

Climate change and its implications for Australia's freshwater fish

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Abstract. Freshwater environments and their fishes are particularly vulnerable to climate change because the persistence and quality of aquatic habitat depend heavily on climatic and hydrologic regimes. In Australia, projections indicate that the rate and magnitude of climate change will vary across the continent. We review the likely effects of these changes on Australian freshwater fishes across geographic regions encompassing a diversity of habitats and climatic variability. Commonalities in the predicted implications of climate change on fish included habitat loss and fragmentation, surpassing of physiological tolerances and spread of alien species. Existing anthropogenic stressors in more developed regions are likely to compound these impacts because of the already reduced resilience of fish assemblages. Many Australian freshwater fish species are adapted to variable or unpredictable flow conditions and, in some cases, this evolutionary history may confer resistance or resilience to the impacts of climate change. However, the rate and magnitude of projected change will outpace the adaptive capacities of many species. Climate change therefore seriously threatens the persistence of many of Australia's freshwater fish species, especially of those with limited ranges or specific habitat requirements, or of those that are already occurring close to physiological tolerance limits. Human responses to climate change should be proactive and focus on maintaining population resilience through the protection of habitat, mitigation of current anthropogenic stressors, adequate planning and provisioning of environmental flows and the consideration of more interventionist options such as managed translocations.

Additional keywords: arid zone, drought, environmental flows, freshwater fish, life history, local adaptation, refugia, threatened species.

Introduction

Climate change is a major threat to global biodiversity and ecosystem functioning (Thomas *et al.* 2004; IPCC 2007) and its effects are already evident across a range of environments and biota (Parmesan and Yohe 2003). The rate and severity of climate changes have, and will, vary across the globe, with particular regions, ecosystems and taxa being differentially affected depending on their susceptibility and level of exposure. Freshwater environments, and the organisms that inhabit them, are particularly vulnerable because they are isolated and fragmented within a terrestrial landscape (Fausch *et al.* 2002). Furthermore, surface water, which determines the quality and availability of aquatic habitat, depends heavily on rainfall and temperature regimes that will be drastically affected by climate change (Carpenter *et al.* 1992; Hobday and Lough 2011). Relatively few studies have explored the implications of climate change for freshwater biota, with the majority of these focussing on northern hemisphere or high-latitude freshwaters (e.g. Xenopoulos and Lodge 2006; Buisson *et al.* 2008; Graham and Harrod 2009; Heino *et al.* 2009; McCullough *et al.* 2009; but see Carpenter *et al.* 1992, for global perspectives, and Chessman 2009 and Kingsford *et al.* 2011, for Australian perspectives). Projected global warming that surpasses or optimises thermal tolerances and requirements is often emphasised as a major driver of assemblage turnover, range shifts and range expansions in these systems because surface water is seldom limiting (but see Xenopoulos and Lodge 2006, for hydrological example). Much less, however, is known of how climate change will affect freshwaters in arid and semiarid regions where surface water is already scarce and likely to become more so (Bates *et al.* 2008).

Australia encompasses a diversity of climates and geography. Its aquatic biota inhabits a broad range of freshwater environments, spanning the naturally variable and unpredictable hydrology of arid and semiarid regions that cover much of the continent, to the highly seasonal yet predictable flows of tropical regions and the more stable and consistent baseflow regimes of some temperate and subalpine regions (Puckridge *et al.* 1998; Kennard *et al.* 2010). Australia's freshwater fish species (~206 native species Allen *et al.* 2002), consequently, exhibit a diverse array of reproductive, morphological and physiological adaptations that facilitate persistence in particular environmental circumstances (e.g. Humphries *et al.* 1999; Pusey *et al.* 2004; Crook *et al.* 2010a). However, the extent to which current populations and assemblages will persist into the future remains unclear. Never before have freshwater fish faced such a magnitude and rate of climate change, coupled with the added pressure of human disturbance (reviewed in Dudgeon *et al.* 2006). It is clear that the projected reductions in surface-water availability resulting from climate change, despite high uncertainty associated with greenhouse gas-scenario selection and model down-scaling (CSIRO and Bureau of Meteorology 2007; Hobday and Lough 2011), pose a significant threat to the viability of freshwater fish populations in many regions of Australia.

At present, information regarding the nature and severity of this threat is fragmented and largely incidental or anecdotal. The aim of the present review is to synthesise this existing information and begin predicting the likely impacts of climate change on Australia's freshwater fish species (Fig. 1). We

conduct regional assessments to explore differences and commonalities in potential fish responses to climate change across the continent, and discuss these in the context of existing anthropogenic stressors. We also consider the potential for species to adapt to projected conditions and discuss management options to some of the issues raised. The review will provide a contextual background to facilitate further research through the identification of key knowledge gaps and will assist managers in forming proactive and effective responses to the threats posed by climate change.

Regional comparisons

Across Australia, significant climatic changes have been observed over the past 50 years (CSIRO and Bureau of Meteorology 2007). Average annual air temperatures have risen by 0.9°C, which is faster than the global average (Lough *et al.* 2011), and rainfall patterns have changed such that some regions are experiencing significant deficits and others increased variability. Droughts are also becoming more severe and less precipitation is falling as snow. Although there are some general patterns associated with climate change, the impacts on hydrology and thus aquatic fauna have not been, and will not be, uniform across the continent (Fig. 2; CSIRO and Bureau of Meteorology 2007; Hobday and Lough 2011; Lough *et al.* 2011). In the following sections, we explore the potential impacts of climate change on freshwater fish across six representative geographic regions of Australia (Table 1, Fig. 3) that loosely correspond to major drainage divisions, hydrological regimes (Haines *et al.* 1988; Kennard *et al.* 2010) and biogeographical provinces of freshwater fish (Unmack 2001). The implications of climate change in the Murray–Darling Basin are considered in more detail by others (Aldous *et al.* 2011; Kingsford *et al.* 2011; Pittock and Finlayson 2011; Balcombe *et al.* 2011; Pratchett *et al.* 2011).

Northern Australia

The freshwaters of northern Australia are diverse, ranging from the complex floodplain–river and billabong systems in the Gulf of Carpentaria, to deeply incised bedrock-controlled rivers of the Kimberley region and geographically isolated streams on upland plateaus. Flow regimes are summer-dominated and vary according to the extent of seasonality, predictability and degree of flow permanence (Kennard *et al.* 2010). Northern Australia, as defined here, constitutes only 17% of the continental area, yet contains ~60% of Australia's freshwater-fish biodiversity (Unmack 2001; Pusey *et al.* 2004). Although most of the floodplain ecosystems are in good ecological condition and reflect the integrity of the surrounding savanna and limited extent of past water-resource development (Woinarski *et al.* 2007; Pusey and Kennard 2009), the fish fauna of the region is increasingly threatened by hydrological alteration and a range of diffuse threats.

The precise nature of changes in northern Australia's rainfall and runoff under various climate scenarios has been notoriously difficult to quantify with high certainty (Cresswell *et al.* 2009). In general, however, the projected trends of slightly reduced discharge, a minor increase in the number of days of zero flow, and increased rates of evapotranspiration (Table 1) suggest that

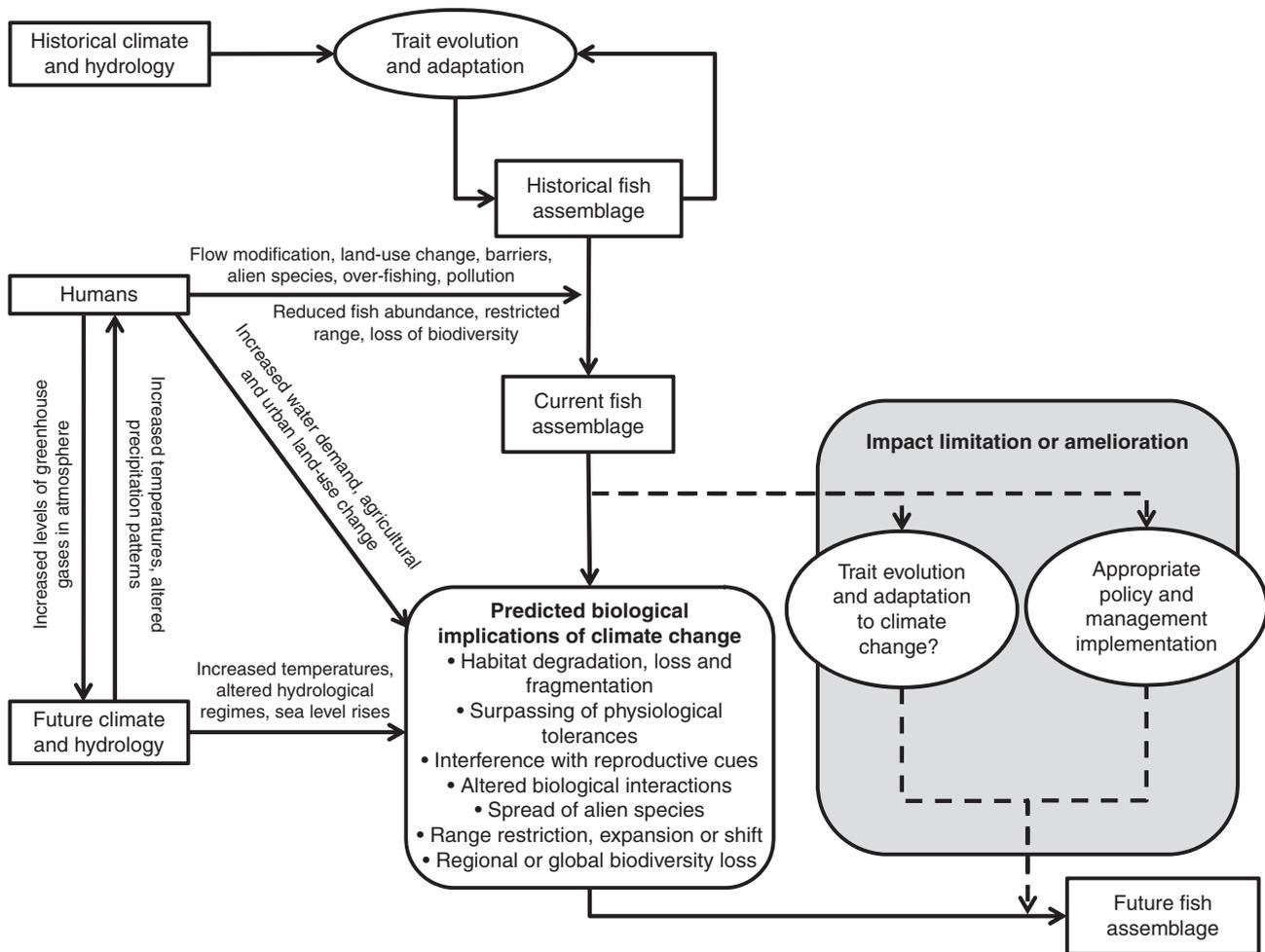


Fig. 1. Schematic diagram highlighting the influences of past climatic and hydrologic regimes, anthropogenic stressors and future climate change, in shaping historical, current and future freshwater fish assemblages. The interdependency of human activity and future climate and hydrology is emphasised, each having both additive and interactive implications for future fish assemblages. Alternate pathways to a future assemblage whereby climate-change impacts are limited or ameliorated by properties intrinsic to the biota or appropriate management interventions that facilitate system adaptation are denoted by dashed lines.

the current trend for increasing intermittency in inland river reaches will intensify. More intense cyclones and individual rainfall events are likely to steepen the flood hydrograph and increase recharge rates of shallow groundwater aquifers (Cresswell *et al.* 2009). The impacts of these minor hydrological changes on the freshwater fish species of the region are difficult to predict, except that any reduction in dry-season flows may potentially exacerbate droughts, reduce the availability of flowing habitats (e.g. riffle habitats used by members of the Terapontidae (grunters) as nursery areas), decrease the extent to which migratory species may move within individual river systems (Chan *et al.* 2011), and decrease the number of refugial habitats if spell lengths exceed refugia permanence. Further, increased rainfall intensity, unaccompanied by an overall substantial increase in total rainfall, may mean that flood events are shorter in duration. This may result in intermittent tributary streams that flow during floods being less likely to provide suitable spawning habitat for a sufficient time to allow hatching,

development and migration back to permanent water for species such as plotosid catfishes.

Northern Australia's coastal freshwater floodplains are extensive (~30% of the region's area) and occur close to the current sea level (D. Ward, pers. comm.); thus, they are vulnerable to sea-level rise. For example, the extensive coastal wetlands of Kakadu are only 0.2–1.2 m above the mean high water level (Eliot *et al.* 1999), which is within the bounds of projected sea-level rises of ~0.3 m by 2030 (Table 1). Likewise, increased intensity of cyclones and associated storm surges further increases the likelihood of saltwater intrusion into coastal freshwater wetlands, with the attendant risk of floristic change (e.g. loss of *Melaleuca* forests and upstream migration of mangroves) and geomorphological transition from freshwater wetlands to saline mudflats (Eliot *et al.* 1999). The transition of wetlands to saline mudflats would occur rapidly (Woodroffe 1995) and locally extirpate wetland-dependent species such as pennyfish (*Denariusa bandata*) and blue-eyes (*Pseudomugil*

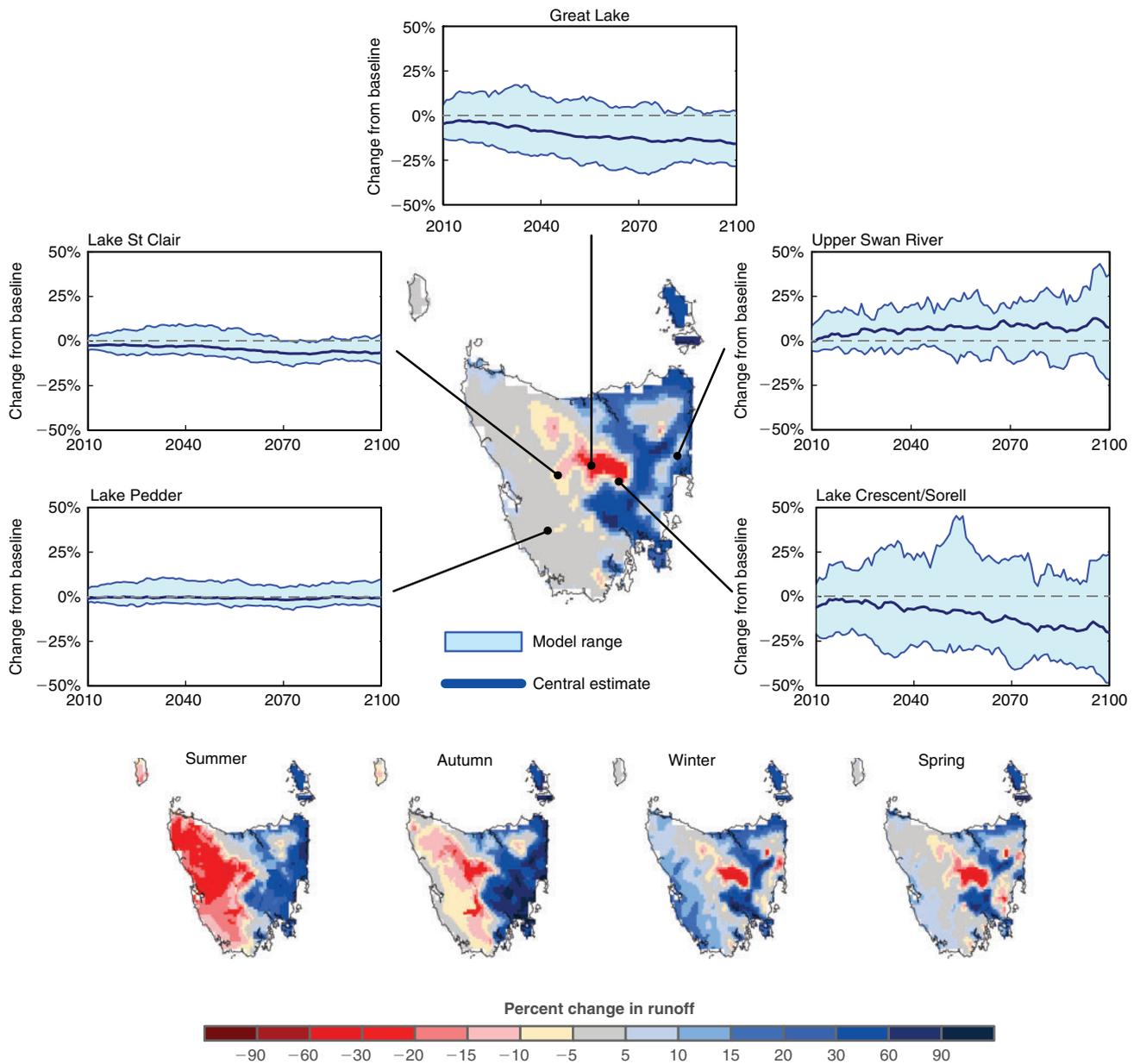


Fig. 2. Example of the spatially and temporally variable impacts that climate change will have on Australia’s hydrology. Within Tasmania, average runoff into some lakes is projected to increase whereas in others it will decline, and the magnitude of these changes will be seasonally dependent. Modelling of inflows to selected Tasmanian lakes for the period 2010–2100 relative to baseline inflows in 1961–1990 (Bennett *et al.* 2010), including a seasonal summary of percentage change in catchment runoff (average of six regional climate projections). Time series show 30-year trailing moving averages of inflows from high-resolution regional climate projections. Central estimate is the mean of six high-resolution regional climate projections, with the ranges showing the wettest and driest regional simulations.

tennellus and *P. gertrudae*) and potentially reduce population sizes of many other species, including the diadromous barramundi (*Lates calcarifer*) for which coastal floodplain wetlands are an important nursery habitat. A shift from a wetland to saline mudflat habitat would have widespread effects on primary production, foodwebs, fish-assemblage structure and overall diversity.

Mean annual air temperatures in northern Australia already range from 30°C to 33°C, and maximum instantaneous water

temperatures frequently exceed this range (e.g. >37°C), particularly during the dry season (Pusey *et al.* 2004; Hamilton 2010). Projected warming in northern Australia, coupled with increased intermittency in rivers that regularly cease to flow (Cresswell *et al.* 2009; Kennard *et al.* 2010), may result in refugial water temperatures exceeding the physiological tolerances, already near their lethal limit, of many species. Although altered thermal regimes might cause a contraction in the distributions of some species in northern Australia, others may

Table 1. Geographical descriptions and projected climatic and hydrologic changes for six Australian freshwater regions covered in the review

Region	Area covered	Historical hydrologic and climatic regimes	Climate-change projections			References
			Rainfall and air temperature	Hydrology	Other	
Northern Australia	Coastal river basins from Kimberley (west) to Cape York Peninsula (east)	Seasonal climate. Flow regime summer dominated. Intermittency and variability increase further from coast, corresponding to gradients in temperature, rainfall, evapotranspiration and water deficit.	+1–3°C by 2070; +1–6% evapotranspiration rate; more intense rainfall events	–1% to +4% change in annual discharge; +7 days of zero flow in Gulf region	Increased intensity of cyclones; 0.25–0.8-m sea-level rise	Eliot et al. 1999; CSIRO and Bureau of Meteorology 2007; Cresswell et al. 2009; McJannet et al. 2009; Pusey and Kennard 2009; Kennard et al. 2010
Wet Tropics	Bloomfield River (north) to Herbert River (south), in narrow strip along Queensland's north-eastern coast	Highly seasonal climate, with low inter-annual variability. Summer rains result in high flows and floodplain inundation. Stable baseflow during dry season. Flow magnitude inversely related to tidal penetration.	+1–3°C by 2070; –10% to +5% change in annual rainfall by 2030; more seasonally variable and intense rainfall	Increased flow seasonality and duration of low-flow periods	Increased intensity of cyclones and storm surges; 0.32-m sea-level rise	Russell et al. 1996; Eliot et al. 1999; Williams et al. 2003; CSIRO and Bureau of Meteorology 2007; McJannet et al. 2007
Lake Eyre Basin	Inland draining rivers of Lake Eyre Basin and central Australia	Hot and dry, with highly variable flows. Monsoon-driven rainfall events occasionally result in filling of the terminal Lake Eyre.	1–3°C increase by 2070; –30% to +20% change in annual rainfall by 2070	Hard to ascertain because of already variable flows; large variation in projected rainfall	More intense cyclones potentially increasing flood magnitude	Puckridge et al. 1998; CSIRO and Bureau of Meteorology 2007
SW Australia	Coastal flowing rivers of SW WA, from Arrowsmith River to Israelite Bay	Mediterranean climate. Highly seasonal and predictable stream flow, many aquatic systems intermittent. Existing drying trends of –10% to –15% in rainfall and 50% reduction in some rivers' discharge over the past 35 years. Highly modified catchments.	Increase in extreme-temperature days (>40°C); –8% median-rainfall reduction by 2030; up to 70% rainfall reduction by 2070	–25% annual runoff by 2030; increase in zero-flow days	Up to 10-m groundwater reductions by 2030	Nicholls et al. 1997; IOCI 2002; Halse et al. 2003; Suppiah et al. 2007; CSIRO 2009a, 2009b
SE Australia	Southern and upland streams of Murray–Darling Basin, coastal streams of Vic., and south-eastern NSW	Temperate climate. Maximum precipitation in winter and spring (including snow in upland areas). Maximum stream flow occurs in spring although this displays significant inter-annual variability. Supra-seasonal droughts common. Highly modified catchments.	+0.9–3.8°C by 2070 increase in extreme-temperature days (>40°C); fewer days <0°C; 2–10% reduction in rainfall, 6–10% increases in evapotranspiration	–5% to –10% annual runoff, possibly >–50% runoff in some catchments by 2070; increase in zero-flow days	Increased bushfire frequency; 30–93% reduction in areas covered by snow for >30 days by 2050	Jones and Durack 2005; Nicholls 2005; CSIRO and Bureau of Meteorology 2007; CSIRO 2008
Tasmania	Island of Tasmania	Wet and cool temperate climate. Moderate to high annual rainfalls (744–2537 mm). Large and small perennial lakes, lagoons, swamps and marshes.	+0.6–3°C by 2100; rainfall decreases across all seasons in Central Plateau, summer decreases and winter increases in the south-west, summer and autumn increases in the east	Large spatial differences in changes to annual runoff, from –30% to >+50%	Increased intensity of rainfall events in the east	CSIRO and Bureau of Meteorology 2007; Bennett et al. 2010; Grose et al. 2010

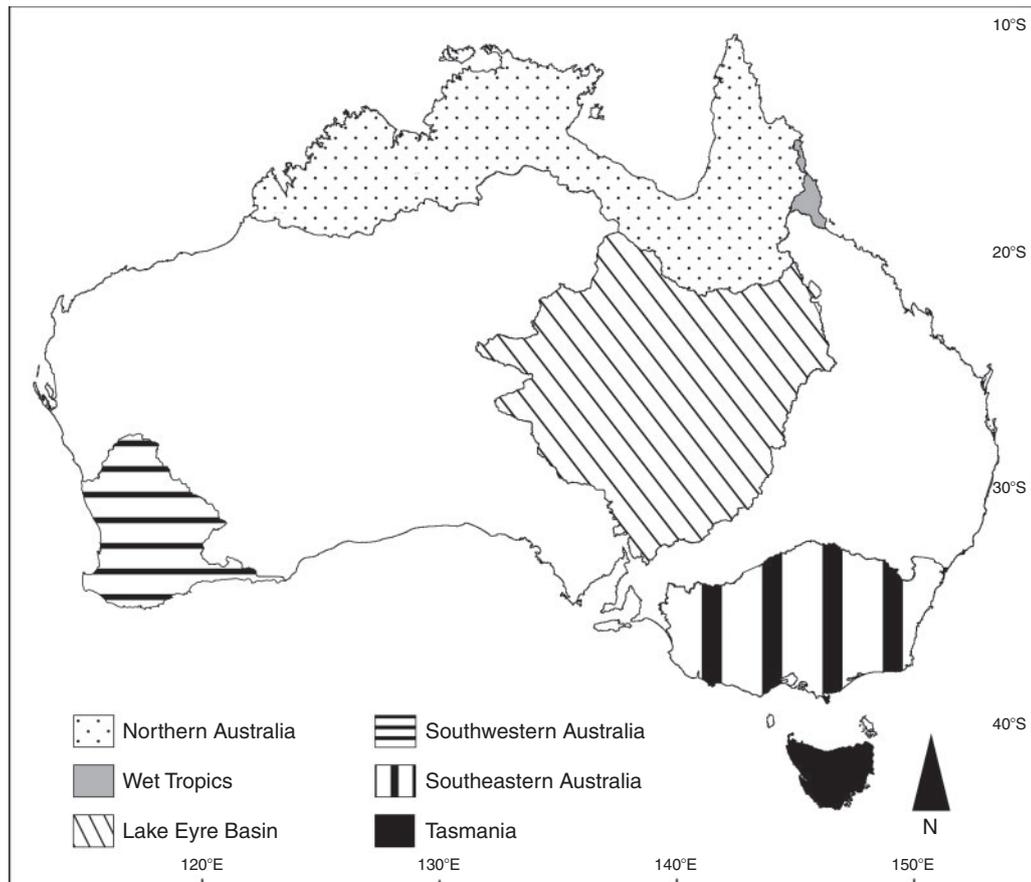


Fig. 3. Australian freshwater regions compared in the review.

experience geographic range shifts and expansions when dispersal is not restricted by barriers. For example, the broad-scale distribution of spangled perch (*Leiopotherapon unicolor*) was suggested to be limited by the 4°C winter isotherm (Llewellyn 1973), whereas more recent research has extended the distribution further south (Schiller *et al.* 1997). Whether this is due to a shift southward of the limiting isotherm, or extension beyond this thermal limit, is unknown. However, range shifts in many other species restricted to this region may be constrained, given the presence of arid zones to the immediate south and the presence of the Great Dividing Range in the east.

Importantly, the generally low levels of human development, near-natural condition of the catchments and flow regimes coupled with the few artificial barriers to fish movement and dispersal mean rivers of northern Australia provide a circumstance where the native fauna is less constrained by human factors in its potential capacity to adjust to system-wide changes as a result of global climate change.

Wet Tropics

Australia's Wet Tropics region is confined to a small and isolated coastal strip in the continent's north-east (Fig. 3) characterised by forested mountain ranges in the upper reaches and cleared alluvial floodplains in the lowlands (Russell *et al.* 1996).

The current climate is highly seasonal, with low interannual variability (Table 1; Kennard *et al.* 2010). During the monsoonal summer months (December–March), air temperature, rainfall and floodplain inundation are at their peaks, whereas stable baseflows extend through the dry season (April–November), maintained by rainfall-recharged groundwater and cloud capture in upland rainforests (McJannet *et al.* 2007). The Wet Tropics region hosts a highly diverse and endemic freshwater fish fauna (~107 species, ~50% of Australia's freshwater fish biodiversity), including representatives from 37 families (Pusey *et al.* 2008). These families can be divided into the following two broad groups: those distinguished by low within-family generic and specific diversity (i.e. one species per family, e.g. Scorpaenidae (bullrout)), and those characterised by higher specific or generic diversity and containing endemics (e.g. Melanotaeniidae (rainbowfishes)). Most of the fish biodiversity is found on the narrow coastal plain, in short, lowland main-channel sections of rivers, owing to natural and anthropogenic instream barriers that limit upstream movement (Pusey and Kennard 1996). However, upland streams are important reservoirs of endemic species because of their prolonged isolation and persistence as refugia through past glacial maxima (Schneider and Moritz 1999).

Climate-change modelling suggests that warming and rainfall changes will be less pronounced on the north-eastern coast

than elsewhere in Australia (CSIRO and Bureau of Meteorology 2007). However, the effects of increased flow seasonality and duration of dry periods (Table 1) is likely to result in greater upstream tidal penetration, longer water-residence times and increased water temperatures (Rayner *et al.* 2008). Increased water extraction for human use also has the potential to exacerbate these effects, with implications for water quality, habitat availability, riparian vegetation structure, instream productivity and ultimately fish assemblages (Pusey *et al.* 2008; Rayner *et al.* 2009). For example, climate-induced alterations to the structure of riparian vegetation communities could affect the availability and consumption of riparian fruits by khaki grunter (*Hephaestus tulliensis*) (Rayner *et al.* 2009). Increases in water-residence time, instream temperature and autochthonous production could advantage alien species such as black mangrove cichlid (*Tilapia mariae*) that consume filamentous algae – a niche that appears under-utilised by native species (Rayner *et al.* 2009). Increases in the intensity of cyclones and rainfall events will result in a concurrent change in flood-disturbance regimes (Eliot *et al.* 1999; Williams *et al.* 2003), and disrupt the seasonal cycle of fish-assemblage structure and function (T. Rayner, unpubl. data).

Cyclonic storm surges will exacerbate the effects of saltwater intrusion associated with sea-level rise (CSIRO and Bureau of Meteorology 2007). Projected sea-level rises are likely to have analogous impacts on the habitat and fishes of the Wet Tropics to those associated with past sea-level rises (e.g. during the Holocene) where between 50 and 400 km of main channel habitat in each catchment was lost (Chivas *et al.* 2001; Yokoyama *et al.* 2001). For example, the lesser salmon catfish (*Arius graeffei*) is not found in the Wet Tropics, whereas it is present in all surrounding systems, where long, low-gradient main channels were maintained during past climate-change events (Pusey *et al.* 2004). In contrast, the presence of high mountains in the region is likely to have buffered fishes from past climate-change events by maintaining flows through cloud capture, especially in small streams. This hypothesis is consistent with the work of Tedesco *et al.* (2005) who found the highest fish species richness in Central and South American and West African drainages that were connected to rainforest refugia during the last glacial maximum. Increases in the basal elevation of orographic cloud formation of 100 m per degree of warming are predicted, with major implications for flow volumes in upland tropical streams (Still *et al.* 1999). Fish species that are restricted to shallow riffle habitats (e.g. Allen's cling-goby (*Stiphodon alleni*), scaleless goby (*Schismatogobius* sp.) and *Glossogobius bellendenensis*; Pusey *et al.* 2004) are particularly vulnerable to extended periods of low rainfall, because their habitats are likely to experience more frequent and extreme drying. Never before have Wet Tropics fish faced the challenge of rapid climate change with the added pressure of human disturbance.

Lake Eyre Basin

Riverine systems in the arid and semiarid interior of Australia are characterised by unpredictable and highly variable hydrology (Puckridge *et al.* 1998). Consequently, rivers persist as a chain of isolated waterholes for most of the time. In the major

catchments, such as the Diamantina/Warburton, Georgina and Cooper, flow and flood events generally occur in summer and occasionally fill large terminal lakes, such as Lake Eyre. The 23 native and 2 alien fish species present in central Australian rivers often have life-history characteristics adapted for these variable habitats (Pusey *et al.* 2004; Balcombe *et al.* 2006; Kerezszy 2010), with the majority of species reproducing throughout the year in permanent waterholes (Balcombe and Arthington 2009). Many fish species from central Australian waterways are also capable of migrating long distances (at least 300 km in the case of *L. unicolor*) in ephemeral desert systems when flow and connection pathways are re-instated (Kerezszy 2010). Additionally, some species such as desert goby (*Chlamydogobius eremius*) and Lake Eyre hardyhead (*Craterocephalus eyresii*) possess specific traits, such as tolerance to hypersaline and hypoxic conditions and the ability to take up oxygen from the air, that enable them to persist in arid environments (Thompson and Withers 2002; McNeil and Schmarr 2009).

Given that arid-zone fish must persist in isolated waterholes for the majority of the time, any prolonged drying of central Australia that exceeds waterhole permanence thresholds would reduce ranges for species in systems where there is already little surface water (Silcock 2009). In extreme cases, such as the Neales catchment in South Australia where only a single permanent waterhole exists (McNeil and Schmarr 2009), prolonged drying could result in catchment-wide extinction of all species. Although most arid-zone fish species have a wide distribution, some are range-limited, and these species would obviously be most at risk if catchments experienced increased drying. Examples include the endemic Cooper Creek catfish (*Neosiluroides cooperensis*) and arid-zone populations of more widespread species such as Australian smelt (*Retropinna semoni*), carp gudgeon (*Hypseleotris* spp.), barred grunter (*Amniataba percoides*) and golden goby (*Glossogobius aureus*). It is important, however, to acknowledge the role of natural environmental variability with, for example, an ephemeral catchment such as the Mulligan containing no water in a dry year and at least seven species of fish following a flood (Kerezszy 2010). Consequently, determining the precise impact of climate change (as opposed to the overall impact of on-going climatic variability) on these arid riverine systems is likely to be difficult.

In contrast, the responses of isolated fish populations in spring complexes to a reduction in the availability of artesian water, associated with less rainfall and groundwater recharge (Fairfax *et al.* 2007), are more predictable. These include range reductions and possible extinction of endangered and endemic species in springs such as Dalhousie in South Australia and Edgbaston and Elizabeth Springs in Queensland. Undoubtedly, the species at most risk from spring drying include the red-finned blue eye (*Scaturiginichthys vermeilipinnis*), which is currently present in only four springs at Edgbaston in western Queensland (Fairfax *et al.* 2007), the Dalhousie endemics (*Neosilurus* sp., *Craterocephalus dalhousiensis*, *Chlamydogobius* sp.) and the Flinders Ranges gudgeon (*Mogurnda clivicola*), which is restricted to two springs in the Northern Flinders Ranges (McNeil *et al.* 2010). These fish species, however, currently face more immediate threats such as alien species (Kerezszy 2009), agricultural development and disease (McNeil and Schmarr 2009). Additionally, water-resource development

in the Lake Eyre Basin is likely to increase under drying climatic conditions, with the possible exploitation of artesian spring resources posing a catastrophic threat to the persistence of these groundwater-dependent species.

South-western Australia

The Mediterranean climate of south-western Australia is characterised by highly seasonal rainfall (Nicholls *et al.* 1997), resulting in seasonal stream flow and significant periods of natural intermittency. As a consequence, the aquatic fauna has evolved under a regime of seasonal inundation of wetlands and annual periods of no-flow in rivers (Bunn *et al.* 1986). However, since 1975, a climatic phase shift has seen significant reductions in rainfall and stream flows (Table 1) (CSIRO 2009a). Furthermore, 80–90% of native vegetation has been cleared for agriculture (Halse *et al.* 2003), resulting in >70% of the Australian continent's secondary salinised areas. Now only ~44% of flow in the largest 30 rivers is fresh (Mayer *et al.* 2005). These current stressors have already caused reductions in the range of aquatic fauna from upstream areas of catchments (e.g. Morgan *et al.* 1998; Halse *et al.* 2003; Davies 2010) and the greatest diversity of freshwater fishes is now found in less-degraded, forested systems (Morgan *et al.* 1998).

Although this region hosts a relatively low-diversity native fish assemblage (10 native, 10 alien species), 80% of these natives are endemic (Morgan *et al.* 1998). Many species have highly restricted distributions; e.g. salamanderfish (*Lepidogalaxias salamandroides*), black-stripe minnow (*Galaxiella nigrostriata*) and mud minnow (*G. munda*) are found almost exclusively in seasonal peat-wetland habitats of the far south-west (Pusey and Edward 1990; Morgan *et al.* 2000). Endemic freshwater fish species of the region breed during high flow periods in winter and spring (Allen *et al.* 2002) and this is the period projected to continue to experience substantial declines in rainfall and discharge (CSIRO 2009a). Many species also move into seasonally inundated tributary or wetland habitats to spawn (e.g. Pen and Potter 1991; Beatty *et al.* 2009). Durational suitability of these habitats has already declined since 1975 and will continue to decline in the face of an additional 25% reduction in annual flow (CSIRO 2009a). The projected additional decreases in rainfall, stream flow and groundwater recharge (CSIRO 2009a, 2009b), and increases in extreme weather events associated with climate change (Table 1), coupled with increased human exploitation of water resources (CSIRO 2009a, 2009b) will only exacerbate current impacts on an already stressed system.

Substantial reductions in groundwater levels will have major implications for habitat availability. For example, groundwater-derived baseflow in the Blackwood River is important in maintaining access to feeding areas (riffles) for freshwater cobbler (*Tandanus bostocki*), with a reduction of just 8% in baseflow discharge predicted to prevent access to riffle zones (Beatty *et al.* 2010b). Further reductions in rainfall will potentially prevent access to these habitats because baseflow magnitude depends on the previous year's rainfall (Golder and Associates 2008). Likewise, projected reductions in groundwater discharge may result in the loss of tributaries as freshwater refugia during baseflow periods (Beatty *et al.* 2009). Further

rainfall and groundwater reductions in the northern region of south-western Australia will threaten the habitats of outlying populations of both *Galaxiella* species (300 km north of common range Morgan *et al.* 1998; Beatty *et al.* 2010a) which are already under pressure from recent flow reductions (Durrant 2009). Reductions in rainfall, delayed onset of the wet season and lowered groundwater levels are likely to seriously threaten the two aestivating species, namely *L. salamandroides* and *G. nigrostriata* (Pusey and Edward 1990). Both species are very small, with limited energetic capacity to persist for many months in the dormant condition; prolongation of this state increases mortality and has serious consequences for subsequent reproductive viability after the onset of winter rains (Pusey 1990).

Salinisation of lotic systems has already altered fish assemblages, causing upstream colonisation by estuarine species and downstream contraction of more sensitive species into remaining fresher habitats (Beatty *et al.* 2009; Beatty *et al.* 2010a). Along with maintaining habitat connectivity, fresh groundwater discharge buffers salinities in the main channel of the Blackwood River (Beatty *et al.* 2010b), resulting in several fishes utilising only the main channel during baseflow periods when most freshwater tributaries cease to flow (Beatty *et al.* 2009). Although the relationship between future rainfall reductions and trends in salinisation of rivers throughout this region is largely unknown (Mayer *et al.* 2005), further reductions in fresh groundwater discharge have the potential to result in the loss of main channel habitat for freshwater fish in many south-western rivers. Some species, such as western minnow (*Galaxias occidentalis*), may be resilient to additional hydrological changes compared with other fish species that have undergone drastic range declines or have highly specialised habitat requirements. This fish has an acute salinity tolerance of 14 g L⁻¹ (Beatty *et al.* 2011) and continues to occupy large areas of inland salinised catchments (Morgan *et al.* 1998; Beatty *et al.* 2011).

Projected increases in the number of extreme-temperature days (i.e. >40°C, Suppiah *et al.* 2007) will increase the risk of the thermal tolerances of fish being exceeded in the small refuge-pool habitats typical throughout the south-west (Davies 2010), which could result in southerly contractions of the region's fish fauna (Booth *et al.* 2011). Temperature is also a critical factor in the reproduction and growth of many freshwater fish species (e.g. Pen and Potter 1991) and changes in prevailing average temperature regimes may lead to a decoupling of the thermal and hydrological conditions essential for reproductive success. Reductions in discharge and elevated temperatures are likely to favour the continued establishment and spread of alien species in south-western Australia, such as mosquitofish (*Gambusia holbrooki*) and goldfish (*Carassius auratus*). In particular, *G. holbrooki* is predicted to increase in prevalence because of its life-history characteristics and high thermal and salinity tolerances (Pyke 2005), with its likely increased dominance of remaining refugia further imperilling the persistence of native species into the future.

South-eastern Australia

South-eastern Australia has a diversity of freshwaters, ranging from coastal rivers to alpine streams (Table 1, Fig. 3) and spans

several biogeographical provinces (Unmack 2001). The seasonally variable climate experiences precipitation peaks in winter and spring, and is frequently punctuated by drought (Murphy and Timbal 2008), with many lowland streams experiencing cease-to-flow conditions for significant periods in most years (Kennard *et al.* 2010). Large areas of this region are heavily developed for agriculture and forestry, or urbanised such that much of the available water is exploited for human consumption. Despite this extensive human disturbance, south-eastern Australia continues to host a relatively high number of native fish species (~54 species, Allen *et al.* 2002; Lintermans 2007). Climate change is predicted to severely affect the freshwaters of this region, with significant declines in rainfall and increases in temperature resulting in less runoff, increased evapotranspiration and decreased groundwater recharge, as well as increased frequency and severity of drought, bushfire and individual rainfall events (Table 1). These additional climatic impacts will add to, or compound, the existing anthropogenic stressors that have already degraded the region's freshwaters.

South-eastern Australia has recently experienced one of the most severe and prolonged droughts on record (Murphy and Timbal 2008). During this 'millennium drought', many small and headwater streams ceased flowing or completely dried out, resulting in the mortality of local fish assemblages and loss of species at the regional level (Bond and Lake 2005; Morrongiello *et al.* 2006). Species particularly affected were river blackfish (*Gadopsis marmoratus*), mountain galaxias (*Galaxias olidus*), southern pygmy perch (*Nannoperca australis*) and the cool-water alien salmonids *Salmo trutta* and *Oncorhynchus mykiss*. These drought conditions reflect projections of longer dry spells and reduced runoff (CSIRO and Bureau of Meteorology 2007) that will intensify cease-to-flow events and potentially lower ground-water levels, thus rendering isolated pool habitats more vulnerable to complete desiccation via evaporation (Lake 2003). Increased drying may also expose acid sulfate soils (Kingsford *et al.* 2011), that when rewetted can seriously affect water quality. The occurrence of locally catastrophic fish kills may increase in the future because flow pulses following extended dry spells have commonly resulted in 'blackwater' events that cause mass mortality of fish because of low dissolved oxygen (Howitt *et al.* 2007) and toxic polyphenols (McMaster and Bond 2008). Reductions in river discharge will increase ephemerality and lead to greater fragmentation and isolation of habitat, potentially limiting genetic exchange among local populations. Although this can result in high levels of genetic structuring within ephemeral streams (e.g. *N. australis* Cook *et al.* 2007), any larger-scale drying may increase the incidence of genetic bottlenecks and the loss of locally adapted genotypes from whole regions.

Fish in many regulated lowland systems of south-eastern Australia probably face fewer acute risks of a drier climate than those in ephemeral systems, although they are still likely to be negatively affected by reduced runoff and increased human water demands. These fish assemblages are already in a generally degraded state and composed of resistant or resilient species (Humphries and Lake 2000). Further reductions in discharge during spring are likely to result in a loss of flow peaks that act as spawning cues for several lowland river fish species (Humphries *et al.* 1999). Reduced flood frequency and magnitude could have

a negative impact on riparian trees such as river red gum (*Eucalyptus camaldulensis*) (Horner *et al.* 2009) and impede the transport of terrestrial organic carbon into the river channel, which helps support the food chain on which fish rely (Robertson *et al.* 1999).

In coastal river systems, most fish species are diadromous and spawn from autumn to winter, coinciding with peaks in river discharge. Recent studies, for example, have found that tupong (*Pseudaphritis urvillii*) (Crook *et al.* 2010b) and Australian grayling (*Prototroctes maraena*) (Koster and Dawson 2009) undertake downstream spawning migrations in response to within-channel flow peaks. O'Connor and Mahoney (2004) also showed that *P. maraena* will reabsorb their eggs and fail to spawn if appropriate flows do not occur during the autumn–winter period. Reductions in the frequency of flow peaks in autumn–winter that trigger spawning behaviour, therefore, present a potential threat to reproduction and recruitment of diadromous species in coastal river systems. Reduced flows are also associated with increased periods of estuary mouth closure and species that exhibit obligate diadromy will not be able to complete their life cycles if they are unable to access the sea at the appropriate time of year (Gillanders *et al.* 2011).

Climatic warming may compound stressors associated with stream drying through raised water temperatures and associated reduced dissolved oxygen, resulting in the physiological tolerances of at least some species being surpassed (McNeil and Closs 2007; McMaster and Bond 2008). Successful spawning and recruitment under such conditions is highly unlikely, even if a pool ultimately retains enough water to permit survival of the resident fish. For example, the maximum sustained tolerable temperatures for adult *G. marmoratus*, *N. australis* and *R. semoni* are within the range 27–29°C, whereas gamete viability and larval survival of *N. australis* and *R. semoni* are very low at these levels (Harasymiw 1983). Projected increases in fire frequency and severity in upland areas could also have catastrophic impacts on fishes, because of acute thermal stress, water quality degradation, habitat loss and sedimentation (Lyon and O'Connor 2008). Species such as barred galaxias (*G. fuscus*), two-spined blackfish (*G. bispinosus*) and Macquarie perch (*Macquaria australasica*) are particularly vulnerable to local extinction because of their already fragmented ranges (Lintermans 2007), whereas aliens such as salmonids will experience range contractions as a result of widespread warming (Bond *et al.* 2011).

A warmer climate may also facilitate increases in the range or abundance of some species in south-eastern Australia normally associated with warmer or more northern freshwaters (Bond *et al.* 2011; Booth *et al.* 2011). For example, the southerly range of golden perch (*M. ambigua*) is partly temperature-limited. Morrongiello *et al.* (2011) found that during the recent drought, the annual growth of *M. ambigua* in south-eastern Australian lakes was negatively correlated with declining water levels; however, this effect was offset by increased growth during warmer years. Despite climatic models projecting significant declines in future water availability, fish growth may increase because of a disproportionate lengthening of the growing season, and thus make these higher latitudes more favourable habitat. Such a pattern is supported by modelling of *M. ambigua*'s distribution under future climate-change scenarios (Bond

et al. 2011). The potential for such range shifts may, however, be retarded by in-stream barriers or geographic features (Booth *et al.* 2011; Morrongiello *et al.* 2011).

Tasmania

Tasmania's unique freshwater environment is characterised by an extensive network of lentic water bodies, particularly in the state's Central Plateau region (Table 1; Hardie *et al.* 2006), resulting in a highly endemic fish fauna (Allen *et al.* 2002). This region's 10 endemic galaxiids naturally have restricted distributions; however, the additional impacts of predation by alien fish species and anthropogenic catchment and waterway manipulations for hydro-electricity generation (Hardie *et al.* 2006; Stuart-Smith *et al.* 2007), irrigation and recreation have resulted in distributions being further constrained. Limited life-history and physiological-tolerance information is available for most of the galaxiid endemics; however, they are thought to be adapted to predictable and relatively benign conditions, and thus to be sensitive to environmental change.

In Tasmania, climate change is projected to result in more seasonally and spatially variable rainfall, with concordant shifts in local hydrology (Fig. 2). In the upper Derwent and Lake St Clair regions, catchment runoff is projected to significantly decline, particularly during summer (Bennett *et al.* 2010). In the Lake Pedder region, rainfall is projected to increase over winter and decline over summer, with no significant change to mean annual levels (Grose *et al.* 2010). Swamp galaxias (*Galaxias parvus*, Lake Pedder) and Clarence galaxias (*G. johnstonii*, Upper Derwent) are endemic to these regions of Tasmania's south-west and rely on marshes and headwater rivulets as important refuges from predation and competition from brown trout (*S. trutta*) and the more widespread climbing galaxias (*G. brevipinnis*) (Crook and Sanger 1998a; Threatened Species Section 2006). Reduced summer runoff is likely to diminish habitat availability and connectivity, which may lead to further population declines for both species, as evidenced by recent surveys that indicate negative drought impacts on several *G. johnstonii* populations (Inland Fisheries Service, unpubl. data). Further, although projected increases in winter runoff may facilitate population connectivity, it may also heighten the risk of refuge invasion by *S. trutta* and *G. brevipinnis* because of increased stream flow and barrier inundation (Crook and Sanger 1998a).

Freshwaters on Tasmania's Central Plateau will experience the most significant declines in runoff, with average projected decreases of between 15% and 35% by 2100 (Bennett *et al.* 2010). Inflow changes for three representative lakes in the Central Plateau region (Great Lake and Lakes Crescent and Sorell) are included in Fig. 2. This area supports six endemic fish species, all likely to be affected by climate change, in addition to significant existing stressors. Declining lake levels have the potential to reduce refuge and spawning habitat for paragalaxiids (*Paragalaxias julianus*, *P. dissimilis*, *P. eleotroides* and *P. mesotes*) and saddled galaxias (*G. tanycephalus*), in turn leading to increased predation, increased risk of recruitment failure and a subsequent reduction in their abundance. Inflow decreases are also likely to influence power generation from these lakes, resulting in increased abstraction and altered water level-management regimes, as well as causing acute and

chronic water-quality deterioration within shallow lakes and lagoons.

Spawning of golden galaxias (*G. auratus*) in Lakes Crescent and Sorell has been linked to rising water levels in late autumn to winter, which are needed to inundate the critical spawning habitat of cobbled littoral areas (Hardie *et al.* 2007). Spawning takes place in water temperatures ranging from 1.4°C to 9.7°C, with spawning peaks recorded in winter when temperatures were below 5°C (Hardie *et al.* 2007). Decreased winter inflows, coupled with projected warming of up to 2.5°C, may reduce spawning success by limiting habitat access and altering thermal cues.

One endemic galaxiid that may not be negatively affected by climate change is Swan galaxias (*G. fontanus*), which inhabits a restricted number of headwater streams around Tasmania's eastern highlands and midlands region (Crook and Sanger 1998b). This species appears to be remarkably tolerant of high temperatures, low oxygen and high chemical concentrations associated with low flows in residual stream-pool habitats (Threatened Species Section 2006); however, a significant number of *G. fontanus* monitoring sites were dry in 2008–2009 (Inland Fisheries Service, unpubl. data). Nonetheless, although climate-change projections indicate that mean annual temperatures will increase in the region by several degrees, modelling (Fig. 2) indicates that inflows are projected to increase in the region and this is likely to decrease the threat of habitat loss resulting from headwater drying. In general, climate change is likely to increase the risk of population decline for many of Tasmania's endemic galaxiids proportional to projected hydrological change. These risks, however, need to be put into perspective with existing threatening processes (Hardie *et al.* 2006), particularly alien species, irrigation development and hydro-electricity generation.

Adaptive potential among and within species

The evolution of Australia's fish species in a variable and unpredictable environment has led, in part, to a depauperate fauna (Allen *et al.* 2002). Yet this has also meant that many species have adaptations that enable survival, exploitation and even dependence on these unique conditions. Equally important, however, is the acknowledgement that other fish species have very localised ranges and narrow tolerances because of isolation and habitat or physiological specificity (Unmack 2001). Population and species persistence under climate change depends on the interplay between ecological and evolutionary processes (Fig. 1; Kinnison and Hairston 2007); the study of variation in life-history traits provides a valuable evolutionary perspective to current and historical ecological processes and facilitates the prediction of species' responses to future climatic scenarios.

Functional traits, such as life-history strategies, have been used to characterise groups of species and predict their response and vulnerability to environmental change (Winemiller 2005). For example, Humphries *et al.* (1999) used reproductive and larval developmental traits to categorise the responses of Murray–Darling species to flow parameters, whereas Crook *et al.* (2010a) explored the sensitivity of south-eastern Australian fish species to the impacts of drought by characterising resistance and resilience traits. The approach of this latter study is potentially useful for exploring the impacts of climate

change, as increasingly drought-like conditions have been projected for much of inland Australia (CSIRO and Bureau of Meteorology 2007). Among-species trait-based approaches have also been used for comparisons among regions such as along hydrologic gradients in southern USA and eastern Australia (Olden and Kennard 2010).

For species to persist in the face of climate change, they require traits that allow them to resist its impacts (1) *in situ* (e.g. thermal tolerances, plastic or adapted life-history characteristics), (2) by moving to more favourable locations (e.g. individual dispersal potential, scope for range shifts) or (3) by rapidly evolving mechanisms that confer resistance or resilience (Parmesan 2006). Australia's variable environment means that many fish species are exposed to different conditions across their range, such that preferential phenotypes in one population may be unfavourable in others. In the absence of constraints, divergent natural selection can result in the adaptation of populations, through specialist genotypes, to their local conditions (reviewed by Kawecki and Ebert 2004). Conversely, temporal environmental heterogeneity or significant gene flow may result in set trait values not being beneficial in unpredictable conditions, or adaptations diluted by immigrants. These conditions favour the evolution of adaptive phenotypic plasticity where genotypes produce different phenotypes of relatively high fitness under all environments, or dominant generalist genotypes with moderate fitness in all environments.

The exploration of within-species trait and genetic variation has only recently begun in Australian freshwater fish species and initial results indicate that significant variation in both is the norm (e.g. *N. australis* reproductive investment, colouration, genetics: Llewellyn 1974; Humphries 1995; Cook *et al.* 2007; Morrongiello *et al.* 2010; *M. ambigua* reproductive behaviour, genetics: Pusey *et al.* 2004; Balcombe *et al.* 2006; King *et al.* 2009; Faulks *et al.* 2010). The degree to which observed trait variability is related to local adaptation or phenotypic plasticity remains largely unknown; however, it does raise the possibility that some populations have an inbuilt adaptive potential to persist under changing environmental conditions. Nonetheless, the rate of climate change and the existence of other current stressors such as habitat fragmentation may render any trait or genetic variability ineffective in saving species from range reductions or extinction.

Management considerations

Future climate impacts on freshwater fish biodiversity and the required adaptation responses will depend not only on the rate and magnitude of climate change, but on the ability to reduce system vulnerability and increase system resilience by treating existing impacts and conserving freshwater habitat (Fig. 1).

Alien species

The introduction and spread of alien species has significantly impacted on freshwater environments worldwide (Dudgeon *et al.* 2006). These impacts now need to be considered in concert with climate change. Alterations to the thermal and hydrological regime of freshwaters will significantly interact with natural and anthropogenic factors, the ability of alien species to become established, their interactions with native fish species and

ecosystem functioning, as well as the control strategies required to ameliorate impacts (Rahel and Olden 2008). Alien species already make up a significant proportion of Australia's freshwater fish diversity (~206 natives: Allen *et al.* 2002; ~43 aliens: Koehn and MacKenzie 2004) and trends indicate that the proportion of aliens is likely to increase (Koehn and MacKenzie 2004; Lintermans 2004). Similarly, at least 53 native species are known to have been translocated, mostly outside their natural range (Lintermans 2004).

The changing impacts of alien species were identified as a major issue in the regional summaries above, suggesting that climate change will alter or intensify the nature of interactions between native and alien species, and increase the prevalence of novel or homogenised fish assemblages (Hobbs *et al.* 2006; Olden *et al.* 2008), which will raise further management implications. Some aliens will benefit from warmer temperatures, habitat degradation and increased modification of natural flow regimes (Bunn and Arthington 2002; Koehn 2004; Kennard *et al.* 2005), whereas others will be detrimentally affected by increases in flow ephemerality, disturbance and the surpassing of physiological tolerances (Closs and Lake 1996; Lyon and O'Connor 2008; Costelloe *et al.* 2010). Identifying the factors that give alien species competitive advantages or disadvantages over native species are key requirements for managing the threat of alien fish species under climate change.

The role of refugia

Refugia are integral properties of the abiotic environment that confer resistance or resilience on biota to disturbance and will play a vital role in facilitating the persistence of the species into the future. By definition, refuge habitats are a relative concept and depend on the species present, their adaptations and the spatial and temporal scale of disturbance (reviewed in Magoulick and Kobza 2003). Intertwined with the natural persistence of refugia into the future are anthropogenic impacts that increase climatic pressures on refuge biota (e.g. water allocation away from refuge habitats, catchment modification and habitat fragmentation). A significant increase in the awareness of refugia and their integration into legislative and management-policy frameworks is required to reduce impacts of future climate change (D. G. McNeil, S. K. C. Gehrig, G. Peters, J. Marshall, K. Cheshire, J. Lobegeiger, S. Balcombe, N. Bond, P. Reich and T. Barlow, unpubl. data). Likewise, more work is needed to fully understand the spatial and temporal extent over which current refugia are effective, the importance of connectivity among refugia, and their likely persistence and form under climate-change scenarios.

Learning from experience

The recent drought in south-eastern Australia has served as a 'dry run' for a drier climatic future, with the fate of many native fish populations dependent on emergency interventions by management agencies. Recently, in Victoria, environmental flows have been released to sustain populations of Murray hardyhead (*Craterocephalus fluviatilis*) and individuals from several *G. fuscus* populations were maintained in captivity to facilitate restocking after their catchments were badly burnt by bushfire. Although reactive rather than proactive, these

measures are likely to have played a vital role in preventing the extinction of both species. In general, however, the allocation of water to protect threatened refuge populations has been difficult to obtain, particularly with increasing human demands. A further problem is that the majority of threatened species and critical refuge habitats exist within unregulated waterways and off-channel habitats, where water delivery may be impossible or unfeasible. Emergency responses such as fish rescues and captive-breeding programs have been widely undertaken in response to the recent drought (see the South Australian Drought Action Plan); however, they do not provide a long-term option for maintaining fish populations under a drying climate future. Management interventions around key fish habitats need long-term and proactive vision, with the aim of ameliorating the impacts of water abstraction and land-use practices. It is imperative that contingencies developed under the recent drought are not forgotten during intervening wet periods and that a focus is maintained on planning for the protection of native fish species under future drought and drying climatic regimes.

Preserving genetic diversity

Understanding the importance of genetic variability in determining how species will respond to climate change is critical to developing strategies to conserve the diversity of fish species in Australian freshwaters (*sensu* Adkison 1995). If trait variation is locally adaptive or dispersal potential low, then a range of populations would need to be protected to ensure that underlying genetic diversity is conserved (Adkison 1995; Hughes 2007). Conversely, if trait variation is plastic, then conservation management should focus on preserving a variety of habitats to ensure that a range of life histories continues to be expressed in wild populations (Beechie *et al.* 2006). Both scenarios bestow on species a capacity to adapt to climate change.

Managed translocation

Many freshwater fish species are particularly vulnerable to the impacts of climate change because they cannot resist *in situ*, lack adaptive potential or are prevented from moving to more favourable environments by natural and anthropogenic barriers. The future conservation of many of these species may therefore rely on proactive managed translocation of individuals to areas, either within or outside natural ranges, where conditions are more favourable (Richardson *et al.* 2009). Although such interventions have obvious appeal, there are ecological and management implications that need to be considered (Olden *et al.* 2011). For example, translocated species (e.g. translocated mouth almighty (*Glossamia aprion*) is suspected of causing the local extinction of Lake Eacham rainbowfish (*Melanotaenia eachamensis*) in Lake Eacham; Barlow *et al.* 1987) or genotypes within species (e.g. freshwater shrimp (*Paratya australiensis*); Hughes *et al.* 2003) may have a detrimental impact on local species or endemic genotypes. Conversely, translocated populations of the threatened *M. australasica* and Pedder galaxias (*G. pedderensis*) have played a vital role in preventing these species going extinct, although the impacts of these translocations on native species in receiving areas is unclear (Hamr 1995; Lintermans 2006). Olden *et al.* (2011) documented a series of recommendations that should be considered before any planned

translocation occurs. These include assessing the trade-offs between the probability of extinction in the donor region versus the probability of causing declines of native species or loss of ecosystem function in the recipient region (e.g. by life-history and ecological traits), the preferential translocation of species within their natural range (dependent on genetic assessments), an examination of the trade-offs between actively facilitating a species' range expansion through barrier removal and habitat restoration and the probability of range expansion by non-natives, and strategically targeting receiving waters to convey the best long-term resistance to climate change on translocated species.

We emphasise, however, that interventionist measures such as managed translocation, although a legitimate option, should be considered as a last resort in dealing with climate-change impacts. Instead, it is better if the resilience of a system or assemblage is maintained through the mitigation of current and well known stressors such as water abstraction, habitat fragmentation and loss, water-quality degradation and the spread of alien species, coupled with the conservation of representative aquatic habitats and fish populations (Kingsford 2011; Kingsford *et al.* 2011; Pittock and Finlayson 2011; Pratchett *et al.* 2011).

Conclusion

Climate change will have differential implications for Australia's freshwater fish, in part dependent on current levels of anthropogenic stress. We predict that a drier, warmer and more variable climate will have a negative effect on many native fish species. Projected hydrological changes will be a particularly important driver because these will affect habitat quality, connectivity and persistence as well as disrupt key life-history processes. Our conclusion differs somewhat from those of other studies worldwide (e.g. Buisson *et al.* 2008; Graham and Harrod 2009; Heino *et al.* 2009; McCullough *et al.* 2009) that have strongly implicated warming as being the major impact on freshwater fish assemblages through the surpassing or optimisation of thermal tolerances. This key difference likely reflects the primary focus of many studies on northern hemisphere or high-latitude freshwater environments where water availability is currently not, and is unlikely to be, limiting. Further research into the implications of climate change on arid and semiarid freshwater systems worldwide is needed because these environments will continue to experience significant water deficits (Bates *et al.* 2008) that will threaten the persistence of fish assemblages into the future.

It is important to recognise that Australia's fish fauna has often (but not always) evolved in a variable and unpredictable environment and this legacy may confer some degree of resistance or resilience to climate-change effects. The danger is that any such adaptive potential has already been eroded by current anthropogenic stress or will be swamped by the rate of climatic change. We encourage further research into the lethal (e.g. physiological tolerances) and sublethal (e.g. reproductive requirements) responses to environmental conditions by species and a more thorough examination of feedback loops involving climate drivers and anthropogenic pressures. This additional knowledge will facilitate more accurate predictions

of climate-change impacts on fish and also pragmatic solutions to managers. However, it is vital that our present understanding of environment–biota interactions is not forgotten but incorporated into current actions via a proactive and adaptive approach to managing the effects of climate change.

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