Hazell et al. 2001).

Fish predation of amphibian eggs and larvae can strongly influence amphibian community structure, although some species are more vulnerable to fish predation than others (Hecnar and M'Closkey 1997, Gillespie and Hero 1999, Gillespie 2001, Ficetola and Bernardi 2004). Frogs can resist predation by producing toxic or unpalatable substances at the tadpole stage, or through behaviours that limit predation (Ficetola and Bernardi 2004). The Australian riverine frogs *Litoria spenceri*, *L. phyllochroa* and *L. lesueuri* are susceptible to predation by introduced trout (Gillespie, 2001), and the introduced Mosquitofish (*Gambusia holbrooki*) is known to displace Green and Golden Bell Frogs (Hamer et al.

2002b). Native fish also prey on amphibians, but the susceptibility to predation may vary among amphibian species; lower rates of predation have been recorded for riverine frogs *Litoria spenceri*, *L. phyllochroa* and *L. lesueuri* compared with the marsh-dwelling frog *Limnodynastes peroni* (Gillespie 2001). Some amphibians, such as the Southern Bell Frog, have long larval stages and require more permanent water to complete their life cycle (Clemann and Gillespie 2010). As permanent water bodies favour the persistence of fish, amphibians with long larval stages that do not have adaptations to coexist with fish may be less common in permanent water bodies than amphibians with short larval stages. Ficetola and Bernardi (2004) found that amphibian diversity in a human-dominated landscape (Milan, northern Italy) was higher in temporary wetlands where fish were absent compared with permanent wetlands that were stocked with predatory fish for recreational fishing.

5.1.2 Movement

Triggers for dispersal

All the habitats that frogs utilise to complete their life cycle may be available in wetlands, necessitating only small migrations, or they may be available only at more distant sites and require larger migrations (Pyke and White 2001). Changes in habitat quality or water availability may also trigger frog movement. For example, the Southern Bell Frog (*Litoria raniformis*) abandons permanent waterbodies in favour of ephemeral waterbodies when they are available, returning again to permanent waterbodies as these sites dry (Wassens et al. 2008). Male Green and Golden Bell Frogs (*Litoria aurea*) make larger migrations to reach ephemeral waterbodies filled by heavy rains than they do to reach permanent waterbodies (Goldingay and Newell 2005, Hamer et al. 2008). The stimulus to utilise more distant ephemeral habitats may be that these sites have a lower risk of predation or more resources. Whatever the reason, occupying many habitat types serves to spread the risk of mortality, thus increasing the chance that some offspring will survive (Hamer et al. 2008). It is not known whether the preference to disperse to newly filled ephemeral waterbodies is a widespread phenomenon in frogs.

Dispersal distances

The maximum dispersal distance reported in European studies varies from 3 km in the toad *Bufo bufo* to 15 km in the frog *Rana lessonae* (Sinsch 1990). Species that migrate overland have been reported to utilise streams to disperse, with distances varying from 2.5 km to 10 km (Sinsch 2006). Research in America concluded that adult amphibians generally have a high site fidelity, rarely moving beyond a few hundred metres from breeding sites, while juveniles are capable of dispersing over larger distances. For example, adult American Wood Frogs (*Rana sylvatica*) have exceptional site fidelity; of 11 195 adults marked in one study, none were recaptured beyond their original pond over the six-year study (Berven and Grudzien 1990). In contrast, about 18% of 356 recaptured juveniles dispersed to other ponds, moving on average 1 126 m. Similar observations in other species have led to the conclusion that juveniles are largely responsible for maintaining amphibian metapopulations (Cushman 2006).

It is unclear to what extent this generalisation can be applied to Australian frogs, where extreme temporal variability in water availability has probably selected for greater mobility. For example, the Green and Golden Bell Frog (*Litoria aurea*) is less faithful to its breeding pond compared with the American Wood Frog, with only 53% of males and 65% of females remaining in the same permanent waterbody (Hamer et al. 2008). Mark–recapture studies demonstrate that this species may disperse up to 3 km (Pyke and White 2001), although sightings up to about 10 km from the nearest possible breeding pond have been made (White and Pyke 2008), and one individual was observed to travel 1.5 km in a single night while foraging (White, unpublished data cited in Pyke and White 2001). Similarly, the Growling Grass Frog (*L. raniformis*), considered among the more vagile frog species, has been reported to move up to 1 km in 24 hours (K. Jarvis, pers. comm. cited in Robertson et al. 2002). In contrast, in urban areas of Melbourne, Growling Grass Frogs that had been marked and recaptured over several seasons dispersed no more than 0.5 km from tagged sites (Heard 2010).

Although a wetland may lie in a frog's dispersal range it may not be occupied because the habitat is unsuitable or the landscape between habitats is difficult to traverse. For example, Hamer et al. (2002a) reported that the probability of Green and Golden Bell Frogs occupying ponds in New South Wales decreased significantly when ponds were more than 50 m apart, even though radio-tracking and mark–recapture studies had shown that this species is capable of moving more than 500 m, sometimes in 24 hours (Hamer et al. 2008). This disparity may be because of habitat preferences, or because the landscape between habitats was inimical for dispersal.

Barriers to dispersal

Movements among habitats, however necessary for survival, also carry a high risk of mortality. When moving among habitats, frogs are vulnerable to predation and, because their skin is permeable to water, also desiccation (Wassens et al. 2008). In temperate landscapes the prevalence and diversity of amphibians declines where the distances among wetlands is large, where road densities are high, or where habitats are surrounded by agriculture or other intensive land uses (Rothermel and Semlitsch 2002, Parris 2006). All these factors decrease the capacity of amphibians to move between habitats and maintain metapopulations.

To minimise the risk of desiccation, movement often occurs during precipitation (Richter et al. 2001, Penchmann and Semlitsch 1986) or flooding (Wassens et al. 2008). To avoid predation and desiccation, some species preferentially move in closed-canopy forest habitats (Vasconcelos and Calhoun 2004). Open habitats such as agricultural fields increase the predation risk, and because temperatures are general higher there the risk of desiccation also increases (Rothermel and Semlitsch 2002). Decreasing forest cover within 2 km of wetlands has been associated with reductions in amphibian and reptile species richness (Findlay and Houlahan 1997). The American Toad (*Bufo americanus*) shows a strong preference for moving beneath forest canopy cover; a movement study by Rothermel and Semlitsch (2002) captured only 3 of 83 toads in open fields. This finding was surprising because adults are found in agricultural landscapes, suggesting that juveniles may be more prone to desiccation than adults.

Roads represent significant barriers to amphibian movement by increasing the risk of death and by exerting psychological or physical constraints on movement (Mader 1984, Gibbs 1998). Ehmann and Cogger (1985) estimated conservatively that 5.48 million reptiles and frogs were killed annually by traffic in Australia. Traffic intensity increases frog and toad kills and reduces population size, as measured by choruses (Fahrig et al. 1995). Increasing road density within 2 km of wetland boundaries has been correlated negatively with amphibian and reptile species richness in 30 wetlands in Ontario, Canada (Findlay and Houlahan 1997).

Significance of dispersal

Because mobility and habitat requirements vary among species, the relative importance of local environmental variables, distances between habitats, and the traversability of the surrounding landscape will vary in shaping the spatial distribution of the frog species. For example, Ficetola and Bernardi (2004) assessed the relationships between wetland features and isolation on the presence or absence of amphibian species in 84 wetlands in a human-dominated landscape in northern Italy. The key finding of their study was that wetland features and wetland isolation both structure amphibian communities. Environmental features that were correlated with amphibian presence were water depth, water permanence, sun exposure and fish presence. Rare species were affected by both environmental features and isolation, whereas common species were less affected by wetland features and were more mobile. In environments where the landscape is inimical to movement, vagile species are probably at greater risk than sedentary species. In other systems the habitat itself may be under threat, and in this case sedentary species are at greater risk than vagile species (Rothermel and Semlitsch 2002).

5.2 Waterbirds

Waterbirds are a diverse group of birds that utilise natural and artificial wetlands both fresh and saline as well as rivers, estuaries, embayments and open shores (Kingsford and Norman 2002). Waterbirds that occur in Victoria's wetlands are listed in Appendix 2 and include: waterfowl (ducks, swans, geese), herons, ibises, spoonbills, rails and coots, as well as pelicans, darters, cormorants and shorebirds (waders). One hundred and forty five waterbird species have been recorded in Victorian wetlands, excluding ocean-going (pelagic) seabirds and a small number of land birds associated with saltmarsh habitats (Appendix 2). Of the 145 species, 83 breed in Victoria and the remainder are regular migrants (29 species) or rare vagrants (29 species). Some of the migrants breed in New Zealand, but most of them travel longer distances to breed in Arctic or sub-Arctic regions of northern Asia or Alaska. Of the 145 species, 13 are mainly associated with coastal waters, 24 with coastal mudflats and beaches, 41 with mudflats or margins of coastal or inland wetlands, and 67 with various types of non-tidal wetland (R. Loyn, Arthur Rylah Institute of Environmental Research, pers. comm.).

Aerial counts of waterbirds in south-eastern Australia over three latitudes encompassing Victoria and the most southerly part of New South Wales show large annual variations in waterbird numbers, with total counts varying from under 20 000 to over 140 000 between 1983 and 2004 (Kingsford and Porter 2006). Habitat depletion has greatly reduced waterbird populations, and several species are classed as threatened (Appendix 2).

5.2.1 Habitat preferences

In comparison to other avian species, populations of waterbirds are characterised by their frequent utilisation of multiple habitats over varying spatial scales to moult, roost, breed and forage, including wetlands, rivers and estuaries (Haig et al. 1998, Kingsford and Norman 2002). Wetland water regimes strongly influence waterbird populations. Floods trigger breeding in many species, and wetland systems that are flooded after a dry period support large numbers of waterbirds compared to permanently flooded sites (Kingsford and Norman 2002, Kingsford and Auld 2005).

Some waterbirds that occur in Victoria are common and familiar birds that occupy a range of habitats (e.g. Pacific Black Duck, Masked Lapwing and White-faced Heron). Others have more specialised requirements and only occupy habitats with certain levels of aquatic vegetation cover and salinity. Some of the less common species tend to be associated with large and complex wetlands that provide a range of habitat resources.

5.2.2 Movement

Waterbirds vary considerably in their habitat requirements and the scale, pattern and frequency of movement among habitat patches (Appendix 2). Waterbirds that are endemic to Australia are typically nomadic (Roshier et al. 2001, Chambers and Loyn 2005). A few species may be classed as somewhat sedentary (e.g. Australian Wood Duck, Chestnut Teal, Australian Shelduck and Purple Swamphen) (Pringle 1985, Ramsey et al. 2010), but even they will sometimes move long distances in response to changes in habitat. For example, Australian Wood Ducks prefer treed habitats and tend to be sedentary. Frith (1959) found that about 75% of banded Wood Ducks moved less than 80 km from the banding location and only 10% moved more than 320 km (Figure 2). In contrast, Grey Teal utilised most wetland types and were highly dispersive, with more than 30% of banded birds recovered farther than 320 km from the banding location, and some travelling an average of 180 km/day (Frith 1959).

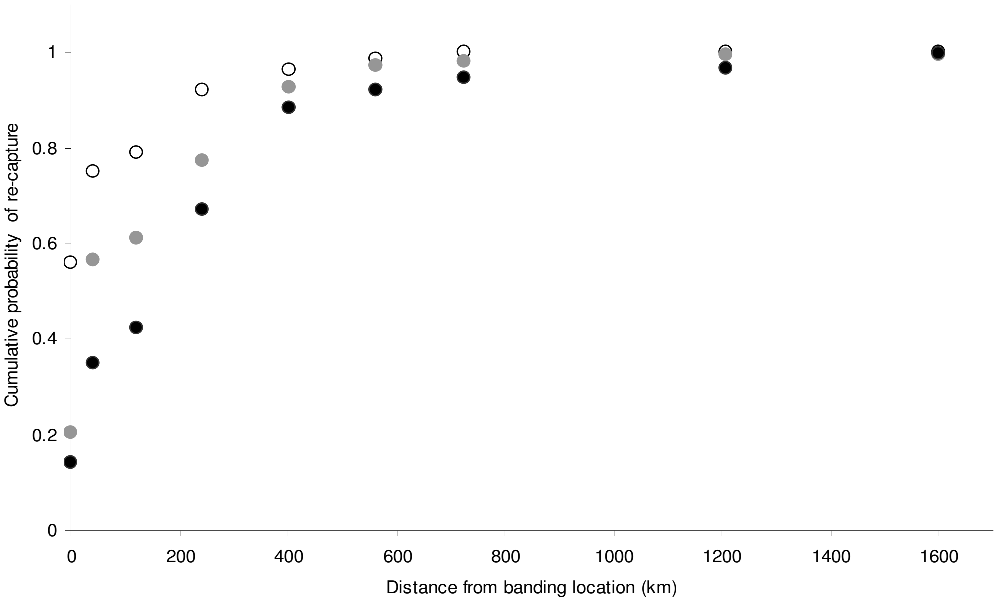

Figure 2. Cumulative probability of recapture as a function of distance from banding location for Grey Teal (black circles), Pacific Black Duck (grey circles) and Wood Duck (white circles). Data based on recaptures of banded birds by Frith (1959).

In Australia, changes in resource availability as wetlands flood and dry strongly influence waterbird dispersal (Kingsford and Norman 2002, Chambers and Loyn 2005). A regular seasonal pattern of movement takes place in response to changes in habitat availability in some species. For example, in summer, many waterbird species in inland south-eastern Australia become concentrated in large swamps as smaller ones dry. As densities increase, a portion of the population disperses. Although dispersal occurs in all directions, most follow the Murray River and its tributaries to South Australia and Victoria and return inland in winter (Frith 1977).

The geographical arrangement of wetlands in the landscape and the dispersal capacity of waterbirds influence the dynamics of waterbird populations. For example, a study of waterbirds in 30 marshes in Iowa, USA, found that clustered wetlands contained more species than isolated wetlands, and the total wetland area within 5 km of each wetland explained the most variation (42%) in species richness among wetlands (Browne and Dinsmore 1986). The clustering of wetlands probably supported higher species richness for two reasons. Firstly, clustering of wetlands of various sizes produces a mosaic of diverse habitats both spatially and temporally as habitats fill and dry at different rates. For example, Pacific Black Duck and other species with limited salt tolerance probably only forage in saline wetlands when freshwater wetlands are accessible nearby (Kingsford and Norman 2002, Loyn et al. 2006). Secondly, the proximity of diverse habitat types allows a wider range of bird species, differing in habitat requirements and dispersal capacity, to utilise them.

On a larger spatial scale, Roshier et al. (2001) examined the availability of wetlands for waterbirds in the Lake Eyre Basin of central Australia, where there are thousands of temporary wetlands. Although the availability of wetland habitats in this arid region is highly variable at small spatial scales, at larger spatial scales habitat availability increases as wetlands fed by different rivers fill and dry at different rates creating a mosaic of wetlands that hold water at different times. This increases the availability of habitats through time and may provide core habitat for waterbirds capable of dispersing the long distances that separate individual wetlands. Highly nomadic waterbirds are able to use habitat patches separated by hundreds of kilometres and are therefore more resilient to habitat loss than more sedentary species.

Although waterbirds are capable of dispersing long distances, movement can be restricted by breeding or moulting. Some waterbirds return to the same breeding or moulting sites each year, producing a narrower pattern of movement than suggested by their mobility (Kingsford and Norman 2002). During breeding, the need to feed and protect flightless juveniles imposes a reliance on nearby wetlands for foraging (Bryan and Coulter 1987). For example, in North America the foraging flights of nesting adults of the Western Great Egret (*Casmerodius albus*), Snowy Egret (*Egretta thula*), Tricolored Heron (*Egretta tricolor*) and American White Ibis (*Eudociumus albus*) were all within 30 km of nesting sites (Smith 1995). Where foraging flights exceed 25-30 km in length breeding success has been found to decline in several ciconiiform wading birds (see Smith 1995). Breeding can also limit movement patterns if juveniles have more specific habitat requirements than adults. Nasal glands that secrete salts and help maintain salt regulation are not fully developed in juvenile ducks (Riggert 1977), so access to freshwater sources is required, restricting habitat utilisation (Halse 1987). These examples illustrate that it is during these critical life stages that the patterning of wetland resources in the landscape probably exerts its greatest influence on waterbird populations.

Although there is some information about the dispersal capacity of waterbirds over large scales, there is little information on the frequencies or patterns of waterbird movements between wetlands over small spatial and temporal scales. Knowledge of these finer-scale movements, particularly during critical life stages, is needed to identify the landscapes elements required to sustain waterbird populations. Haig et al. (1998) has suggested that critical information gaps exist in understanding seasonal movements between multiple sites, including:

- how well waterbirds survey habitats before breeding sites are selected
- whether early nest failure prompts movement to new sites to re-nest
- utilisation of foraging areas away from nest sites
- utilisation of brood rearing habitat away from the nest site
- moult migration
- movement of young adults to access age-specific resources
- movement within migration and winter sites.

The high level of diversity in movement patterns and habitat requirements of waterbirds means that assessing landscape elements that optimise waterbird populations is complex. Some general principles that should be considered are outlined below:

- wetting and drying cycles are important in providing food resources for waterbirds
- floods of sufficient size and duration are needed to trigger waterbird breeding
- mosaics of wetlands that fill and dry over different cycles increase habitat availability over time
- the influence of temporal and spatial patterns of wetland types in the landscape probably exert their greatest effects on waterbird populations during critical life stages (breeding and moulting), when dispersal capacity is more limited and resource requirements are more specialised
- for waterbirds with more limited capacity to migrate large distances, cluster of wetlands separated by a small distance are likely to be beneficial
- temporary habitats can provide stepping stones that facilitate movement among habitats but also have the potential to trap less mobile waterbirds when they dry

5.3 Freshwater fish

In Victoria, 32 native fish species frequently occupy wetlands, and many of those prefer still or slow-flowing water (Appendix 3). Almost half of the species are listed as threatened or vulnerable (Appendix 3). Several species are diadromous and migrate between freshwater and marine habitats to complete their life cycles. A number of introduced species also utilise wetland habitats, including Common Carp (*Cyprinus carpio*), Goldfish (*Carassius auratus*), Weather Loach (*Misgurnus angullicaudatus*), Mosquitofish (*Gambusia holbrooki*), Redfin Perch (*Perca fluviatilis*) and Tench (*Inca tinca*). Brown Trout (*Salmo trutta*) and Rainbow Trout (*Oncorhynchus mykiss*) are introduced species that mainly occur in lakes and farm dams. Many introduced fish are detrimental to native fish populations because of predation, competition for resources, habitat modification and the introduction of diseases and parasites (Crowl et al. 1992, Rowe et al. 2008). Understanding the processes that govern fish movement between freshwater habitats will inform the management of native species and identify mechanisms for controlling the spread of introduced species.

5.3.1 Habitat preferences

A variety of fish species utilise wetland habitats as nursery grounds, to access food resources and spawn, and as refuges from predation or competition (Poisal and Crivelli 1997). The type of wetland habitat varies from permanent to temporary and fresh to saline, and includes billabongs, anabranches, lakes, marshes and floodplains (Humphries et al. 1999).

5.3.2 Movement

Exploratory movements in waterways are often undertaken by fish in search of alternative habitat, but the pattern, scale and constraints of fish movements among wetlands is not well studied. Movement abilities differ among fish species and will influence community assemblages and species distributions in the landscape. For example, the propensity for dispersal varies among fish species with some species being sedentary and others dispersive. Large bodied fish are generally able to disperse over greater distances than small bodied fish, but as water depth must be at least 1.5 x body depth for fish to swim, shallow water can present a barrier to movement in large fish (Lucus and Baras 2001). Conversely, small fish can disperse in shallow water but may avoid deep water as the risk of predation is higher (Harvey and Stewart 1991).

Fish movements in a network of seasonal wetlands and a lake in Florida, USA were studied for over a year by Hohausova et al. (2010). The study found dispersal routes varied with the size and species of fish, and both hydrology and human disturbances influenced movement patterns. The depth of water connecting habitats was an important factor influencing dispersal, with shallow water favouring the dispersal of smaller bodied fish (e.g. Mosquitofish) which dispersed farther than large bodied fish. Dispersal distances of fish varied from 0.7 to 4 km.

In temporary wetlands, where fish populations undergo frequent local extinctions associated with drying, the ability of species to recolonise these systems is a key determinant of community assemblage structure (Snodgrass et al. 1996). The role of connectivity in structuring fish assemblages in 24 temporary wetlands in Florida was examined by Baber et al. (2002). This study found that 71% of the study wetlands were colonised by fish. The most common species was the Mosquitofish, which inhabited all wetlands where fish were recorded. Fish were absent from wetlands that were:

- isolated from permanent water bodies that provided sources of fish for recolonisation
- had shorter wetting cycles (hydroperiods) that imposed frequent local extinctions
- were surrounded by a large proportion of higher land that confines water and limits hydrological connections to other waterbodies.

Wetlands with diverse fish assemblages were connected to permanent water bodies and also positioned in a mosaic of wetlands. Deeper wetlands with a long hydroperiod also supported more diverse fish communities. Other studies similarly report that fish diversity in temporary wetlands is enhanced by connectivity to other waterbodies and the number of wetlands in the landscape

(Snodgrass et al. 1996, Taylor 1997). Although hydrological connectivity was found to increase species diversity, Mosquitofish were also prevalent in hydrologically connected systems. In Australia, where the Mosquitofish is invasive and has been implicated in the decline of native fish, hydrologic connectivity in regions where this species (or other introduced species) occur may have negative effects on fish diversity (Rowe et al. 2008).

River–floodplain movement — The ability of fish to migrate to floodplain wetlands is influenced by a variety of factors, including hydroperiod, distance, elevation gradient and the presence of water control structures such as canals, levees, and dams (Hohausova et al. 2010). In Australia, 50% of floodplain wetlands on developed rivers may be isolated from their source rivers (Kingsford 2000), presenting limitations on fish movement and local persistence. In some cases, structures such as channels, culverts and weirs can artificially connect wetlands, providing either permanent or periodic access depending on the type and method of operation (Beesley et al. 2011).

Although many species of fish occupy both streams and wetland habitats, the significance of river–floodplain connections in maintaining fish populations is still not well understood in Australia. The flood pulse concept (FPC) proposed by Junk et al. (1989) posits that optimal conditions for fish recruitment occurs when floodplain inundation coincides with warmer temperatures. As some fish species spawn in the warmer months, floods that coincide with warmer temperatures allow larvae and juveniles to access and exploit plentiful resources available on productive floodplains. The FPC is well supported empirically in tropical regions of the world, where flood pulses regularly coincide with warmer temperatures (Junk et al. 1989; Humphries et al. 1999).

In Australia, however, temporal variability in the flood pulse can uncouple floodplain inundation and warmer temperatures, making the significance of river–floodplain linkages to fish recruitment less clear (Humphries et al. 1999; King et al. 2003). For example, in the unregulated Ovens River in Victoria, native fish failed to recruit in inundated floodplains, probably because temperature thresholds for spawning were not synchronised with floods in this region; but Common Carp, which are capable of spawning at lower temperatures, successfully recruited (King et al. 2003). Beesley et al. (2011) reported that the colonising potential, recruitment success and fish abundance in floodplain wetlands in the Murray–Darling Basin was influenced by the source (river or irrigation channel) and mode of water delivery to floodplain (e.g. pipes, pumps, regulated and unregulated channels). Fish responses were poor when water was sourced from irrigation channels and pumped into floodplain wetlands.

Movements across catchments — For most freshwater fish, dispersal between catchments is constrained by the inability to traverse terrestrial or estuarine environments (Wong et al. 2004). Some salt-tolerant species may successfully cross estuaries to reach different catchments, but for most species seawater represents a physiological barrier to dispersal. Genetic studies have shown that there are higher levels of genetic differentiation between populations of freshwater fish than between populations of estuarine or marine fish, supporting the notion that dispersal is more constrained in freshwater fish (Gyllensten 1985, Ward et al. 1994). However, hydrologic connections between drainages can occur when floods connect waterways, producing plumes of freshwater in the sea that permit temporary passage of freshwater species to other catchments (Grimes and Kingsford 1996, Pusey and Kennard 1996). Fish passage to other catchments can change over geological time-frames as rivers shift coarse (McGlashan and Hughes 2000) and as sea levels change (Bermingham and Avise 1986).

The Pacific Blue-eye provides one example of connectivity over a large spatial scale. It is a widespread, salt-tolerant and putatively vagile species that inhabits coastal drainages across much of eastern Australia. It occupies a range of rivers and wetland habitats, from rainforest streams to estuaries. Genetic studies revealed that northern and southern populations along the east coast of Australia are genetically divergent, probably because of a dry corridor in mid-coastal Queensland (Wong et al 2004). At the southern end of the species range, populations were genetically more similar among drainages, suggesting that floods may be important in maintaining connectivity among populations.

5.4 Aquatic invertebrates

Aquatic invertebrates disperse to new sites either actively or passively. Active dispersal is mostly limited to winged insects, although some molluscs, flightless beetles and crayfish are capable of moving small distances overland, although most require wet terrain (Bilton et al. 2001; see Table 1). Wingless taxa disperse when small dormant eggs or cysts are carried by wind, water or animal vectors.

Table 1. Classification of freshwater invertebrate taxa as active dispersers or as passive dispersers (adapted from Bilton et al. 2001 and Verberk et al. 2008). Passively dispersed taxa (order or family) rely on vectors such as wind, water and animals to dispersal dormant life stages (typically eggs or asexual propagules) that are tolerant of environmental extremes and are usually capable of asexual reproduction or parthenogenesis.

Active dispersers	Passive dispersers
Strong flyers	Porifera (sponges)
Coleoptera (beetles)	Rotifera (wheel animals)
Dytiscidae (diving beetles)	Bryozoa (moss animals)
Hemiptera (true bugs)	Cladocera (water fleas)
Gerridae (water-striders)	Copepoda
Corixidae (water-boatmen)	Branchiopoda
Diptera (true flies)	Mollusca
Culicidae (mosquitoes)	
Chaoboridae (phantom midges)	
Chironomidae (non-biting midges)	
Odonata (dragonflies and damselflies)	
Lepidoptera (butterflies, moths)	
Weak flyers	
Ephemeroptera (mayflies)	
Trichoptera (caddisflies)	

5.4.1 Active dispersal in winged invertebrates

Scale of dispersal

A number of aquatic invertebrate taxa, including mosquitoes (Culicidae), dragonflies and damselflies (Odonata), have winged adult stages that can actively dispersal (Bilton et al. 2001). The capacity for flight is highly variable (Table 1). Some taxa, such as butterflies and moths (Lepidoptera) and dragonflies, have a remarkable capacity for flight and may travel hundreds or thousands of kilometres (Williams 1957, Feng et al. 2006, Wikelski et al. 2006). The dragonfly *Pantala flavescens* migrates seasonally over the sea from China to Beihuang Island and has been detected with radar at altitudes of 200–500 m, flying continuously at speeds of 5–11 m/s for up to 10 hours and dispersing up to 400 km in a single flight (Feng et al. 2006). In Australia, the Bogong Moth (*Argotis infusa*) migrates up to 1000 km from the inland plains of eastern Australia to the Snowy Mountains of New South Wales and the Victorian Alps, where they aestivate in rock crevices (Green et al. 2001). Even in these more mobile groups the dispersal capacity is variable. Substantially shorter dispersal distances — over 5 km and less than 1 km — have been reported in adult mosquitoes (Service 1993, Bilton et al. 2001).

Although winged taxa are able to disperse through active flight, it is often facilitated by winds (Dingle 1972). Many winged taxa probably utilise high altitude winds to increase the distances they disperse (Dingle 1972). Moths migrate above the temperature inversion layer, where wind speeds tend to exceed the moth's flight speed and dispersal is largely passive (Drake and Farrow 1988). Weak flyers such as stoneflies, mayflies, caddisflies and some members of the Diptera also probably disperse largely as aerial plankton (Table 1).

The river network provides an important conduit for the movement of invertebrates and inturn influences movement among floodplain wetlands. The dendritic structure of river systems can impose constraints on dispersal with rates of dispersal declining at higher levels in the stream hierarchy:

dispersal within stream > among streams > among subcatchments > among catchments

For taxa with a strong flight capacity, lateral movement from the river across the terrestrial landscape can permit dispersal to different watercourses and associated wetlands. Movement upstream along a watercourse may also allow some individuals to move from one headwater stream to another, and hence to a different watercourse (Bilton et al. 2001). Studies examining genetic differentiation of aquatic insect populations from different positions in the stream hierarchy conclude that many winged aquatic insects are able to disperse among river catchments (Kelly et al. 2001, Miller et al. 2002, Hughes 2007).

Triggers for dispersal

Winged insects are thought to disperse in order to escape unsuitable conditions and colonise new sites. Flight duration, and hence the potential for dispersal, is greatest soon after the moult to adulthood and declines thereafter. In females this is because the stimulus to disperse occurs before egg production (oogenesis) and is lost during reproduction. In some taxa such as the Heteroptera, energy for reproduction is harnessed through the histolysis of the flight muscles, a phenomenon referred to the oogensis-flight syndrome (Johnson 1963). In contrast to females, dispersal in males is not consistently linked to reproduction (Johnson 1963).

Dispersal can be triggered by environmental conditions. In the Heteroptera and Coleoptera, increasing temperature and falling water levels trigger dispersal (Velasco et al. 1998 cited in Bilton et al. 2001). Environmental conditions may also control dispersal indirectly by influencing development. As sexual maturation inhibits migratory flight (at least in females), environmental conditions that favour rapid development, such as long day length, low population density and ample food, will tend to shorten the time over which migratory flights occur. The influence of habitat condition on migration is expressed in some taxa through wing dimorphism, with a higher frequency of wingless forms occurring under stable conditions (Bilton et al. 2001).

Dingle (1972) reported that take-off on migratory flights requires suitable body temperature, sunshine and wind. During take-off, insects exhibit a strong positive response to the ultraviolet light of the sky, but during settlement the cue is replaced by a positive response to the green-yellow wavelengths of the surface (Johnson 1963). In contrast, others studies report that migratory flights commonly take place at night in larger insects and are usually initiated at dusk. Nocturnal migration may be favoured to avoid predation or heat stress, or because aerodynamic conditions are more favourable at this time (Drake and Farrow 1988, Feng et al. 2006).

Barriers to dispersal

In some cases geographic boundaries or limited flight capacity constrain dispersal. Although examples for wetland taxa are lacking, studies of stream-dwelling invertebrates illustrate the potential for these variables to limit dispersal. For the stream-dwelling stonefly *Yoraperla brevis*, which occupies deep rocky canyons, movement between rivers is likely to be prevented by large cliffs that bound rivers. This geographical feature probably explains the higher levels of genetic differentiation found in populations of *Y. brevis* among rivers than among sites within rivers (Hughes 2007).

The midge *Elporia barnardi* has a very limited ability for flight and also shows high levels of genetic differentiation among populations suggesting restricted dispersal. At high altitudes, low air temperatures most likely restrict flight in stoneflies, and this may limit dispersal (Brittain 1990). In

Australia the stonefly *Thaumatoperla flaveola*, which lives at high altitudes, has lost the capacity for flight (Brittain 1990, Pettigrove 1991).

5.4.2 Passive dispersal of invertebrates

Aquatic invertebrates that lack the mobility provided by wings, move among habitats by the passive dispersal of their resting stages by wind, water or animal vectors. Many aquatic invertebrates have small dormant stages that are resistant to desiccation and temperature extremes and reduce the risk of mortality associated with dispersal. For example, both the dormant eggs of cladocerans (water fleas) and the asexual propagules (statoblasts) of bryozoans (moss animals) are enclosed by chitinous plates that provide physical protection and resistance to desiccation. Dormancy can last for several years; for example, statoblasts of the bryozoan *Lophopodella* can germinate after more than four years of drying, and tardigrades (water-bears) are capable of extended hibernation (cryobiosis) as adults.

Many resting stages have adaptations to facilitate vector mediated dispersal. Spines, hooks and protective casings facilitate animal mediated dispersal (Bilton et al. 2001), whereas buoyant propagules enhance dispersal in water. Apart from their small size and tolerance to desiccation, there appears to be no elaborate adaptation for invertebrate propagules to disperse in wind, unlike plant seeds. The timing of propagule release may be synchronised to match the availability of a dispersal vector. For example, Okamura and Hatton-Ellis (1995) reported that propagule release by Fairy Shrimps coincides with waterbird migration. In some cases the morphological characteristics of propagules are plastic. For example, the freshwater bryozoan *Plumatella repens* produces sessoblasts that attach to the colony and prevent dispersal when the colony is small; but when the colony is large, floating statoblasts are produced that facilitate dispersal and provide a mechanism to escape resource limitation (Karlson 1992).

Direct measurements of the dispersal potential of aquatic invertebrate have been assessed by intercepting propagules carried by vectors, observing the colonisation of experimental ponds by invertebrates, or by using genetic markers to infer dispersal. Genetic markers provide information about spatial patterns of dispersal, but tend to underestimate dispersal because they only capture dispersal events that have resulted in colonisation. Moreover, genetic markers do not provide information about the dispersal pathway.

Wind-mediated dispersal

Only a small number of studies have attempted to assess the types of species carried by wind or the distances they disperse. The data so far suggests that wind can disperse many aquatic invertebrate species but is probably effective only over small spatial scales. For example, Cáceres and Soluk (2002) found that 65% of the invertebrate taxa present in source ponds colonised experimental ponds 10–200 m away in two years. In total, 26 taxa colonised the experimental pond, including rotifers (13 taxa), copepods (2 taxa), cladocera (7 taxa) and 4 other taxa. A similar experiment by Cohen and Shurin (2003) found that distances of up to 60 m had no effect on the ability of invertebrates to colonise experimental ponds. Vanschoenwinkel et al. (2008) intercepted propagules of 17 taxa using wind socks placed around temporary rock pools on a mountaintop in South Africa, and found that the number of propagules declined significantly 10–20 m from the rock pools. Although these studies suggest that dispersal distances are small, they may be sufficient to permit dispersal over longer distances by a stepping stone process.

Studies that quantify aerial dispersal over longer distances are needed to develop a clearer understanding of the spatial scales over which wind may disperse propagules. In particular, convective currents may be an important mechanism for the dispersal of invertebrates. An understanding of propagule traits may help identify invertebrate propagules that are likely to be lifted by convective air currents and dispersed over large distances. The potential for long-range aerial dispersal, however, is likely to be lower for invertebrate propagules than plant seeds because they lack adaptations for flight observed in plants. Moreover, plant seeds are often released above the water or soil surface, sometimes many metres above it, whereas invertebrate propagules must be lifted from the water surface or from exposed soil by the wind. Although invertebrate propagules may lack adaptations for wind dispersal, adaptation for dispersal by water and animal vectors are evident.

Water-mediated dispersal

In freshwater systems, drift is a common means of dispersal downstream (Bilton et al. 2001), and many resting egg stages of invertebrates float when reflooded (Van de Meutter et al. 2006). The significance of water corridors in the dispersal of invertebrates was demonstrated by Michels et al. (2001), who found that genetic distances among populations of the water flea *Daphnia ambigua* matched stream distances between populations more than geographic (straight line) distances. Havel et al. (2002) used patterns in the invasion of the Missouri lakes by *Daphnia lumholtzi* to assess dispersal distances. Invasion probability was modelled as a function of local site characteristics and distance to all known source populations. The model found that site characteristics were the most significant predictors, but dispersal along with local site condition improved the fit. The number of propagules was estimated to decline sharply 20–30 km from a source and remained relatively constant at greater distances.

Rates of dispersal in water can vary among invertebrate species, and diurnally in some species. Van de Meutter et al. (2006) found that rates of dispersal between interconnected pools differed between taxa in the following pattern:

Chironomidae > Baetidae and Physidae > all other families

where 'all other families' included Acroloxidae, Coenagrionidae, Corixidae, Culicidae, Dixidae, Limnoiidae and Pyralidae. In the Choaboridae and Chironomidae, dispersal rates were greater at night than during the day.

Animal-mediated dispersal

A variety of animals have been shown to mediate the dispersal of invertebrates, including fish, mammals, amphibians, waterbirds, and aquatic insects that have been parasitised (Green et al. 2002b, Green and Sanchez 2006, Pollux et al. 2006, Green et al. 2008).Waterbirds are probably the most important animal vector, and certainly the most studied (Figeurola and Green 2002a, Figeurola and Green 2002b, Green et al. 2002a, Green et al. 2002b, Figeurola et al. 2003, Figuerola et al. 2005, Green et al. 2005, Green and Sanchez 2006, Green et al. 2008).

Waterbirds disperse invertebrates propagules that become attached to the feet, feathers or bill, or are consumed and survive gut passage. Invertebrate propagules found to survive gut passage in waterbirds include: Brachiopoda (eggs), Cladocera (epphipia), Bryozoa (statoblasts) and Corixidae (eggs) (Figeurola et al. 2003; Green et al. 2008,). Very few studies have assessed external dispersal, but Croll and Holmes (1982) recovered zooplankton eggs as well as algae and plant seeds from waterbirds feathers.

In Australia only two studies (Green et al. 2008, Raulings et al. 2011) have examined the role of waterbirds in dispersing aquatic organisms, and only Green et al. (2008) assessed the potential of waterbirds to disperse invertebrates. They measured the number, type and viability of invertebrate propagules in fresh faecal samples collected from Grey Teals (*Anas gracilis*), Eurasian Coots (*Fulica atra*) and Black Swans (*Cygnus atratus*) and one Australian Pelican (*Pelecanus conspicillatus*). Samples were collected in temporary to permanent wetlands of the Macquarie Marshes in New South Wales. The study found that 84% of the 71 samples tested contained intact invertebrates propagules, and across all samples a total of 759 propagules were detected. Ostracod eggs were dominant and represented 75% of the recovered propagules.

Although the number of recoverable propagules from waterbirds is small, and the number of viable propagules is even smaller, the abundance and frequency of waterbird movement among habitats suggests that waterbirds play an important role in dispersal (Raulings et al. 2011). Waterbirds are particularly significant vectors as they can mediate the dispersal of organisms to hydrologically isolated sites over large spatial scales.

Evidence for dispersal

The cosmopolitan distribution of many zooplankton species (e.g. cladocerans, copepods and rotifers) is often used to support the notion that dispersal is common and widespread (De Meester et al. 2002). This claim has been contested by Jenkins and Underwood (1998) who point out that many zooplankton species do not have cosmopolitan distributions. Bohonak and Jenkins (2003) claimed that taxonomic revisions have shown that in some cases what was considered to be a single species with a widespread distribution has proven to be many cryptic species, each with a more limited distribution. Although this suggests that long-distance dispersal in invertebrates may not be as common as once thought, genetic studies do demonstrated the significance of waterbirds in the dispersal of invertebrates. Waterbird movements (based on band recovery data) explain a significant portion of gene flow occurring between North American populations of the water fleas *Daphnia ambigua* and *D. laevis* (Taylor et al. 1998, Figuerola et al. 2005) and the bryozoan *Cristatella muceodo* (Freeland et al. 2000). However, waterbird movement does not contribute to gene flow in *Sida crystallina*, a daphnid with propagules that are more susceptible to desiccation (Figuerola et al. 2005).

5.5 Wetland plants

Wind, water and waterbirds are the most important natural dispersal pathways for wetland plant seeds and vegetative fragments (collectively propagules). The dispersal pathways available to plants are determined by a range of factors, including:

- plant habit and morphology
- propagule traits (e.g. buoyancy)
- the availability of dispersal vectors.

For example, submerged and floating plant species release propagules directly into the water column and are largely dependent on water and waterbirds for dispersal. Emergent and riparian vegetation release seeds into the air, and therefore have the potential to disperse initially by wind and subsequently by water and waterbirds. Wind, water and waterbirds are likely to differ in the suites of species they transport and the distance, time and direction of propagule movement. Each of these vectors will therefore produce a different temporal and spatial pattern of dispersal in the landscape. The spatial patterning of dispersal varies over time as seeds are released, habitats flood, winds strengthen and abate, and waterbirds vary in abundance.

5.5.1 Wind-mediated dispersal

Wind is an important dispersal pathway for wetland plants as it is a widely available vector and has the potential to transport seeds to hydrologically isolated sites and to upstream wetlands over long distances (Soon 2006). A high proportion of wetland species have adaptation to disperse in wind, particularly species occurring in rainwater or groundwater fed wetlands that lack connections to other aquatic habitats via surface water flows (37–46% of species) (Soons 2006).

Propagules are dispersed by wind in two ways: (1) very light seeds can be uplifted by thermal currents to high altitudes and dispersed over long distances; and (2) under turbulent conditions seeds can be uplifted and carried in the wind (Soons 2006). The distance propagules disperse in wind is also influenced by the height of seed release and seed traits. Seeds that are released high above the ground and are very small and light or have specialised adaptation for flight, such as plumes or wings, remain airborne for longer and disperse farther (Tackenberg 2003, Soons 2006). The falling speed of seeds in still air (once they have reached a constant falling speed) is referred to as their terminal velocity and is a good indicator of how well they are adapted for flight; that is, the lower the terminal velocity, the longer the seed will remain airborne. Soons (2006) grouped plants into three broad wind-dispersal categories based on seed terminal velocities.

Seed with terminal velocities below 0.3 m/s

The first dispersal category represents seeds that fall very slowly — at terminal velocities below 0.3 m/s. This group has the greatest potential for long-distance dispersal in wind because their seeds can be lifted by convective currents or wind turbulence, extending their dispersal range to many kilometres (Wright et al. 2000, Tackenberg 2003, Soons 2006). The widely distributed tall emergent aquatic plants, *Typha* spp. and *Phragmites* spp., which occur in Victoria, have seeds with terminal velocities of 0.14 and 0.21 m/s (Soons 2006, van Diggelen 2006). Models simulating the spread of *Typha angustifolia* and *Phragmites australis* via wind from source populations of 576 m^2 predicted they could spread over 83 hectares and 2.6 hectares, respectively. The greater spread of *T. angustifolia* results from its exceptional seed production — 2.6 million seeds/m^2, compared with 18 000 seeds/m^2 in *P. australis* (van Diggelen 2006). Genetic analysis of *P. australis* populations revealed little genetic differentiation between populations from different water drainages, suggesting frequent wind-mediated dispersal (Tomáš and Zdenka 2009). In south-eastern Victoria, genetic structuring of *P. australis* has been detected at a separation of 20 km (L. James, Royal Botanic Gardens Melbourne, pers. comm.), which again indicates long-distance seed and/or pollen dispersal.

Seed with terminal velocities **of** *0.3–2 m/s*

The second dispersal category identified by Soons (2006) represents plants with terminal velocities of 0.3–2 m/s. These seeds are too heavy to be lifted by convective currents but may be carried long distances by turbulent winds during storms. The dispersal distance varies from tens of metres to several kilometres, depending on the terminal velocity, seed release height and wind speed.

Seed with terminal velocities above 2 m/s

In the third dispersal category, plants have heavy seeds with terminal velocities above 2 m/s. These plants are not adapted for wind dispersal, and seed is deposited close the plant.

Data on seed terminal velocities for Australian aquatic plants are limited, although Laurent (2009) measured falling speed (m/s) over 3.9 metres for several native and introduced Victorian species associated with wetlands (Table 2). For some seeds a constant falling rate may not be reached over this distance and rates using this approach are considered less accurate that measures of terminal velocity.

Although wind is an important dispersal pathway for wetland plants the size of the source population is an important driver in determining the effectiveness of wind as a dispersal vector. When plant populations are large, more seeds are dispersing, and this increases the number of individuals that reach more distant sites. For example, dispersal models predict that only 1 in 10 000 seeds of *Hypochaeris radicata* (a common weed in Australia) would disperse 2.4 km (Soons 2003). This plant produces about 380 seed per plant (Hovenden et al. 2007), so only a small population of about 30 plants is sufficient for at least one seed to disperse this far.

Even when seed abundance is high, the scale and pattern of dispersal are governed by wind speed and direction, the prevalence of thermals, and the spatial arrangement of aquatic habitats in the landscape. Wind dispersal will be enhanced when habitats experience strong winds and are close together and aligned with the direction of the prevailing wind. For example, where the prevailing winds are from the east or west, wetlands that are aligned along a west–east axis will be more strongly connected by wind dispersal than those aligned along a north–south axis. Habitats with the longest axis perpendicular to the prevailing wind will intercept more propagules than wetlands that have the longest axis parallel to the prevailing wind. The nature of the surrounding landscape can also impinge on the capacity for wind dispersal. For example, tall neighbouring vegetation has been shown to reduce the transport of wind dispersed seed (Davies and Shely 2007).

Table 2. Dispersal categories based on falling speeds for some native and introduced plant species associated with wetlands. Data from Laurent et al. 2009 are based on falling speed (m/s) over 3.9 m. Data from Soons et al. (2006) represent terminal velocities.

Falling speed	Species	Reference
< 0.3 m/s	*Typha latifolia*	Soons et al. 2006
	Typha angustifolia	Soons et al. 2006
	Phragmites australis	Soons et al. 2006
0.3–2 m/s	*Cassinia longifolia*	Laurent 2009
	Crassula peduncularis	Laurent 2009
	Melaleuca ericifolia	Laurent 2009
	Holcus lanatus	Soons et al. 2006
	Isolepis inundata	Laurent 2009
	Anthoxanthum odoratum	Soons et al. 2006
	Alisma plantago-aquatica	Laurent 2009
> 2 m/s	*Bidens tripartita*	Laurent 2009
	Rumex crispus	Laurent 2009
	Ranunculus sceleratus	Laurent 2009
	Eucalyptus tereticornis	Laurent 2009
	Persicaria decipiens	Laurent 2009
	Eleocharis acuta	Laurent 2009
	Plantago lanceolata	Laurent 2009
	Potamogeton ochreatus	Laurent 2009
	Acacia mearnsii	Laurent 2009
	Triglochin procerum	Laurent 2009

There have been very few attempts to quantify seed dispersal by wind in aquatic habitats. Neff and Baldwin (2005) intercepted wind dispersed seed arriving in a coastal marsh over seven months. Thirty nine species were captured over the study with an average of 18 seeds/m^2 per month; temporal changes in the seed catch were not reported. Morris et al. (2011) assessed the arrival of seeds by wind into wetlands in south-eastern Australia and found that seed dispersal peaked in February. At this time seed abundance was dominated by the native grass *Lachnagrostis filiformis*, with over 28 000 seedlings germinating from 83 samples. A total of 379 seeds from 33 other taxa germinated.

5.5.2 Water-mediated dispersal

Water can disperse vast numbers of plant propagules, and many plant species in river and floodplain systems and contributes to local species richness (Schneider and Sharitz 1988, Boedeltje et al. 2004, Merritt and Wohl 2006). Seeds of many wetland species remain buoyant for extended periods — about 40% of the 50 species tested by van den Broek et al. (2005) floated for more than 70 days, increasing their potential for long-distance dispersal. Dispersal in water is also directed, in that it deposits propagules at wet sites that favour establishment (How and Smallwood 1982, Soons 2006).

Directionality of dispersal

In rivers, habitat patches are connected longitudinally by the movement of plant propagules downstream. This unidirectional movement implies that downstream populations will have greater genetic diversity than populations upstream, but support for this hypothesis is equivocal. Some studies have found higher genetic diversity in downstream populations compared with upstream populations (Gornall et al. 1998, Liu et al. 2006), but other studies have not (Tero et al. 2003, Prentis et. al. 2004, Chen et al. 2007).

Sites are connected laterally when propagules move between the river and the floodplain, but in sloping areas the lateral spreading of water flow is limited and dispersal of plant propagules can be constrained in water drainages at very small spatial scales. The isolating effect of slope was demonstrated in populations of the stream lily *Helmholtzia glaberrima* in south-eastern Queensland, which were genetically isolated between micro-drainages only 10–15 m apart (Prentis and Mather 2007).

Dispersal distances

The distances propagules travel in water increases greatly with increasing steam velocity (Anderson et al. 2000, Riis and Sand-Jensen 2006, Groves et al. 2009) and the duration of propagule buoyancy (Middleton 1999, Boedeltje et al. 2004). Stream features such as sinuosity and woody debris can retain seeds and reduce dispersal distances. Floods are important dispersal events because they flush seeds that have accumulated in vegetation into streams, and they can fragment and uproot plants that will then be dispersed in floodwaters to distant sites. Floods may disperse seeds vast distance in rivers. For example, Nilsson et al. (1991) calculated that seeds could travel over 90 km/day along a river stretch during spring floods in northern Sweden. Large floods were thought to have resulted in the distribution of genetically identical individuals of *Phragmites australis* up to 10.8 km apart (Tomáš and Zdenka 2009).

Timing of dispersal

The flood pulse concept describes how the seasonal pulse of water movement between the river channel and floodplain shapes aquatic ecosystems (Junk et al. 1989, Middleton 1999). For aquatic vegetation, flood waters not only deliver seeds to floodplain wetlands but influence establishment success. During floods, buoyant seeds become stranded at the highest water level and germinate as water levels fall. Some species rely on flood water to deliver them to elevated sites suitable for establishment, e.g. Swamp Cypress and Cottonwood (Middleton 1999, Middleton 2000). In Australia, patterns of seed release in River Red Gum (*Eucalyptus camaldulensis*), Cajuput Tree (*Melaleuca leucadendra*), Swamp Gum (*Eucalpytus rudis*) and Swamp Paperbark (*Melaleuca rhaphiophylla*) along rivers in Western Australian are synchronised with the natural hydrological regime (Pettit and Froend 2001)

Barriers to dispersal

In Australia, river regulation has produced a highly modified flow regime and degraded river systems (Arthington and Pusey 2003, Kingsford 2000). Water storages such as dams and weirs can disrupt the longitudinal movement of propagules from upstream to downstream sites (Jansson et al. 2000, Merrit and Wohl 2006). For example, dams in the southern Rocky Mountains in Colorado, USA, reduced the abundance of propagules in the water column by 70–94% (Merrit and Wohl 2006), and Nilsson et al. (1997) found that that riparian vegetation of regulated rivers were more depauperate than free-flowing rivers. In regulated rivers, propagules that remain floating on the water surface for long periods have a greater chance of passing through barriers such as weirs or spillways than those that sink early (Jansson et al. 2000). In support of this hypothesis, Jansson et al. (2000) found that the riparian vegetation along regulated rivers in Sweden had a higher portion of species with long-floating propagules compared with unregulated rivers. Dams not only act as barriers to dispersal but alter the hydrologic regime, reducing the frequency and magnitude of river discharges and often altering the seasonal patterns of discharges, in some cases inverting them (Maheshwari et al. 1995, Reid and Brooks 2000). Reduced flows can limit the distances propagules may disperse before they sink. Under very low flows, winds may sweep propagules floating on the water surface to the shore (Jansson et al. 2000), and when the prevailing wind blows upstream, dispersal downstream may be halted.

Changes to the natural hydrologic pattern can lead to a loss of synchronicity between hydrological events and plant life stages and produce profound changes in the structure of riparian and floodplain vegetation. Ward and Standford (1995) reported that the diversity of pioneer floodplain vegetation of the Prairie River in North America declined following river regulation, and in the Platte River flow regulation reduced spring floods and transformed a previously unwooded braided river to a forested channel. In Australia, flow regulation in the Murray River has reduced the frequency and duration of winter floods while the frequency of summer floods has increase eightfold (Mayence et al. 2010). These changes have altered the distribution pattern of key species. For example, dominance shifted from Moira Grass (*Pseudoraphis spinescens*) prior to river regulation in 1945 to River Red Gum (*Eucalyptus camaldulensis*) in 1985 following regulation (Bren 1992). In more recent years, Giant Rush (*Juncus ingens*) has expanded its range in the Barmah Forest in Victoria, favoured by summer floods, and contributed to further reductions in the distribution of Moira Grass, which has declined by about 80% in area since the 1930s (Mayence et al. 2010).

A major consequence of river regulation has been the alienation of the floodplain (Mueller 1995, Kingsford 2000). In Australia, Kingsford (2000) estimated that more than 50% of floodplain wetlands on developed rivers are alienated from the river. Many floodplain wetlands remain connected to rivers only through water control structures. These may impact on dispersal in a number of ways:

- inflows may not be managed in a way that is synchronised to key dispersal events
- regulatory structures may obstruct the entry of buoyant propagules
- inflows may be too slow to capture stochastic dispersal events.

Moreover, inflows through water control structures probably do not mimic disturbance created by over-bank flows and propagules are less likely to be deposited at elevated sites.

Evidence for dispersal

Several studies of gene flow in amphibious aquatic plant populations provide some evidence that dispersal in water is important in structuring aquatic plant populations. Populations of the submerged macrophyte *Vallisneria spinulosa* in lakes of the Yangtze River in China had high levels of genetic diversity within populations but low genetic diversity among populations, indicating that gene flow was maintained among populations (Chen et al. 2007). Similarly water-mediated and waterbird-mediated dispersals were identified as important pathways in maintaining gene flow among populations of the submerged macrophytes *Potamogeton malaianus* in lakes distributed along 1400 km of the Yangtze River (Chen et al. 2009).

Another way to assess the importance of dispersal in structuring communities is to analyse how well spatial variables — typically distance among habitats —explains patterns of community structure compared with environmental variables. Using this approach, Capers et al. (2009) found that the composition of submerged and floating plants in 98 lakes and ponds across Connecticut, USA, were shaped by both environmental and spatial processes. Plant communities became less similar with increasing distance between lakes, even after accounting for increasing differences in environmental conditions with distance. The data indicated that both environmental conditions and dispersal limitation shaped community composition in the lakes. Variation in the dispersal ability of plants influenced their distribution in the landscape. Free-floating plants and those capable of vegetative reproduction were present at more distant sites than plants without these traits.

5.5.3 Waterbird-mediated dispersal

As with the dispersal of some aquatic invertebrates, waterbirds disperse plant propagules when they become attached to the feet, feathers or bill, or when they are consumed and survive gut passage (Charalambidou and Santamaría 2002, Figuerola and Green 2002a). Although the number of viable propagules recovered from waterbirds is small, the abundance, frequency and scale of waterbird movement among habitats indicate that waterbirds play a unique role in dispersing aquatic plants. Waterbirds are of particular significance because they can spread plants to hydrologically isolated habitats not reached by wind. Waterbirds may also disperse species that are not dispersed readily by other vectors.

Only two studies have assessed the role of waterbirds in dispersing aquatic plants in Australia (Green et al. 2008, Raulings et al. 2011). Green et al. (2008) recovered viable propagules of 14 plant taxa from a total of 60 waterbird faecal samples collected from Grey Teal (*Anas gracilis*), Eurasian Coot (*Fulica atra*) and Black Swan (*Cygnus atratus*) in wetlands of the Macquarie Marshes in New South Wales. Raulings et al. (2011) assessed both internal and external transport of plant propagules in Grey Teal, Black Duck (*Anas superciliosa*) and Chestnut Teal (*Anas castanea*) harvested during the duck-hunting season (March) in Gippsland, Victoria. Viable propagules of seven plant taxa were recovered from the lower intestine of 63 birds, and viable propagules of six plant taxa were recovered from the feet and feathers of 29 birds. A summary of plant taxa carried by waterbirds in Australia is provided in Table 3.

The significance of waterbird-mediated dispersal can be gauged from estimates of waterbird abundance and the probability of seed carriage. The maximum probabilities of seed carriage calculated by Raulings et al. (2011) for Grey Teal, Black Duck and Chestnut Teal was about 0.36, demonstrating that, when numbers are high, waterbirds are important dispersal vectors of plant propagules. Aerial surveys by Kingsford provide an index of waterbird abundance throughout eastern Australia. Based on these surveys the annual average waterbird population between 1996 and 2004 was about 238 000, and surveys that covered Victoria and the southern part of New South Wales counted 80 000 waterbirds in 2004.

Different species of waterbirds are likely to produce different patterns of connectivity among aquatic habitats, shaped by differences in habitat and feeding preference, rates and distance of movement, and local abundances. For example, Green et al. (2008) found differences in the types of plant species carried by species of waterbirds. Even when the types of seeds carried do not differ among waterbird species, differences in the scale of movement may still produce different patterns of dispersal in the landscape (Raulings et al. 2011). For example, based on the recovery of banded birds by Frith (1959) and Normal (1971), Grey Teals are likely to carry seed farther than Black Ducks, which are likely to carry seeds farther than Chestnut Teals. The distance that internally transported seeds may be dispersed by these birds will depend on gut retention time and the bird's flight speed.

Barriers to dispersal

Changes in land use can alter waterbird movement patterns and affect dispersal. The loss of suitable waterbird habitat has altered waterbird migration routes (Sutherland 1998), and feeding patterns of waterbirds have shifted towards agricultural crops and grasslands (Santamaría and Klaassen 2002). This has implications for the dispersal of native aquatic organisms among sites and the introduction of agricultural and terrestrial weeds into aquatic habitats.

Evidence for dispersal

There is strong evidence that waterbirds could disperse aquatic plants, but whether this potential is realised through the establishment of populations remains untested, except for a study by Mader et al. (1998). They established that gene flow among populations of the submerged macrophyte *Potamogeton pectinatus* across Britain, Sweden and Crete was higher in habitats visited by migratory Bewick's Swans (*Cygnus columbianus bewickii*), demonstrating the significant role that waterbird dispersal can play in structuring plant communities.

Table 3. Plant species dispersed by waterbirds in Australia.

Plant taxa dispersed		**Waterbird taxa carrying seeds**			
Plant Family	**Scientific name**	**Common name**	**Scientific name**	**Seed viability**	**Ref**
Asteraceae	*Aster subulatus**	Grey Teal	*Anas gracillus*	V	R
Asteraceae	*Conyza bonariensis**	Chestnut Teal	*Anas castanea*	V(ext)	R
Asteraceae	*Conyza* sp.	Grey Teal	*Anas gracillus*	V	R
Asteraceae	*Cotula coronopifolia**	Chestnut Teal	*Anas castanea*	V	R
		Grey Teal	*Anas gracillus*	V	R
Asteraceae	*Lactuca serriola**	Black Duck	*Anas superciliosa*	V	R
Asteraceae	*Senecio glomeratus*	Chestnut Teal	*Anas castanea*	V(ext)	R
Asteraceae	*Sonchus* sp.*	Black Duck	*Anas superciliosa*	V	R
		Chestnut Teal	*Anas castanea*	V	R
Characeae	*Nitella*	Black Swan	*Cygnus atratus*	NV	G
		Australian Pelican	*Pelecanus conspicillatus*	V	G
		Grey Teal	*Anas gracillus*	V	G
Cyperaceae	*Bolboschoenus fluviatilis*	Mallard	*Anas platyrhynchos*	V	G
Cyperaceae	*Bolboschoenus medianus*	Black Duck	*Anas superciliosa*	V	R
Cyperaceae	*Eleocharis acuta*	Mallard	*Anas platyrhynchos*	V	G
		Black Duck	*Anas superciliosa*	V	R
		Chestnut Teal	*Anas castanea*	V	R
		Grey Teal	*Anas gracillus*	V	R
Cyperaceae	*Eleocharis pallens*	Mallard	*Anas platyrhynchos*	V	G
Cyperaceae	*Eleocharis pusilla*	Black Duck	*Anas superciliosa*	V	R
		Grey Teal	*Anas gracillus*	V	R
Cyperaceae	*Eleocharis sphacelata*	Mallard	*Anas platyrhynchos*	V	G
Cyperaceae	*Isolepis* sp.	Grey Teal	*Anas gracillus*	V	R
Cyperaceae	*Schoenoplectus tabernaemontani*	Chestnut Teal	*Anas castanea*	V	R
Cyperaceae	*Schoenoplectus validis*	Mallard	*Anas platyrhynchos*	NV	G
Fabaceae	*Medicago polymorpha**	Black Swan	*Cygnus atratus*	V	G
Fabaceae	*Trifolium cernuum**	Grey Teal	*Anas gracillus*	V	R
Fabaceae	*Trifolium glomeratum**	Black Duck	*Anas superciliosa*	V(ext)	R
		Grey Teal	*Anas gracillus*	V	R
Haloragaceae	*Myriophyllum crispatum*	Australian Pelican	*Pelecanus conspicillatus*	NV	G
		Black Swan	*Cygnus atratus*	NV	G
		Eurasian Coot	*Fulica atra*	NV	G
		Grey Teal	*Anas gracillus*	V	G
Juncaceae	*Juncus gregiflorus*	Grey Teal	*Anas gracillus*	V	R
Juncaceae	*Juncus pallidus*	Grey Teal	*Anas gracillus*	V	R
Juncaceae	*Juncus* sp.	Grey Teal	*Anas gracillus*	NV	G
Juncaginaceae	*Triglochin striata*	Grey Teal	*Anas gracillus*	V	R
		Chestnut Teal	*Anas castanea*	V	R
		Black Duck	*Anas superciliosa*	V	R
Lemnaceae	*Lemna disperma*	Eurasian Coot	*Fulica atra*	NV	G
		Grey Teal	*Anas gracillus*	NV	G

(Continued on next page)

Table 3. continued

Plant taxa dispersed		**Waterbird taxa carrying seeds**			
Plant Family	**Scientific name**	**Common name**	**Scientific name**	**Seed viability**	**Ref**
		Australian Pelican	*Pelecanus conspicillatus*	V	G
Plantaginaceaae	*Plantago coronopus**	Black Duck	*Anas superciliosa*	V(ext)	R
Poaceae	*Lachnagrostis filiformis*	Black Duck	*Anas superciliosa*	V(ext)	R
		Chestnut Teal	*Anas castanea*	V(ext)	R
Poaceae	unidentified sp.	Grey Teal	*Anas gracillus*	NV	G
Polygonaeaceae	*Polygonum arenastrum**	Black Swan	*Cygnus atratus*	V	G
Portulaceae	*Portulaca* cf *oleraceae*	Grey Teal	*Anas gracillus*	V	G
Ranunculaceae	*Ranunculus scleratus**	Grey Teal	*Anas gracillus*	V	G
Typhacaeae	*Typha domingensis*	Eurasian Coot	*Fulica atra*	V	G
Typhacaeae	*Typha orientalis*	Australian Pelican	*Pelecanus conspicillatus*	V	G
		Black Swan	*Cygnus atratus*	V	G
		Eurasian Coot	*Fulica atra*	V	G

*Introduced species; V, Viable; NV, not viable; ext, indicates that seed was carried externally on feet, feathers or bill. All other seed were carried internally.

6 Assessing landscape connectivity

The dispersal characteristics of wetland biota are varied and will result in diverse temporal and spatial patterns of connectivity in the landscape. Based on an understanding of the biological processes that connect wetlands, models of wetland connectivity can be generated to help guide the management of wetlands at a landscape scale. Attempts to assess connectivity have so far focused on terrestrial systems; models of wetland connectivity have not yet been attempted. Assessing wetland connectivity requires a multispecies approach to represent the diverse biota of wetland systems. Such an approach would require that patterns of connectivity be developed for key groups that share similar modes of dispersal. These models could then be integrated to provide a system-based connectivity model.

Connectivity at a landscape-scale can be assessed using a range of modelling approaches. These vary in complexity from those that consider only the structural characteristics of the landscape to those that consider how the dispersal biology of the focal organism(s) may be modified by elements of the landscape. In this chapter, modelling approaches to assess connectivity at a landscape-scale are appraised to identify a suitable approach for developing connectivity maps for wetland biota across Victoria.

6.1 Structural connectivity

Structural connectivity infers dispersal from the geographical arrangement of habitats in the landscape (Calabrese and Fagan 2004). Metrics related to distance or the patterning of habitats is typically used.

Distance metrics — Two types of distance metrics are used: (1) nearest-neighbour distance, and (2) neighbourhood metric. Nearest-neighbour distance is the more commonly used distance metric. It uses the shortest straight line (Euclidean) distance between a focal habitat patch and its nearest neighbour to infer dispersal, assuming that the smaller the inter-patch distance the greater the likelihood of dispersal. The potential for all other patches in the landscape to contribute dispersers is ignored (Moilanen and Nieminen 2002). In contrast, the neighbourhood metric does consider the distances between a focal habitat patch and all patches. As the likelihood of dispersal declines exponentially with increasing distance, a negative exponential function is used to score connectivity from these dispersal metrics.

Spatial pattern metrics — A host of spatial pattern metrics have been developed to characterise various landscape elements that influence connectivity, including patch quality, patch number, patch area, core area, patch perimeter, contagion, perimeter–area ratio, shape index, fractal dimension, patch cohesion, extent, shape, and spatial arrangement of landscape elements (Calabrese and Fagan 2004, Schuemaker 1996).

Measures of structural connectivity are appealing as they provide a rapid assessment of connectivity for large areas. However, they should be applied cautiously as species dispersal abilities are not considered and patterns of connectivity may fail to represent real patterns in nature (Jacobson and Peres-Neto 2010). Even where a relationship between spatial metrics and dispersal are established the relationship may not hold in different landscapes or for different species (Calabrese and Fagan 2004).

6.2 Potential connectivity

Potential connectivity is an indirect measure of connectivity that combines spatial information of landscape structure and the dispersal biology of the focal organism(s). The ecological realism of models is enhanced by incorporating detailed information on species-specific habitat requirements and dispersal behaviours, including:

- species habitat requirements for all or critical life stages
- mode of movement between habitats
- maximum distance of dispersal

- spatial and temporal pattern of movement
- factors that may impede or facilitate movement among habitat patches.

The simplest models assess connectivity according to whether the distances between habitats patches are within the dispersal ability of the species of interest. More complex models map dispersal routes based on the permeability of the landscape, as perceived by the species.

Graph theory, least cost analysis and circuit theory are three key modelling techniques used to assess potential connectivity at a large spatial scale. Two other techniques — buffer radius and incidence function — are best applied to detailed studies of connectivity at smaller spatial scales (Moilanen and Nieminen 2002) and are not discussed here.

6.2.1 Graph theory

Graph models calculate all possible pair-wise connections among habitat patches using information on dispersal distance and indices of landscape structure (Keitt et al. 1997, Bunn et al. 2000, Calabrese and Fagan 2004). In graph models the habitat patches are represented as nodes (also called vertices), and dispersal between habitat patches are represented as links (Urban and Keitt 2001, Urban et al. 2009). Habitats (nodes) are often weighted by area and sometimes by quality, which serve as proxies for population size and provide some indication of the strength of dispersal (Calabrese and Fagan 2004). In graph models, links are the shortest straight line distance between habitat nodes. Habitat nodes are connected by links if they are in the assigned dispersal distance (Keitt et al. 1997). However, species change their route in response to the traversability of the terrain and graph models do not account for this. Graph models therefore provide only a coarse representation of dispersal.

Graph models are attractive because they provide a visual representation of the overall structure of habitat connections for large areas that is not possible with more complex models. They also offer the utility of assigning directionality to dispersal pathways. Basic graph models can provide ecological information about the system (Urban and Keitt 2001), including that indicated below.

- **Connectivity maps.** These visually represent connections between habitat patches in the landscape.
- **Critical linkages.** These are habitats that, because of their position in the landscape, enable access to multiple habitats. They are identified by estimating how often a habitat patch lies between pairs of other habitat patches, generating a 'betweenness centrality' score. Nodes with high betweenness centrality are considered essential for maintaining core connectivity.
- **Connected mosaics.** These are groups of connected habitats called components. Different components are not connected and organisms can not move from one component to another.
- **Degree of connectivity.** The number of habitat patches joined to a focal habitat indicates the level of connectivity.

Graph-based models can also be used to evaluate the effects of landscape-scale management strategies on connectivity. For example, the importance that different habitat patches have to connectivity can be evaluated by deleting a node and assessing what effect this has on connectivity. Conversely, the benefits of creating or restoring habitat patches in the landscape can be assessed by inserting a node or changing the attributes of a node (e.g. habitat quality or size) and re-assessing connectivity.

A review by Calabrese and Fagan (2004) proposed that graph theory represents the best trade-off between the level of information generated from the model and its data requirements. Despite these benefits, graph models do not take into account landscape permeability, and this limits their use to situations where the mobility of the focal taxa is largely unaffected by landscape elements, or where landscapes do not contain features that constrain movement. Graph models also do not identify multiple pathways, although overlaying graph models may enable multiple pathways to be assessed.

6.2.2 Least cost analysis and circuit theory

Least cost analysis and circuit theory methods are based in graph theory, but ecological realism is increase by considering the ability of focal species to traverse the non-habitat matrix. Least cost analysis identifies dispersal pathways among habitat patches by assigning permeability scores to the intervening landscape. Dispersal distances along a single path of greatest permeability — or least cost — is measured, rather than simply the geographic (straight line) distance. Least cost analysis has been used to inform conservation planning for over a decade (McRae 2006, McRae and Beier 2007, McRae et al. 2008).

Circuit theory, also called isolation by resistance (IBR), is similar to least cost analysis in that it identifies pathways through the intervening landscape that offer the lowest resistance to movement between habitat patches. It is analogous to electrical circuits as it represents connectivity as circuit diagrams (Fig 6.1). The main advantage of circuit theory is that it can model multiple dispersal pathways between habitats (McRae and Beier 2007). Circuit theory models can assess connectivity between multiple habitats but are computationally demanding when the number of habitats is large.

6.2.3 GIS approaches

Neighbourhood analysis and cost distance analyses are two approaches that can be applied to assess connectivity in a GIS framework (VEAC 2010). These approaches, like circuit theory and least cost analysis, increase realism by incorporating rules around landscape permeability and the direction and scale of movement for the organism(s) of interest. In both neighbourhood analysis and cost distance analysis the landscape is represented as grids, and cells are assigned a permeability score based on the dispersal constraints for the organism of interest, with habitat cells having the highest permeability.

Neighbourhood analysis and cost distance analyses represent connectivity in slightly different ways. Cost distance analysis only assesses the permeability of cells surrounding habitats that are in the dispersal range of the organism of interest. This approach provides a detailed representation of connectivity among habitats but provides no information on the permeability of the landscape beyond the specified dispersal distance. In contrast, Neighbourhood analysis assesses the permeability of the landscape surrounding each cell in the landscape, which identifies permeable corridors that are not revealed by least cost analysis. Combining outputs from both analyses is more representative of connectivity than the outputs of the individual analyses.

6.3 Conclusion

Least cost analysis, circuit theory and GIS methods all offer greater realism in modelling connectivity, provided responses of organisms to landscape elements are known and the resolution of the landscape is sufficient to accurately assign resistance or permeability values. For many organisms our understanding of dispersal distances and movement behaviour limits the potential to accurately model connectivity.

Our appraisal of landscape connectivity models indicate that only a few approaches are capable of incorporating rules for landscape permeability, and the direction and scale of movement to produce realistic maps of connectivity for an organism(s) of interest. Although circuit theory accommodates most of these requirements it is computationally demanding, and this currently limits its application at a state-wide scale. GIS approaches offer similar level of realism but processing times are comparatively modest; at present they are the best option for modelling the connectivity of Victoria's wetlands.

An ecosystem-based model of wetland connectivity that integrates patterns of connectivity for multiple species is desirable to guide strategic investment and planning, and to improve our understanding of how wetlands systems interface with other ecosystems. Producing an ecosystem-based wetland connectivity map could be achieved by integrating connectivity models for individual groups. Although such a map would be a useful tool for guiding policy, an understanding of the patterns of connectivity at a group or species level is needed to inform more targeted management.

Identifying wetlands that are connected for multiple species may assist in prioritising wetlands site for conservation or restoration. This could be achieved by ranking wetlands based on the number of pathways for which they have a high connectivity score.

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Appendix 1. Description of amphibians recorded in Victoria

Table A1. Description of amphibians recorded in Victoria including: conservation listing (CL) in Victoria (DSE 2007), mobility and habitat use. The genus *Litoria* belongs to the family Hylidae, all the other genera belong to the family Myobatrachidae.

Species name	Common name	CL	Altitudinal range (m)	Habitat use	Mobility
Litoria aurea	Green and Golden Bell Frog	Vu	10–720	generalist	high
Litoria booroolongensis	Booroolong Tree Frog	CE, FFG	210–260	stream	unknown
Litoria citropa	Blue Mountains Tree Frog		10–590	stream	unknown
Litoria dentata	Bleating Tree Frog			generalist	unknown
Litoria ewingii	Southern Brown Tree Frog		10–1510	generalist	unknown
Litoria lesueuri	Lesueur's Frog		10–1460	stream	unknown
Litoria littlejohni	Large Brown Tree Frog	DD, FFG	110–1160	generalist	medium
Litoria nudidigita	Leaf Green Tree Frog		10–1390	stream	unknown
Litoria paraewingi	Plains Brown Tree Frog		20–1730	generalist	medium
Litoria peronii	Peron's Tree Frog		10–1030	generalist	unknown
Litoria raniformis	Growling Grass Frog	E, FFG	10–1140	generalist	high
Litoria spenceri	Spotted Tree Frog	CE, FFG	310–1700	stream	unknown
Litoria verreauxii alpina	Alpine Tree Frog	CE, FFG	1000–1720	specialist	unknown
Litoria verreauxii verreauxii	Verreaux's Tree Frog		10–980	generalist	unknown
Crinia parinsignifera	Plains Froglet		20–850	generalist	unknown
Crinia signifera	Common Froglet		10–1950	generalist	unknown
Crinia sloanei	Sloane's Froglet		80–210	generalist	unknown
Geocrinia laevis †	Southern Smooth Froglet		10–720	specialist	low
Geocrinia Victoriana †	Victorian Smooth Froglet		10–1730	specialist	low
Heleioporus australiacus†	Giant Burrowing Frog	Vu, FFG	60–830	unknown	unknown
Limnodynastes dumerilii	Pobblebonk Frog		10–1700*	generalist	medium
Limnodynastes fletcheri	Barking Marsh Frog		20–300	generalist	unknown
Limnodynastes interioris	Giant Bullfrog	CE, FFG	80–400	generalist	medium
Limnodynastes peronii	Striped Marsh Frog		10–1180	generalist	unknown
Limnodynastes tasmaniensis	Spotted Marsh Frog		10–1150	generalist	unknown
Mixophyes balbus	Southern Barred Frog	CE, FFG	200–970	stream	unknown
Neobatrachus pictus	Mallee Spadefoot Toad		30–370	generalist	unknown
Neobatrachus sudelli	Common Spadefoot Toad		10–440	generalist	unknown
Paracrinia haswelli	Haswell's Froglet		10–910	generalist	unknown
Philoria frosti †	Baw Baw Frog	CE, FFG	810– 1570	specialist	low
Pseudophryne bibroni †	Brown Toadlet	E, FFG	10–1090	specialist	low
Pseudophryne dendyi †	Dendy's Toadlet	DD	10–1710	specialist	low
Pseudophryne semimarmorata †	Southern Toadlet	Vu	10–1500	specialist	low
Uperoleia laevigata	Smooth Toadlet	DD	190–950	generalist	unknown
Uperoleia martini	Martins Toadlet	DD	20–210	generalist	unknown
Uperoleia rugosa	Rugose Toadlet	Vu, FFG	100–200	generalist	unknown
Uperoleia tyleri	Tylers Toadlet	DD	20–210	generalist	unknown

Habitat use: generalist, species that utilise most wetland types; specialist, species with narrow habitat requirement; stream, stream dwelling species. Mobility ratings are based on expert opinion: Unknown; Low, < 0.5 km; Medium, < 1 km; High, > 1 km. Conservation listing in Victoria (DSE 2007): RE, regionally extinct; CE, critically endangered; E, endangered; Vu, vulnerable; DD, data deficient; FFG, listed as threatened under the FFG Act 1988.

*Elevation data may be compilation of subspecies; †species that do not breed in ponds; Tyler's Toadlet and Martins Toadlet may be the same species (taxonomy unresolved).

Sources: Robinson (1998); M. Scroggie, N. Clemann and S. Saddlier, ARI, pers. comm.

Appendix 2. Waterbirds recorded in Victoria that are associated with wetlands

Table A2. List of waterbirds associated with wetlands that have been recorded in Victoria, the types of wetlands in which they occur, status of occurrence and conservation listing in Victoria. Movement patterns associated with breeding, feeding and moulting are also listed. Pelagic seabirds, vagrants and land birds using saltmarsh are excluded from this list. Species are grouped by taxon number according to Christidis and Boles (2007). This table was compiled by R. Loyn, Arthur Rylah Institute for Environmental Research, Department of Sustainability and Environment.

CL = conservation listing; MB = movements between breeding and non-breeding habitat; MF = movements between feeding, roosting and moulting habitats. See key on page 52.

Common Name	Scientific Name	Habitat	Status	CL	MB	MF
Magpie Goose	*Anseranas semipalmata*	F	RI	NT	L	L
Plumed Whistling-Duck	*Dendrocygna eytoni*	F	RB		A	L
Musk Duck	*Biziura lobata*	FST		Vu	A	L
Freckled Duck	*Stictonetta naevosa*	F		E, FFG	IA	L
Cape Barren Goose	*Cereopsis novaehollandiae*	FS		NT	C	R
Feral Goose	*Anser anser*	F	I		L	L
Black Swan	*Cygnus atratus*	FST			A	M
Australian Shelduck	*Tadorna tadornoides*	FST	G		A	M, F
Australian Wood Duck	*Chenonetta jubata*	F	G		A	L
Pink-eared Duck	*Malacorhynchus membranaceus*	FS	G		IA	L
Australasian Shoveler	*Anas rhynchotis*	FS	G	Vu	A	L
Grey Teal	*Anas gracilis*	FST	G		IA	L
Chestnut Teal	*Anas castanea*	FST	G		A	T
Mallard	*Anas platyrhynchos*	F	I		L	L
Pacific Black Duck	*Anas superciliosa*	F	G		A	L
Hardhead	*Aythya australis*	F	G	Vu	IA	L
Blue-billed Duck	*Oxyura australis*	FS		E, FFG	A	L
Australasian Grebe	*Tachybaptus novaehollandiae*	F			L	L
Hoary-headed Grebe	*Poliocephalus poliocephalus*	FST			IA	L
Great Crested Grebe	*Podiceps cristatus*	FST			A	L
Darter	*Anhinga novaehollandiae*	F			L	L
Little Pied Cormorant	*Microcarbo melanoleucos*	FST			A	T
Great Cormorant	*Phalacrocorax carbo*	FST			A	T
Little Black Cormorant	*Phalacrocorax sulcirostrus*	FST			A	T
Pied Cormorant	*Phalacrocorax varius*	FST		NT	L	T
Black-faced Cormorant	*Phalacrocorax fuscescens*	C		NT	C	T
Australian Pelican	*Pelecanus conspicillatus*	FST			A	F, T
Australasian Bittern	*Botaurus poiciloptilus*	F		E, FFG	A	L
Australian Little Bittern	*Ixobrychus dubius*	F	S		A	L
Black Bittern	*Ixobrychus flavicollis*	FT	RB	Vu, FFG	A	L
White-necked Heron	*Ardea pacifica*	F			IA	F
Eastern Great Egret	*Ardea modesta*	FST		Vu, FFG	IA	F
Intermediate Egret	*Ardea intermedia*	FT		CE, FFG	IA	F
Cattle Egret	*Ardea ibis*	F	W		A	F, R

(continued on next page)

Appendix 2 (continued)

Common Name	Scientific Name	Habitat	Status	CL	MB	MF
White-faced Heron	*Egretta novaehollandiae*	FST			L	F
Little Egret	*Egretta garzetta*	FST		E, FFG	A	F
Eastern Reef Egret	*Egretta sacra*	T	RNB		A	T
Nankeen Night-Heron	*Nycticorax caledonicus*	F		NT	A	F
Glossy Ibis	*Plegadis falcinellus*	F		NT	IA	R
Australian White Ibis	*Threskiornis molucca*	FST			A	R
Straw-necked Ibis	*Threskiornis spinicollis*	F			IA	R
Royal Spoonbill	*Platalea regia*	FST		Vu	A	T
Yellow-billed Spoonbill	*Platalea flavipes*	F			IA	F
Eastern Osprey	*Pandion cristatus*	C	RNB		A	F
White-bellied Sea-Eagle	*Haliaeetus leucogaster*	FST		Vu, FFG	A	F, T
Whistling Kite	*Haliastur sphenurus*	FT			A	L
Swamp Harrier	*Circus approximans*	FS			A	R
Brolga	*Grus rubicundus*	F		Vu, FFG	A	L, M
Purple Swamphen	*Porphyrio porphyrio*	FS			L	L
Lewin's Rail	*Lewinia pectoralis*	FST		Vu, FFG	L	L
Buff-banded Rail	*Gallirallus philippensis*	FST			L	L
Baillon's Crake	*Porzana pusilla*	F	S	Vu, FFG	A	L
Australian Spotted Crake	*Porzana fluminea*	FST			A	L
Spotless Crake	*Porzana tabuensis*	F			A	L
Black-tailed Native-hen	*Tribonyx ventralis*	F			A	L
Dusky Moorhen	*Gallinula tenebrosa*	F			L	L
Eurasian Coot	*Fulica atra*	F			A	L
Pied Oystercatcher	*Haematopus longirostris*	T			C	T
Sooty Oystercatcher	*Haematopus fuliginosus*	T		NT	C	T
Black-winged Stilt	*Himantopus himantopus*	FS			A	L
Red-necked Avocet	*Recurvirostra novahollandiae*	FST			IA	F
Banded Stilt	*Cladorhynchus leucocephalus*	S			IA	F
Pacific Golden Plover	*Pluvialis fulva*	T	S	NT	NH	T
Grey Plover	*Pluvialis squatarola*	T		NT	NH	T
Red-capped Plover	*Charadrius ruficapillus*	FST			A	T
Double-banded Plover	*Charadrius bicinctus*	FST	W		NZ	T
Lesser Sand Plover	*Charadrius mongolus*	T	S	Vu	NH	T
Greater Sand Plover	*Charadrius leschenaultii*	T	S	Vu	NH	T
Oriental Plover	*Charadrius veredus*	FS	RNB		NH	F
Inland Dotterel	*Charadrius australis*	FS		Vu	A	F
Black-fronted Dotterel	*Elseyornis melanops*	F			L	L
Hooded Plover	*Thinornis rubricollis*	T		Vu, FFG	C	L
Red-kneed Dotterel	*Erythrogonys cinctus*	FS			IA	L
Banded Lapwing	*Vanellus tricolor*	FS			L	L
Masked Lapwing	*Vanellus miles*	FST			L	L
Australian Painted Snipe	*Rostratula australis*	FS		CE,FFG	A	L
Latham's Snipe	*Gallinago hardwickii*	F	S	NT	NH	L

(continued on next page)

Appendix 2 (continued)

Common Name	Scientific Name	Habitat	Status	CL	MB	MF
Black-tailed Godwit	*Limosa limosa*	FST	S	Vu	NH	T
Bar-tailed Godwit	*Limosa lapponica*	T	S		NH	T
Little Curlew	*Numenius minutus*	FS	RNB		NH	L
Whimbrel	*Numenius phaeopus*	T	S		NH	T
Eastern Curlew	*Numenius madagascariensis*	T	S	NT	NH	T
Terek Sandpiper	*Xenus cinereus*	T	S	E, FFG	NH	T
Common Sandpiper	*Actitis hypoleucos*	FST	S	Vu	NH	L
Grey-tailed Tattler	*Tringa brevipes*	T	S		NH	T
Common Greenshank	*Tringa nebularia*	FST	S		NH	T
Marsh Sandpiper	*Tringa stagnatilis*	S	S		NH	L
Wood Sandpiper	*Tringa glareola*	F	RNB	Vu	NH	L
Ruddy Turnstone	*Arenaria interpres*	T	S		NH	T
Great Knot	*Calidris tenuirostris*	T	S		NH	T
Red Knot	*Calidris canutus*	T	S	NT	NH	T
Sanderling	*Calidris alba*	T	S	NT	NH	T
Red-necked Stint	*Calidris ruficollis*	FST	S		NH	T
Long-toed Stint	*Calidris subminuta*	F	RNB	NT	NH	L
Pectoral Sandpiper	*Calidris melanotos*	FS	RNB	NT	NH	L
Sharp-tailed Sandpiper	*Calidris acuminata*	FST	S		NH	T
Curlew Sandpiper	*Calidris ferruginea*	FST	S		NH	T
Broad-billed Sandpiper	*Limicola falcinellus*	T	RNB		NH	T
Ruff	*Philomachus pugnax*	F	RNB		NH	L
Oriental Pratincole	*Glareola maldivarum*	FST	RNB		NH	L
Australian Pratincole	*Stiltia isabella*	FS	S	NT	A	L
Little Tern	*Sternula albifrons*	C		Vu, FFG	C, NH	T
Fairy Tern	*Sternula nereis*	C		E, FFG	C	T
Gull-billed Tern	*Gelochelidon nilotica*	FST		E, FFG	A	F
Caspian Tern	*Hydroprogne caspia*	FST			A	T
Whiskered Tern	*Chlidonias hybrida*	FS		NT	A	F
White-winged Black Tern	*Chlidonias leucopterus*	FST	S	NT	NH	F
White-fronted Tern	*Sterna striata*	C	W	NT	NZ	T
Common Tern	*Sterna hirundo*	C	S		NH	T
Crested Tern	*Thalasseus bergii*	C			C	T
Pacific Gull	*Larus pacificus*	C		NT	C	T
Kelp Gull	*Larus dominicanus*	C			C	L
Silver Gull	*Chroicocephalus novaehollandiae*	FST			A	F, T
Azure Kingfisher	*Ceyx azureus*	F		NT	L	L
Australian Reed-Warbler	*Acrocephalus australis*	F	S		A	L
Little Grassbird	*Megalurus gramineus*	FST			L	L

(continued on next page)

Key for Appendix 2.

Wetland habitats (main habitats used by each species)

C	Coastal waters
F	Freshwater wetlands (may be vegetated or open, favoured by different species)
FS	Freshwater or saline wetlands, but rarely tidal
FST	Freshwater, saline or tidal wetlands
FT	Freshwater or tidal wetlands (e.g. among paperbarks and mangroves in tropics, mostly freshwater in Victoria)
S	Saline wetlands (may use freshwater or tidal habitats locally or periodically)
ST	Saline or tidal wetlands
T	Tidal mudflats or beaches

Status

I	Introduced to Australia
RI	Re-introduced to Victoria after extinction in early 20th century
RB	Rare breeding species
RNB	Rare non-breeding visitor to Victoria
G	Classed as a game species (in some years not all these species are allowed to be taken)
S	Mainly summer visitor
W	Mainly winter visitor

Note that vagrants (recorded on rare occasions, presumably as lost individuals) are not included in this table.

Victorian Conservation Status (Source: DSE 2007)

CE	Critically Endangered
E	Endangered
Vu	Vulnerable
NT	Near Threatened
FFG	Listed under the *Flora and Fauna Guarantee Act 1988*

Movements between breeding and non-breeding habitat

A	Migratory or nomadic movements in Australia (not including subset below)
IA	Nomad , breeding mainly in inland Australia during floods and largely vacating coastal habitats in those times
NH	Migrant, breeding in Northern Hemisphere
NZ	Migrant, breeding in New Zealand
C	Mainly coastal, may make movements along coasts or to breed on coastal islands
L	Mainly local movements (< 50 km)

Note, there are some regular seasonal patterns in nomadism in Australia, but they may be over-ridden by major flood events

(continued on next page)

Key for Appendix 2 (continued)

Movements between feeding, roosting and moulting habitats

T	Regular (twice-daily) movements up to 20 km between feeding areas and high-tide roosts on spits, islands or saltmarsh. (Species that use tidal and non-tidal habitats typically make shorter daily movements when feeding in non-tidal habitats.)
R	Regular daily movements up to 20 km between feeding and roosting habitats
F	Regular movements up to 10 km between alternative feeding habitats
M	Annual movements to suitable moulting habitat
L	Mainly local movements (< 5 km)

Appendix 3. Native Victorian fish that occur in wetlands

Table A3. List of native fish recorded in Victorian wetlands. Distribution in Victoria is indicated as: N, Murray Darling Basin; S, coastal; t, translocated. Habitats are indicated as: FW, freshwater; M, marine; Est, estuaries; and S, saline. Conservation list (CL) in Victoria (DSE 2007): RE, regionally extinct; CE, critically endangered; E, endangered; Vu, vulnerable; DD, data deficient; NT, near threatened; FFG, listed as threatened under the *Flora and Fauna Guarantee Act 1988*.

Common Name	**Species**	**Location**	**Habitat**	**CL**
Olive Perchlet	*Ambassis agassizii*	N	FW	
Short-finned Eel	*Anguilla australis*	S	FW, M	
Long-finned Eel	*Anguilla reinhardtii*	S	FW, M	
Small-mouthed Hardyhead	*Atherinosoma microstoma*		Est, FW	
Silver Perch	*Bidyanus bidyanus*	N	FW	
Murray Hardyhead	*Craterocephalus fluviatilis*	N	S	CE, FFG
Unspecked Hardyhead	*Craterocephalus stercusmuscarum fulvus*	N	FW	DD, FFG′
River Blackfish	*Gadopsis marmoratus*	N+S	FW	
River Blackfish, U. Wannon R. form	*Gadopsis marmoratus*	S	FW	CE, FFG
Broadfin Galaxias	*Galaxias brevipinnis*	S+N^t	FW, M	DD
Common Galaxias	*Galaxias maculatus*	S+N^t	FW, M	
Flat-headed Galaxias	*Galaxias rostratus*	N	FW	Vu, FFG
Spotted Galaxias	*Galaxias truttaceus*	S+N^t	FW	
Dwarf Galaxias	*Galaxiella pusilla*	S	FW	Vu, FFG
Striped Gudgeon	*Gobiomorphus australis*	S	FW	
Western Carp Gudgeon	*Hypseleotris* species complex	N + S^t	FW, S	
Murray Cod	*Maccullochella peelii*	N	FW	Vu, FFG
Golden Perch	*Macquaria ambigua*	N	FW,S	
Murray Darling Rainbowfish	*Melanotaenia fluviatilis*	N	FW	DD, FFG
Southern Purple-spotted Gudgeon	*Mogurnda adspersa*	N	FW	RE, FFG
Southern Pygmy Perch	*Nannoperca australis*	N+S	FW	
Yarra Pygmy Perch	*Nannoperca obscura*	S	FW	NT, FFG
Variegated Pygmy Perch	*Nannoperca variegata*	S	FW, S	E, FFG
Bony Herring	*Nematalosa erebi*	N	FW, S	
Australian Mudfish	*Neochanna cleaveri*	S + N^t	FW, Est	CE, FFG
Flat-headed Gudgeon	*Philypnodon grandiceps*	N + S	FW, S, Est	
Dwarf Flathead Gudgeon	*Philypnodon macrostomus*	N + S	FW, S, Est	
Tupong	*Pseudaphritis urvillii*	S	FW, Est	
Western Blue-spot Goby	*Pseudogobius olorum*	S	Est, FW	
Eastern Blue-spot Goby	*Pseudogobius* sp. 9	S+N	Est, FW	
Australian Smelt	*Retopinna semoni*	N+S	FW, S	
Freshwater Catfish	*Tandanus tandanus*	N	FW	E, FFG
Lagoon Goby	*Tasmanogobius lasti*	S	Est, FW	

Note: Murray Cod occurs only occasionally in wetlands.

Sources: T. Raadik, ARI, pers. comm.; Beesley et al. (2011); Drew (2008); Closs et al. (2006).

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