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Climate-change threats to native fish in degraded rivers and floodplains of the Murray–Darling Basin, Australia

Stephen R. Balcombe[A,E], *Fran Sheldon*[A], *Samantha J. Capon*[A], *Nick R. Bond*[B,C], *Wade L. Hadwen*[A], *Nick Marsh*[D] *and Sofie J. Bernays*[A]

[A]Australian Rivers Institute and eWater Cooperative Research Centre, Griffith University, Nathan, Qld 4111, Australia.
[B]School of Biological Sciences and eWater Cooperative Research Centre, Monash University, Clayton, Vic. 3800, Australia.
[C]Present address: Australian Rivers Institute, Griffith University, Nathan, Qld 4111, Australia.
[D]Yorb Pty Ltd, 906 Sandgate Road, Clayfield, Qld 4011, Australia.
[E]Corresponding author. Email: s.balcombe@griffith.edu.au

Abstract. Many aquatic ecosystems have been severely degraded by water-resource development affecting flow regimes and biological connectivity. Freshwater fish have been particularly affected by these changes and climate change will place further stress on them. The Murray–Darling Basin (MDB), Australia, represents a highly affected aquatic system with dramatically modified flow regimes. This has impaired the health of its rivers, and potentially limited the adaptive capacity of its biota to respond to a changing climate. Here, we present our predictions of the potential impacts of climate change on 18 native fish species across their distributional ranges against the back-drop of past and continuing water-resource development (WRD). Because most of these species are found across a wide range of geographical and hydrological settings, we classified the MDB into 10 regions to account for likely variation in climate-change effects, on the basis of latitude, elevation and WRD. Cold water-tolerant species will be under greater stress than are warm water-tolerant species. In some regions, the negative impacts on exotic fish such as trout are likely to improve current conditions for native species. Because the impacts of climate change on any given species are likely to vary from region to region, regional fish assemblages will also be differentially affected. The most affected region is likely to occur in the highly disturbed Lower Murray River region, whereas the dryland rivers that are less affected in the northern MDB are likely to remain largely unchanged. Although climate change is a current and future threat to the MDB fish fauna, the continued over-regulation of water resources will place as much, if not more, stress on the remnant fish species.

Additional keywords: conceptual models, native fish, regionalisation, riparian vegetation, water-resource development.

Introduction

Climate change, with associated changes in land use, atmospheric CO_2 concentration, nitrogen deposition and acid rain, as well as introductions of exotic species, is considered one of the most important determinants of current declines in global biodiversity (Sala *et al*. 2000). The challenge for ecologists is to predict the likely responses of species and communities to climate change over and above the background natural ecological variability (Verschuren *et al*. 2000) and, in heavily modified areas, above and beyond the effects of human development.

Humans already withdraw ~50% of available freshwater resources globally (Szöllosi-Nagy *et al*. 1998), with requirements increasing almost 10-fold during the 20th century (Biswas 1998). The effects of this development on aquatic ecosystems have been severe, evidenced by the numerous global and regional assessments that depict accelerating losses of biodiversity and declines in ecosystem function (Vörösmarty *et al*. 2000). These impacts in freshwater ecosystems stem from changes to the natural flow regime (Poff and Zimmerman 2010), loss of river–floodplain connectivity (Tockner *et al*. 2008) and channelisation and construction of in-stream barriers, to name a few. The added effects of climate change in already stressed ecosystems will only further exacerbate the decline in freshwater biota (Pittock and Finlayson 2011).

In Australia, most of the larger rivers in the south-east of the country suffer from extensive agricultural and rural development and a consequent decline in river ecosystem health (Mercer and Marden 2006). The most notable are the rivers of the Murray–Darling Basin (MDB) located in the south-east of Australia. The MDB occupies ~14% of the continent's surface area (1.07 million km^2), produces ~40% of the country's annual agricultural production (Crabb 1997) and annually contributes ~AU$18 billion worth of produce to the national economy (MDBA 2010). As a focus for intensive agricultural production, there is intense interest in the condition of aquatic ecosystems in

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the MDB, as well as the possible impacts of climate change (Davies *et al*. 2010).

There has been widespread degradation of both riverine and floodplain biota in the MDB, with large tracts of floodplain forest transitioning to terrestrial ecosystems (Pittock and Finlayson 2011). In their assessment of fish species, hydrology and macroinvertebrates, Davies *et al*. (2010) found 20 of the 24 river basins to be in poor or very poor condition. The impacts of flow modifications, including thermal pollution, have been implicated in the demise of native fish in the MDB-regulated rivers, because of their impacts on physiology, spawning and movement (Gehrke and Harris 2001; Growns 2008). Native fish numbers are now only 10% of pre-European levels (MDBC 2004) because of factors such as changes to the natural flow regime, habitat degradation and barriers to biological connectivity (Pratchett *et al*. 2011). Assessing how climate change will affect fish species in the MDB must consider these previous and continuing impacts.

Much in-stream fish habitat has been lost as a result of wood removal across the MDB (Koehn *et al*. 2004). Disruption of riparian–riverine linkages and the loss of riparian and floodplain flora will continue to result in impacts to MDB fish, aside from the direct impacts of river regulation. In the present review, we begin by exploring the effects of water resource and climate change on riparian and in-stream vegetation in the MDB. We then assess how climate change might alter native fish assemblages across the MDB by focussing on 18 individual species, spanning the majority of fish within any local assemblage within the MDB (largely on the basis of distribution maps from Lintermans (2007)). These impacts are presented in a regional context to demonstrate how responses are likely to differ across climate zones and levels of water-resource development.

Climate change impacts in the Murray–Darling Basin

Projected changes to temperature, rainfall and evaporation, particularly in inland Australia, will alter the frequency and magnitude of heavy rain events, floods and droughts, and affect runoff, soil moisture and salinity on a regional basis (Pittock 2003). In the northern and southern MDB, declines of between 8% and 12% of median runoff, with <5% change in the central, eastern and southern upland regions, are predicted (PMSEIC 2007). The frequency of drought is predicted to increase by 20–40% by 2030 (compared with 1975–2000 average) (PMSEIC 2007). Most global climate models indicate that future winter rainfall is likely to be lower across the MDB, particularly in the southern MDB (CSIRO 2008), which is significant because most of the rainfall and runoff occurs in winter in this region.

Although the median 2030 climate projections suggest an overall reduction of 11% in average surface-water availability across the MDB, there are strong regional variations, with reductions of 3% in the Paroo catchment, 12% for the Murray River at Wentworth and 21% in the Wimmera (CSIRO 2008). These changes in runoff- and surface-water availability must be set against a backdrop of historical levels of water use in the basin of ~50%, which have already caused widespread changes in the nature of riverine and floodplain ecosystems.

Predicted impacts on riparian and floodplain vegetation in the Murray–Darling Basin

River red gum (Eucalyptus camaldulensis)

River red gums are the iconic trees of the MDB and contribute significant structural woody habitat and finer organic material (Koehn *et al*. 2004) that provide shelter from predators, food and nutrients. River red gums form extensive forests within the Murray and Murrumbidgee catchments (e.g. Barmah–Millewa Forest) and fringe most of the main rivers and tributaries throughout the basin (Roberts 2001). The species is found across a large temperature gradient and can utilise a range of water sources, including surface- and groundwater sources (Thorburn *et al*. 1994). Their distribution, density and condition, however, are closely linked to flooding, particularly flood frequency (Roberts 2001). Consequently, changes in flood frequency are usually associated with changes in river red gum condition. In the Barmah Forest, for example, river red gum trees have historically withstood an absence of flooding for up to 18 months during droughts in 1982 and perhaps also during droughts of a similar duration in 1904, 1915, 1944 and 1967 (Bren *et al*. 1987). The extreme drought in the lower MDB since the mid-1990s, however, has stressed or killed a large number of river red gums.

Impacts of water-resource development on river red gums have occurred as a result of changes in flood frequency, duration and magnitude (Cunningham *et al*. 2007). Where parts of the floodplain have been permanently inundated, large stands of river red gum have perished. Individual trees and river red gum forests in other locations are stressed because of a lack of flooding of sufficient duration and frequency. Reductions in flooding associated with river regulation and water abstraction have probably impaired recruitment. Increased groundwater salinity, also associated with river regulation in parts of the MDB, has further contributed to declining river red gum health (Overton *et al*. 2006).

Climate-change impacts on river red gums are most likely to manifest themselves through changes in the frequency and magnitude of floodplain inundation events. Trees and forests already stressed by water-resource development may exhibit mass mortality as a result of the increased stress associated with further reductions in flooding caused by climate change. Increased duration of dry spells, along with higher temperatures, may reduce survivorship of seedlings. Such impacts to river red gums, leading to less structural woody habitat, will have significant implications for fish, such as Murray cod (*Maccullochella peelii*) (Koehn 2009) and trout cod (*Maccullochella macquariensis*) (Nicol *et al*. 2007). Reduced inputs of organic matter from finer material such bark and leaves will also have an impact on food supply for small-bodied fish and cascade upwards through food webs, whereas the loss of stream-side canopy may increase algal growth and further exacerbate rising water temperatures as a result of reduced shading.

Lignum (Muehlenbeckia florulenta)

Lignum shrubland occurs throughout the MDB, with large stands on the floodplains of the lower Warrego River, Barwon–Darling River and northern Darling tributaries (Roberts 2001). In the eastern MDB, it fringes the more ephemeral or temporary waterbodies. Lignum is very tolerant of drought conditions and can survive as a leafless shrub for several years on low rainfall with little to no flooding (Craig *et al*. 1991; Capon 2003). After long dry spells, lignum responds quickly to either flooding or rainfall through rapid leaf growth and flowering (Capon *et al*. 2009). Lignum shrubland is particularly significant in the MDB as breeding habitat for colonial waterbirds, especially where it comprises large, mature shrubs in intermediately flooded areas (Capon *et al*. 2009).

Impacts of water-resource development on lignum shrubland in the MDB are likely to have been minimal in comparison with the widespread historic clearing of this species. Lignum is intolerant of prolonged flooding (Roberts 2001; Capon 2003), so reductions in flood frequency and duration associated with water-resource development do not appear to have resulted in significant declines in the health of remaining lignum stands. Instead, this may have allowed lignum to increase its range into areas that were previously flooded more frequently or for longer durations, such as in the terminating wetlands of the northern MDB dryland rivers.

Higher air temperatures and reductions in rainfall and flood frequency and duration associated with climate-change scenarios may alter the character and condition of lignum stands throughout the MDB and, therefore, their value as habitat. Lignum recruitment appears to be closely linked to hydrology (Capon *et al*. 2009) and further alterations to flooding patterns may change the population structure of lignum stands as well as facilitating the further encroachment into channels and open water areas by seedlings. Such impacts are likely to have implications for fish populations in the MDB by altering habitat and food-web structure, via flow-on effects of impacts to piscivorous waterbirds that rely on lignum shrublands for habitat and via changes to inputs of organic material (e.g. lignum leaves).

Aquatic grasses, reeds, rushes and sedges

Emergent macrophytes, including grasses, sedges, reeds and rushes, are widespread across the MDB's floodplains, wetlands and waterway fringes. Prominent and ecologically significant species include grasses such as couch (*Cynodon dactylon*), Moira grass (*Pseudoraphis spinescens*), water couch (*Paspalum distichum*) and common reed (*Phragmites australis*) as well as bulrushes (*Typha* spp.) and sedges such as *Eleocharis* spp. and *Cyperus* spp. Most species exhibit some tolerance to both inundation and drying, although life-history responses vary widely, reflected by species distributions (Roberts 2001). Some species (e.g. Moira grass and water couch) require frequent, seasonal inundation, whereas others (e.g. common reed) can persist through considerable periods of drought both as mature plants and as persistent rhizomes in the soil. In contrast, bulrushes grow in water to 2 m deep and, although they can tolerate water regimes that vary from permanently wet to seasonally or periodically dry, they do not tolerate permanent flooding over 2 m deep and can only tolerate dry conditions for short periods after the growing season (Roberts 2001).

The impacts of water-resources development are likely to have varied amongst species in this group, depending on their particular environmental tolerances and life histories. Anecdotal evidence, for instance, suggests that common reed was historically more widespread in terminal floodplains of the MDB and the decline in the extent of this species may reflect reductions in flood frequency, as well as grazing pressure, in such areas (Roberts 2001). Moira grass plains on floodplains of the Murray River are also threatened as a result of water-resources development, both as a direct result of changes in flood frequency, duration and timing on the life history of this species, as well as indirectly as a result of their encroachment by both river red gum and giant rush because of altered flooding patterns (Bren 1992; Roberts 2001).

Further reductions in the duration and frequency of flooding, which are likely under many climate-change scenarios, will have a major impact on many plant species in this group, and further reductions in the extent of Moira grass plains and stands of common reeds are of particular concern. Higher air temperatures, combined with lower humidity, have the potential to affect germination and regeneration of these species through reduced soil moisture. Survival of persistent propagules (e.g. rhizomes) may also decline as a result of declining soil moisture and flood frequency. Bulrushes are also likely to be affected by altered flooding patterns associated with water-resources development and climate change.

Although *Typha* stands may well expand in certain regions of the MDB under climate-change scenarios, favoured by warm, nutrient-rich conditions, in other areas where water levels and soil moisture decline and the periods between flooding are extended, *Typha* stands may disappear. Such loss of grasses and reeds, particularly in terminating and off-channel wetlands, are likely to have a significant impact on smaller-bodied fish species, such as pygmy perch and carp gudgeons, that rely on them for both cover and food. Furthermore, plants such as reeds and grasses that fringe river channels also provide significant organic inputs to fish food webs; losses would reduce fish abundance and diversity (Fig. 1).

Conceptual models of predicted climate-change impacts on some iconic MDB fish species

Environmental filters have been used to predict changes in fish species presence on the basis of their physiological and habitat requirements (Poff 1997; Bond *et al*. 2011). However, patchy information on environmental tolerances of many MDB fish taxa limits predictions of impacts from climate change. Many MDB fish species appear to be ecological generalists (flexible breeding strategies, diet and habitat), given their wide distribution across varying climatic and geographical regions (Lintermans 2007). Therefore, the main climate-change drivers for generalist fish within the MDB will relate to flow (and therefore changes in habitat availability) and to physiological impacts felt through increased water temperatures influencing spawning times and reduced oxygen levels impairing fitness and survival (Fig. 2; Pankhurst and Munday 2011). Given the overriding impacts of current levels of water-resource development on fish throughout the MDB, our predictions of climate-change impacts acknowledge how individual species have already been affected, and will continue to be so, by water-resource development (MDBC 2004).

The impact of climate change on invasive species will also be relevant to native fish. Invasive species are expected to undergo a mix of responses to climate change, reflecting the diverse

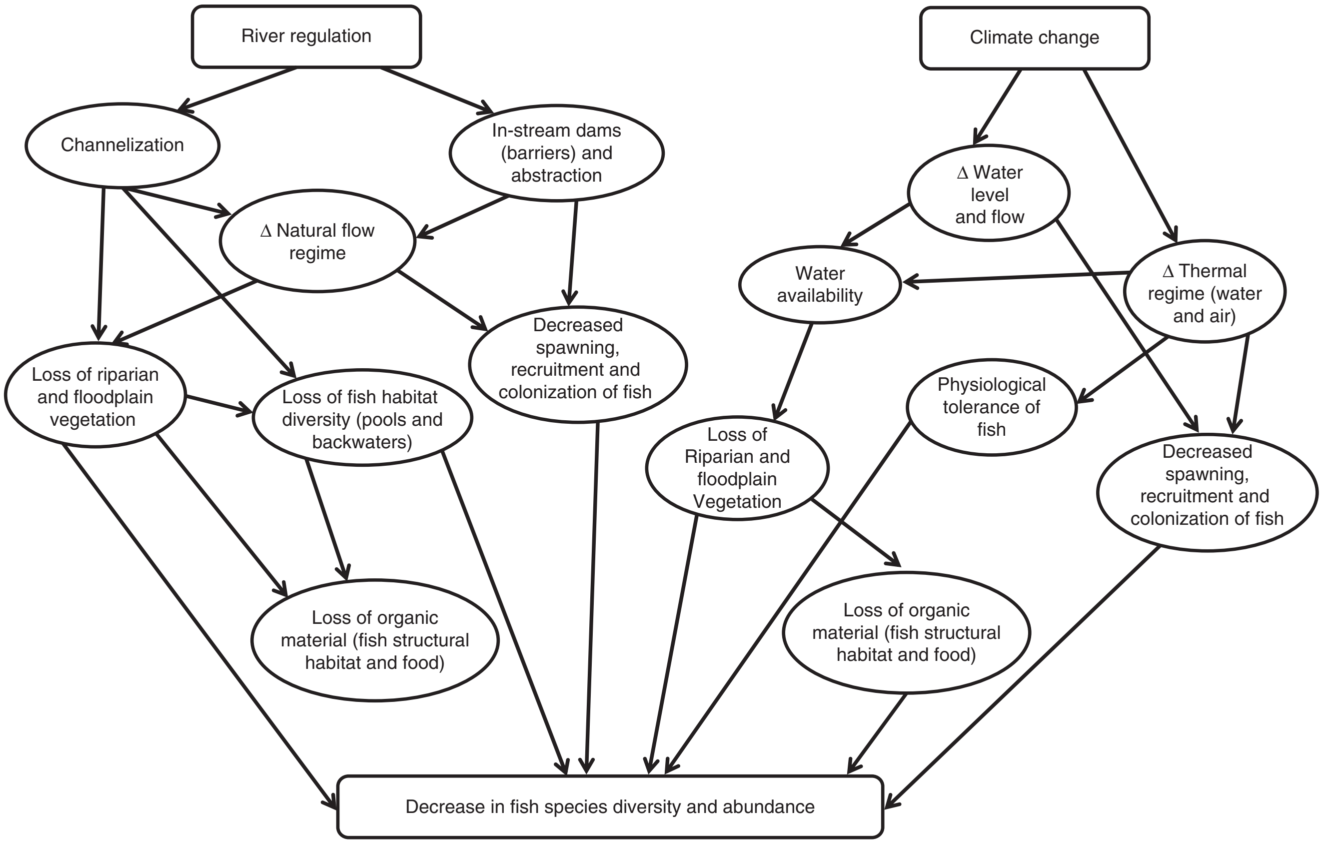

Fig. 1. Conceptual model of some possible impacts of river regulation and climate change on fish the diversity and abundance of species in the Murray–Darling Basin. Figure adapted and simplified from Pusey and Arthington (2003) and Boulton and Brock (1999).

range of climatic conditions under which they originally evolved (Rahel and Olden 2008). For example, Bond *et al*. (2011) predicted a contraction in the distribution of brown (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) in the southern part of the MDB. The reduction of these species, especially in upland regions, would be expected to benefit many native species. Morrongiello *et al*. (2011) suggested that gambusia may benefit from increased water temperatures, again, especially in the south. Any increase in the distribution and abundance of this species is likely to be negative, especially for small-bodied native fish. Common carp (*Cyprinus carpio*) has opportunistic recruitment patterns and high rates of population growth that allow it to persist in suboptimal conditions (Koehn 2004). Hence, this fish species is unlikely to be affected by climate change and will probably increase in some places, as a result of increased temperature and thus breeding and growth response when periodic recruitment opportunities (occasional floods) occur.

On the basis of the conceptual model in Fig. 2, we developed five derivative models for different groups of MDB fish species. Fish were grouped according to ecological similarities in diet, breeding strategies (such as spawning flexibility and type of spawning cue), habitat associations (e.g macrophytes, snags, open water) and temperature tolerances (e.g cold water and warm water). For brevity, only two of these models are presented here to demonstrate how we assessed climate-change impacts on species diversity and abundance.

The first model predicts the abundance of Murray cod (Fig. 3). This model demonstrates two pathways of effect, as follows: (1) decreased precipitation leading to reduced water levels and flow, affecting spawning and recruitment, and (2) increased temperature influencing the timing of spawning and physiological tolerance, ultimately reducing Murray cod abundance (Table 1). Overall, Murray cod will decline across the MDB, especially in the northern regions where reduced flows will exacerbate impacts of loss of hydrological connectivity and reduce thermal (summer) refugia because of the loss of deep pools (Table 1). There may be some localised increases in populations where stream temperature rises partially negate impacts of cold-water pollution below bottom-release dams (Table 1). Additionally, there are likely to be longer-term indirect impacts throughout the MDB where riparian and floodplain trees are lost, given they provide significant habitat and food for Murray cod (Table 1).

Our second example (Fig. 4) demonstrates some of the key drivers influencing five medium- to large-bodied fish species that are either widely distributed across the whole MDB (yellowbelly (*Macquaria ambigua*), eel-tailed catfish (*Tandanus tandanus*) and silver perch (*Bidyanus bidyanus*)) or across the northern MDB (Hyrtl's tandan (*Neosilurus hyrtlii*) and spangled perch (*Leiopotherapon unicolor*)) (Table 1). Increased temperature will directly influence predator–prey relationships by affecting lower levels of the food web, including primary productivity, potentially creating more niches for these fish.

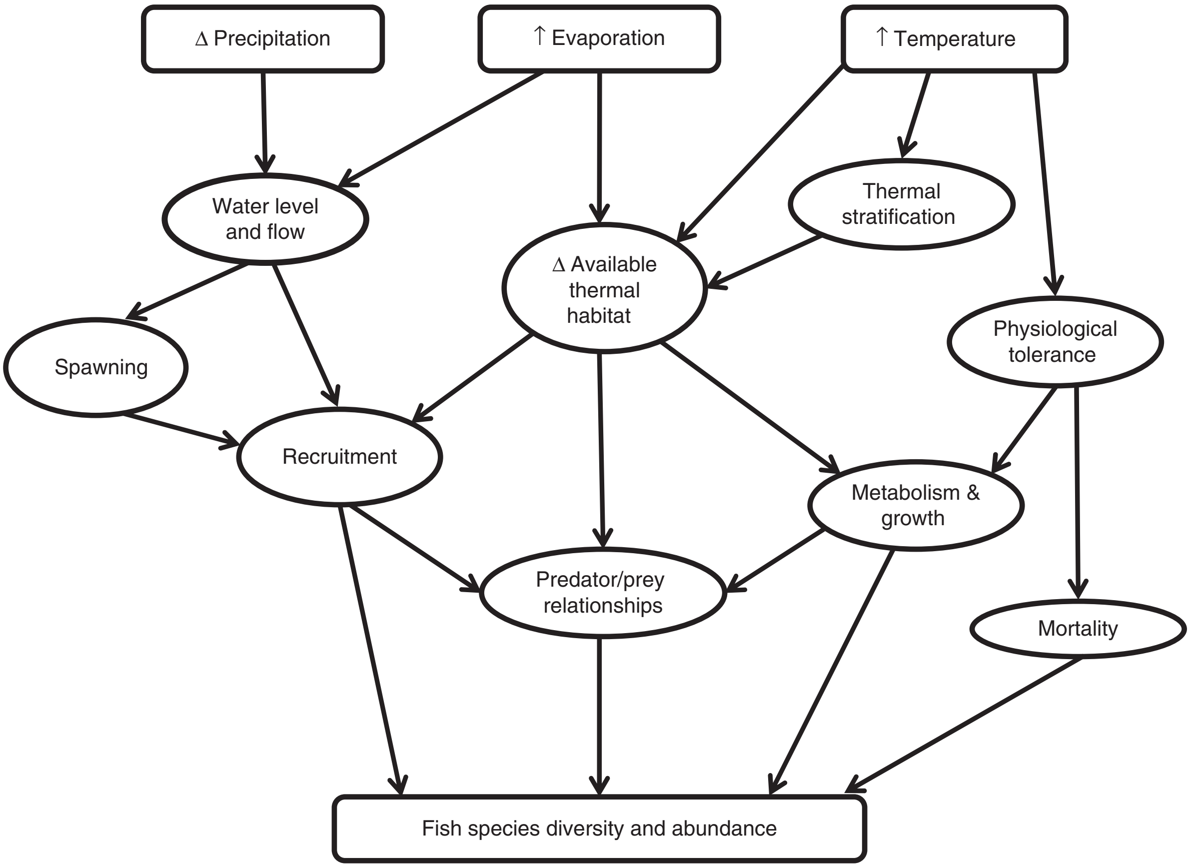

Fig. 2. Conceptual model of the predicted impact of climate change (mediated though changes in precipitation, increased temperature and increased evaporation) on the diversity and abundance of fish species. $\Delta =$ change, $\uparrow =$ increase.

Changes in precipitation and evaporative loss will reduce the amount of water in the river, impairing connectivity and recruitment of these species. In the northern MDB, increased temperatures will allow species such as yellowbelly, spangled perch and Hyrtl's tandan with high temperature tolerances and opportunistic breeding strategies to take advantage of the high primary productivity (Table 1). Silver perch and eel-tailed catfish are unlikely to gain much benefit from such changes in the northern MDB because the drier climate will have a further impact on hydrology, particularly connectivity (Table 1). In the southern MDB, however, these two species will probably benefit from increases in stream temperature, given how much they have been affected by cold-water pollution (Table 1).

Of the remaining species presented in Table 1, we grouped them as follows: Group A, including carp gudgeons and bony bream; Group B, including river blackfish, two-spined blackfish, trout cod, mountain galaxiids and Macquarie perch; and Group C, containing Australian smelt, un-specked hardyhead, southern pygmy perch, flat-headed gudgeon and Murray–Darling rainbowfish. Group A fish tolerate an extremely wide range of environmental conditions and their abundance is often strongly linked to levels of primary productivity (Table 1). The increase in temperature resulting from climate change should, therefore, increase the food base of these fish directly and any change to flows is likely to have no major influence on them (Table 1).

The distributions of Group B fish all extend into the cooler upland streams of the MDB (Lintermans 2007) and these fish could be loosely termed as 'cold-water tolerant'. Increased stream temperatures are likely to have a direct physiological effect on these fish, particularly where they are located at their high temperature limits (e.g. river blackfish and mountain galaxiids in the northern MDB, Table 1). In the southern MDB, increased temperatures may lead to increased abundances in local populations of fish such as trout cod, two-spined blackfish and Macquarie perch affected by cold-water pollution (Table 1). Such changes in temperature regime could affect larval recruitment success of species such as trout cod and Macquarie perch with short breeding seasons, by affecting the timing of zooplankton emergence, for example (Table 1). It is likely that all of the species within this group have been largely affected by the presence of exotic trout, so the expected decline of trout (Bond *et al*. 2011) because of increased stream temperatures may lead to more native species in these rivers (Table 1).

Group C comprises smaller-bodied fish, often found in wetlands and off-river channel waterbodies often associated with macrophytes (Table 1). The reduction since European settlement of species such as Murray–Darling rainbowfish, un-specked hardyhead and southern pygmy perch can be largely attributed to a loss of connectivity within riverine ecosystems (Table 1). Distributions of these species will become further

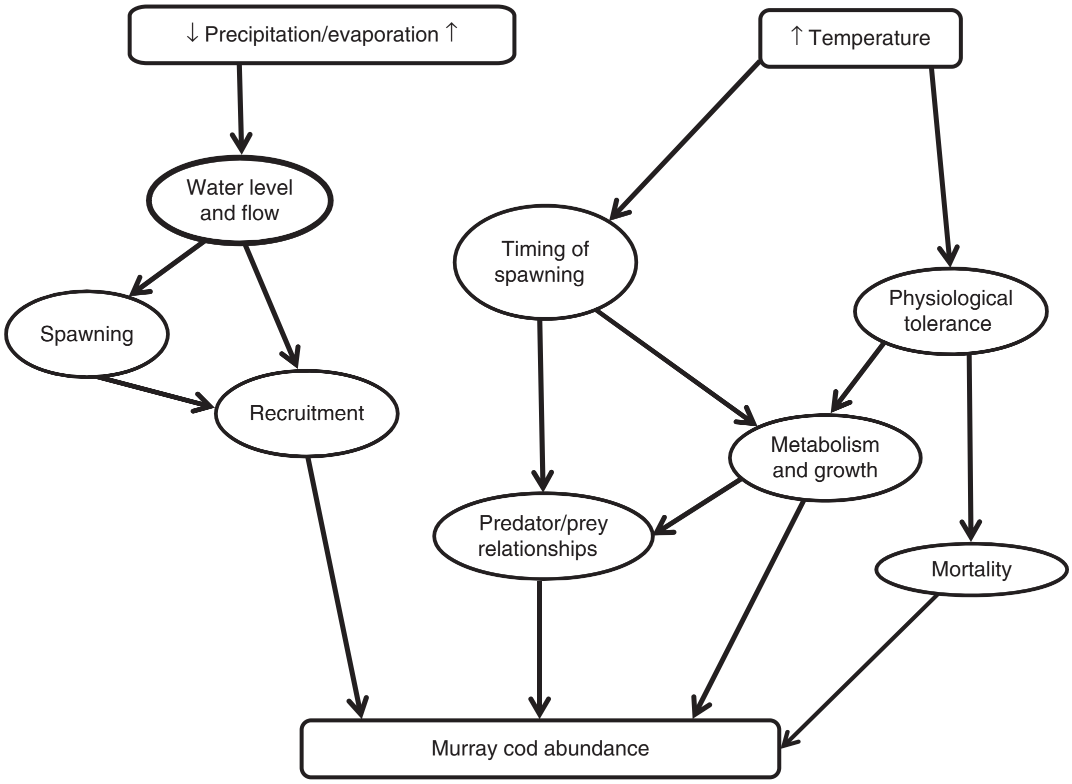

Fig. 3. Simplified conceptual model of climate-change impacts on Murray cod in the Murray–Darling Basin. ↑ = increase, ↓ = decrease.

fragmented as flow diminishes as a result of climate change. Losses of floodplain vegetation (e.g. rushes and reeds in floodplain wetlands) will also further affect fish such as flat-headed gudgeons and southern pygmy perch associated with macrophytes (Table 1). Increased temperatures will also have an impact on small-bodied fish with short breeding seasons and relatively narrow diet ranges, such as Australian smelt, also found in many floodplain habitats (Table 1). These fish are likely to be affected because any shift in seasonal thermal regime is likely to disrupt the synchrony between the seasonal peak in smelt larvae and specific species and size classes of their zooplankton prey.

Regional impacts on fish assemblages in the MDB

Given that the impacts of climate change are predicted to vary with latitude as well as with the degree of flow modification, we classified the MDB into 10 regions on the basis of their latitudinal position and the degree of flow management (Fig. 5). Ecological communities will tend to vary over an elevation gradient, so we used the largely elevation-driven regionalisation boundaries in the Sustainable Rivers Audit (Davies *et al*. 2008) to differentiate uplands from lowlands and to distinguish the alpine region. By using this classification and the predicted effects of climate change on individual species (Table 1), we can predict regional changes in fish assemblages throughout the MDB.

Northern and eastern uplands

Both of these regions, located in the northern MDB, with rivers ultimately flowing into the Darling River (Fig. 5), represent highly regulated rivers because of the presence of water storages (Table 2). There are significant effects of cold-water pollution in these regions, owing to bottom-release off-takes in water storages. Therefore, any warming as a result of climate change will confer an advantage to those fish species that have been reduced in their range and abundance from cold-water pollution. It would be expected that both range and abundance of Murray cod and river blackfish could increase slightly in both of these regions because increased water temperatures partially mitigate effects such as reduced spawning and growth from thermal pollution (Table 1). Although increased temperatures could also facilitate the range expansion of generalist fish species such as yellowbelly, eel-tailed catfish, silver perch and bony bream, these highly regulated rivers are likely to have less water overall. As a result, drought refugia will dry out faster, leaving fewer suitable habitats across the landscape and probably cancelling out any gains made though increased water temperature.

Southern uplands

The rivers of the southern MDB comprise a mixture of regulated and unregulated rivers. Most predicted changes in this region relate to increased water temperatures, although in the regulated rivers, effects will be further exacerbated by reduced flows

Table 1. Predicted effects of climate change on the main drivers of abundance and distribution of specific native fish species in the Murray–Darling Basin (MDB)

↓ = decreased distribution and abundance, ↑ = increased distribution and abundance. Where there is both a positive and negative response this will be region-specific

Common name	Key factors (distribution biology, physiology, response to water-resource development (WRD))	References	Response to climate change	Overall response
Murray cod (*Maccullochella peelii*)	Widely distributed throughout lowland regions of whole MDB. Seasonal spawning linked to temperature and enhanced by flow. Most populations panmictic (high genetic mixing). Subject to thermal stress at high temperatures, affected by cold-water pollution. Likely impact from reduced flows resulting from WRD, leading to fewer deep-water refugia. Presence of in-stream barriers reduces connectivity and limits migration and dispersal. Change to flow seasonality has an impact on recruitment processes.	Koehn 2001; King *et al*. 2003; Koehn and Harrington 2006; Lintermans 2007; Rourke 2007; Sherman *et al*. 2007	Higher temperatures will result in more fish kills, but will partially offset some impacts of cold-water pollution below dams. Fewer flow events and increased drying will lead to reduced fitness of populations from lowered biological connectivity, also fewer refugia (deep pools). Where floodplain (especially woody) vegetation is lost (e.g. river red gums), longer term loss of habitat and food resources.	↓
Yellowbelly (*Macquaria ambigua*)	Widespread throughout lowland habitats of entire MDB. High temperature-tolerant generalists, with very flexible life history, habitat and diet. Populations are highly panmictic and many individuals are known to undertake significant migrations. Lower abundance and poorer recruitment in regulated rivers. Affected by cold-water pollution.	Koehn 2001; King *et al*. 2003; Balcombe *et al.* 2006, 2007; 2011; Lintermans 2007; Ebner *et al*. 2009*a*; Faulks *et al*. 2010*a*	Likely to be favoured by increased temperatures across MDB in comparison to many other species. Yellowbelly thrives in highly warm and productive systems. Where cold-water pollution has limited their numbers, they will also increase as stream temperatures and productivity rise. Although connectivity is important, their ability to respond to isolated flow events with high recruitment will probably negate any negative impacts of less flow. Loss of floodplain vegetation will result in less in-stream habitat structure and food resources.	↑
Eel-tailed catfish (*Tandanus tandanus*)	Found across most of the basin in slower-flowing streams, with wider distribution in the northern basin. Carnivore, mostly on macroinvertebrates. Wide spawning window. Temperature tolerant to both high and low temperatures. Affected by high salinities. Generally, low genetic variation across the basin Heavily affected by loss of connectivity from WRD. Widespread, but low in the southern basin.	Lintermans 2007; Rayner *et al*. 2008; Rourke *et al*. 2010	Some increased range as a result of temperature increase, particularly in cold-water regions below dams. May be further affected in particularly dry regions where major abstractions occur if there is increased salinity. Loss of woody floodplain vegetation will have negative effects	↑↓
Silver perch (*Bidyanus bidyanus*)	Patchy distribution across the whole MDB in lowland rivers. Generalist omnivores. Temperature tolerant of warm waters. Heavily affected by WRD because of loss of connectivity disrupting migration and reproduction. Heavily affected by cold-water pollution.	Koehn 2001; Mallen-Cooper and Stuart 2003; King *et al*. 2009; Lintermans 2007	Increased temperatures will advantage these fish, particularly where cold-water pollution occurs; also being temperature tolerant, they are likely to increase in range. Such gains, however, are likely to be negated to some extent by reduced flow, with less connectivity and opportunities for migration. Loss of woody floodplain vegetation will have negative effects.	↑↓
Hyrtl's tandan (*Neosilurus hyrtlii*)	Restricted to the northern basin only. Tolerant of high temperatures. Significant migrations associated with flow. Strong recruitment associated where flow and high temperature co-occur. Populations are panmictic. Unknown impact of WRD, but in-stream barriers likely to be significant, along with cold-water pollution	Pusey *et al.* 2004; Balcombe *et al*. 2006; Lintermans 2007; Balcombe and Arthington 2009; Kerezsy *et al*. 2011	Likely range increase as a result of rising water temperature. Potential eastern and southern migration. Reductions in flows will disrupt spawning migrations and could reduce juvenile recruitment success.	↑

(*Continued*)

Table 1. (Continued)

Common name	Key factors (distribution biology, physiology, response to water-resource development (WRD))	References	Response to climate change	Overall response
Spangled perch (*Leiopotherapon unicolor*)	Widespread in the northern basin only. Generalist carnivore. High temperature tolerant habitat generalists. Susceptible to low temperatures. Seasonal spawning largely associated with flow and high temperatures. Highly migratory in response to flow. WRD likely to have impacted their distribution and abundance in regulated systems where multiple barriers exist. Likely to be affected by coldwater pollution.	Pusey *et al.* 2004; Balcombe *et al.* 2006, 2007; 2011; Balcombe and Arthington 2009; Lintermans 2007	Reduced flows, especially where multiple barriers exist, will limit the migration ability; however, this is offset by their ability to rapidly breed and migrate when flow events occur. Increased temperatures are likely to result in fish extending their range south and further into upland areas and into regulated sections below bottom-release dams.	↑
Bony bream (*Nematolosa erebi*)	Widespread across the basin, mostly in lowland rivers. Mostly algivorous and detritivorous. Extremely variable life history; can breed and recruit rapidly over a range of hydrological conditions. Tolerant of high temperatures and poor water quality. Susceptible to low temperatures. Likely impact with WRD only associated with cold-water pollution.	Pusey *et al.* 2004; Balcombe *et al*. 2006; Lintermans 2007; Sternberg *et al*. 2008; Balcombe and Arthington 2009	Increases in temperature are likely to increase algal productivity and thus food source. The species will also increase its range, especially because the climate change will negate some cold-water impacts.	↑
Carp gudgeons (*Hypseleotris* spp.)	Widespread across the entire basin. Temperature-tolerant generalist carnivores. Variable life history with long spawning season. Likely to have been advantaged by WRD, especially with more stable hydrology resulting in greater density of macrophyte habitat.	Williams and Williams 1991; Bren 1992; Balcombe and Closs 2004; Balcombe and Humphries 2006; Lintermans 2007	Increased primary productivity driven by higher temperatures is likely to increase secondary production and thus carp gudgeon distribution and abundance. Also reduction in effects of cold-water pollution will advantage these generalists. Potential reduced abundance in locations where macrophytes are affected.	↑
Trout cod (*Maccullochella macquariensis*)	Restricted distribution to Murrumbidgee and mid- to upper Murray catchments, with only three self-sustaining populations. Short, seasonal spawning linked to temperature and enhanced by flow. Habitat specificity: snags and in-stream habitat mostly associated with pools. Subject to thermal stress at high temperatures, affected by cold-water pollution. WRD has led to less in-stream habitats, riparian vegetation and increased competition from generalist species, all likely to have played a role in its now limited distribution.	Brown *et al*. 1998; Koehn 2001; Koehn and Harrington 2006; Lintermans 2007; King *et al*. 2009	Higher temperatures will partially offset some impacts of cold-water pollution, but also increase potential competitor (for food and habitat) abundance. Less flow will reduce refugia and create greater competition with more generalist (including exotic) species.	↓
Macquarie perch (*Macquaria autralasica*)	Distribution mostly limited to cooler upland sections of southern MDB. Temperature-related spawning. Generalist diet. High genetic diversity suggests fragmentation of populations throughout MDB. Affected by cold-water pollution, loss of habitat and reduced connectivity through WRD.	Koehn 2001; Lintermans 2007; Faulks *et al*. 2010*b*; Tonkin *et al*. 2010	Less flow will further fragment habitats and thus populations, leading to reduced fitness. Increased temperature will partially offset cold-water pollution effects, but will also affect spawning season and food availability.	↓
Two-spined blackfish (*Gadopsis bispinosus*)	Restricted to cool, clear upland streams in the south-east of MDB. Spawning is temperature related, with short spawning season. Inhabits deeper sections of streams with ample cover, absent from smaller headwater streams. Affected by cold-water pollution, sedimentation and altered hydrology. Also likely to have been affected by exotic trout species.	Maddock *et al*. 2004; O'Connor and Zampatti 2006; Lintermans 2007	Increased temperatures will partially reduce cold-water pollution effects and favour fish by affecting trout populations. Temperature increase will affect blackfish breeding and recruitment and potential losses from thermal stress during summer.	↑↓

Northern river blackfish (*Gadopsis marmoratus*)	Widely distributed in upland streams basin-wide, extending to lowland streams and rivers in the southern basin. Spawning is temperature related, with a relatively long spawning season. Generalist diet and habitat, but requires cover of some sort. Affected by cold-water pollution, sedimentation and altered hydrology. Likely to have been affected by trout species. Northern MDB populations placed at their upper thermal limits.	Jackson 1978; Koehn and O'Connor 1990; Khan *et al*. 2004; Lintermans 2007; Koster and Crook 2008	Main climate-change effects will be the impact of higher temperatures on distribution. Significant reductions in northern populations already situated close to their upper thermal limits. Reduced flows will have an impact on both connectivity among habitats and refuges during low-flow periods	↑↓
Mountain galaxias (*Galaxias olidus*)	Widely distributed in upland streams basin-wide, extending to lowland streams and rivers in the southern basin. Generalist carnivore. Wide spawning period cued by temperature. Temperature tolerant over a wide range, although likely to be at upper the thermal limit in northern MDB where it co-occurs with river blackfish.	Koehn and O'Connor 1990; Bond and Lake 2003; Lintermans 2007	Potential reduction of range in the northern basin with increased temperature. Main impacts are likely to have been caused by interactions with trout; any reduction in trout numbers (from temperature increase) will lead to an increase in the numbers of Mountain galaxia.	↑
Australian smelt (*Retropinna semoni*)	Widespread throughout the MDB in lowland areas. Habitat and food specific (pelagic planktivores). Seasonal spawners cued by temperature. Some evidence of genetic structure in disconnected habitats which have increased in some parts of the MDB from extraction of water. Evidence of limited dispersal within intermittent systems.	Lintermans 2007; Ebner *et al*. 2009*b*; Woods *et al*. 2010; Kerezsy *et al*. 2011	Diet speciality combined with a short breeding season will make the species vulnerable to temperature and season shifts because these may uncouple specific the availability of zooplankton with appearance of larvae/juveniles. Increased salinity will also affect smelt food resources across the MDB	↓
Un-specked hardyhead (*Craterocephalus stercusmuscarum fulvus*)	Restricted distribution mostly to the northern basin. Often found in wetlands and backwaters or slow-flowing channels. Probably, distribution has been reduced as a result of overall reduction in connectivity between channels and wetlands.	Lintermans 2007; Wedderburn *et al*. 2007	Less connectivity linking their range of habitats is likely to reduce the distribution, particularly in southern MDB. Losses of floodplain and wetland vegetation will have a negative impact owing to loss of habitat and food sources.	↓
Southern pygmy perch (*Nannoperca australis*)	Restricted range to the southern basin only. Largely associated with structured habitats, especially macrophytes in backwaters, billabongs and wetlands. Limited dispersal, with high population structure over small geographic distances. Refuge habitats extremely important during drought	Cook *et al*. 2007; Lintermans 2007; Tonkin *et al.* 2008	Reduction in the range, with more tolerant species being likely to displace them. Reduced connectivity and number of refugia, during drought also will reduce their population viability. Losses of floodplain and wetland vegetation will have a negative impact owing to loss of habitat and food sources.	↓
Flat-headed gudgeon (*Philipnodon grandiceps*)	Restricted distribution, particularly in the northern MDB, reasonably common in parts of the southern MDB, particularly in wetlands associated with macrophytes. Tolerant of high temperatures. Dispersal largely by larval drift. Reduced connectivity because of the presence of weirs and flow alteration are likely to have resulted in decreased distribution throughout the MDB.	Koehn and O'Connor 1990; Humphries *et al*. 2002; Pusey *et al*. 2004; Lintermans 2007	Common in wetlands in the lower Murray; alterations (less flow. fewer wetlands and macrophytes) will reduce numbers. Increased temperature may lead to an expansion of fish distribution where they may displace less temperature-tolerant species. Losses of floodplain and wetland vegetation will have a negative impact owing to loss of habitat and food sources.	↑↓
Murray–Darling rainbowfish (*Melanotaenia fluviatilis*)	Restricted to lowlands of north-eastern rivers and patchy throughout the lower basin (largely eastern). Generalist carnivore. Spawning associated with macropyhtes. Affected by cold-water pollution and potential losses of macrophytes and connectivity because they are known to migrate.	Koehn and O'Connor 1990; Humphries *et al*. 2002; Pusey *et al.* 2004; Lintermans 2007	Losses as a result of WRD are most likely already felt and any further hydrological change will have a limited impact. Losses of floodplain and wetland vegetation will have a negative impact owing to loss of habitat and food sources. There may be some localised increase in the downstream sections below weirs where cold-water pollution may be partially mediated by an increase in temperature.	↓

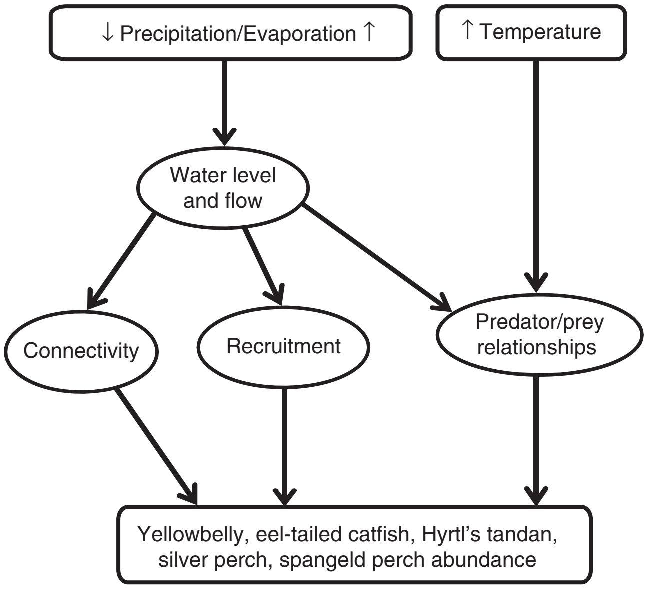

Fig. 4. Simplified conceptual model of climate-change impacts on yellowbelly, eel-tailed catfish, silver perch, Hyrtl's tandan and spangled perch in the Murray–Darling Basin. ↑ = increase, ↓ = decrease.

(Table 2). These increases are likely to affect cold water-tolerant species such as river and two-spined blackfish and trout cod, reducing their breeding activities and thus overall abundance (Table 1). However, balanced against these predicted reductions in native species will be the likely displacement of exotic trout (Bond *et al*. 2011), which currently has a significant impact on native riverine food webs as a major predator of invertebrates and fish (Lintermans 2007). Such an impact on trout could facilitate increases in vulnerable species such as mountain galaxias and the two blackfish species.

Alpine

The Alpine region contains many headwater streams of the Murray and Murrumbidgee rivers in the eastern MDB (Fig. 5). For the regulated rivers, the impacts of water-resource development would outweigh any small changes to flow regime brought about by climate change. Therefore, the impacts of climate change will be mostly restricted to increases in stream temperatures that alter the distributions of the cold water-tolerant species, especially two-spined blackfish (Table 2). It is likely that temperature increases will reduce river blackfish distributions at lower altitudes and affect the spawning time and food availability for Macquarie perch. As with the southern uplands, we predict that significant impacts on exotic trout will greatly benefit native fish species such as mountain galaxias and the two blackfish species through reduced competition and predation.

Dryland

The dryland region in the upper western corner of the MDB (Fig. 5) consists largely of the unregulated semiarid rivers. While there are no major diversion weirs or water storages on these rivers, there are many low-level weirs that currently impose the largest threat to fish migration and breeding patterns in the region (Table 2). The fish of these rivers are mostly ecological generalists, adapted to cope with the highly variable flows of these rivers (Gehrke *et al*. 1995; Balcombe *et al*. 2006, 2011). It is unlikely that climate change will substantially change these fish assemblages, given the ability of the species to cope with extremes of climate. However, where the impact of climate change interacts with the effects of barriers on fish migration (such as low flows), the fish species that migrate as part of their breeding cycle (e.g. Hyrtl's tandan, Balcombe and Arthington 2009; Kerezsy *et al*. 2011) could be affected in some rivers. There are likely to be some localised impacts of less flow reaching terminal wetlands (climate change added to water-resource development), affecting floodplain and wetland vegetation, especially encroachment from lignum. This could enhance the local abundance of fish species, including exotic species such as carp and gambusia, because of the presence of added structural habitat and increased organic input when these systems are flooded.

Darling tributaries

Originating in the northern and eastern upland region, the Darling tributaries region refers only to the lowland section of these rivers (Fig. 5). All are affected by water-resource development to varying degrees because of the presence of headwater storages, low-level weirs and significant levels of water abstraction for irrigation (Table 2). Climate change is likely to lead to fewer refuge pools (remaining pools will also be shallower) during dry periods, which will have a flow-on effect for fish that are close to their upper thermal limits, such as Murray cod. Generalist species such as eel-tailed catfish, yellowbelly and bony bream may increase in abundance in response to declines in Murray cod. Balanced against this is the potential expansion of the distributions of exotic fish, particularly of common carp and gambusia, which are established and significant competitors for food resources in these rivers (Gehrke *et al*. 1995; Balcombe *et al*. 2011). The combined effects of reduced flows and reduced connectivity from development will also have an impact on species, including carp gudgeons, Murray–Darling rainbowfish and un-specked hardyheads, that use more marginal waterbodies such as anabranches and billabongs (Lintermans 2007).

Darling lowland

The Darling lowland region in the mid-western MDB (Fig. 5) has been significantly affected by water-resource development, with major abstractions and many low-level weirs (Table 2). Because of the high levels of water-resource development and the associated decline of the fish assemblages in the region, climate-change impacts are not likely to cause too many further changes. However, further reductions in flow and increased temperatures may decrease available drought refugia for Murray cod. Furthermore, bony bream may increase its abundance in such refuge habitats in response to fewer predators and because of its ability to capitalise on increased algal resources associated with high water temperatures. These increases in primary productivity in degraded habitats could also favour common carp (Koehn 2004), placing further stress on native fish. Lignum may

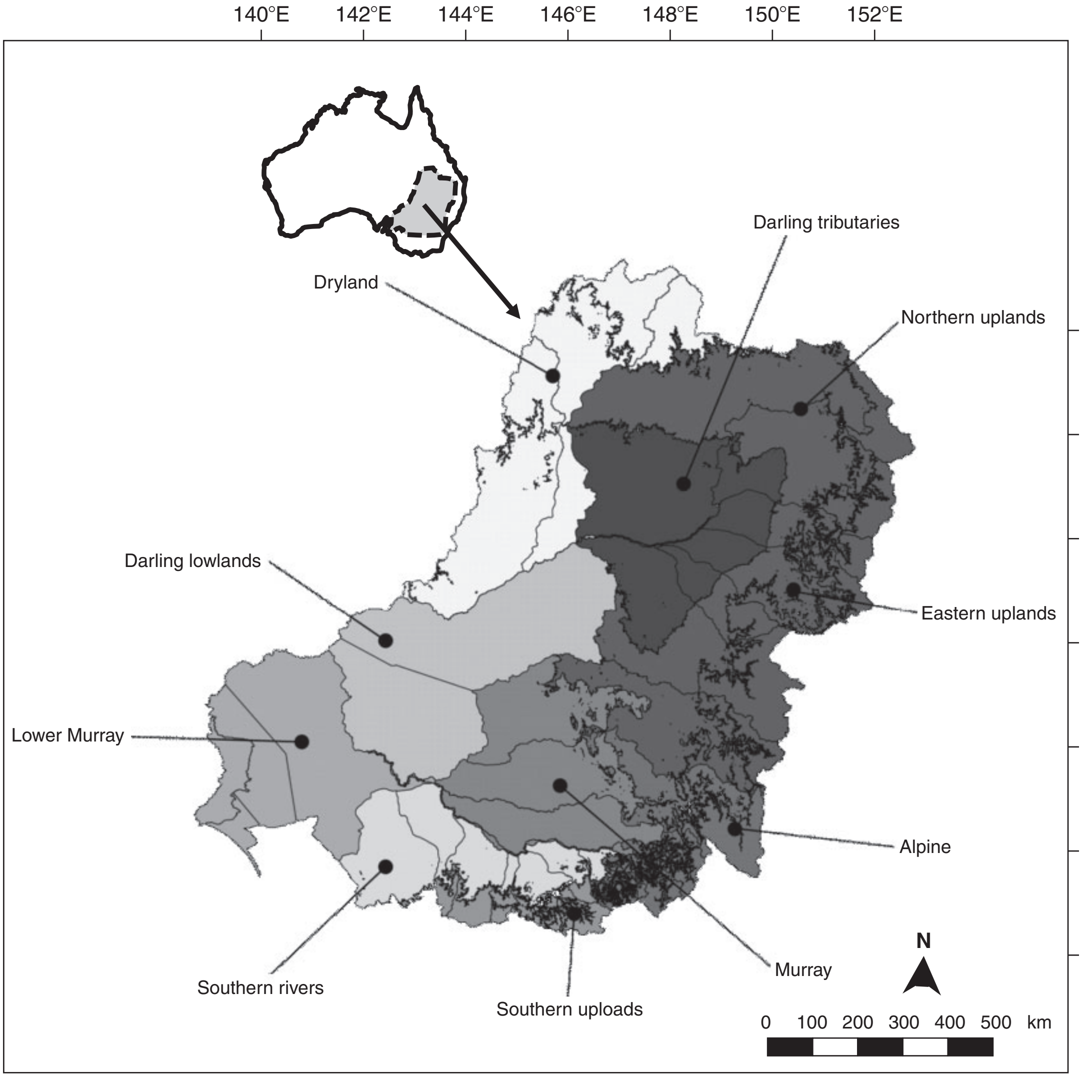

Fig. 5. Location of the Murray–Darling Basin within Australia and its subsequent classification into different regions on the basis of latitudinal position, altitude and degree of flow management.

encroach into drier sections of rivers such as wetlands, which could exacerbate impacts of exotic fish.

Murray

The Murray region in the lower MDB (Fig. 5) is a highly regulated riverine system with many weirs and locks. Flows are managed via release from major water storages. Fish stocks have been largely affected by cold-water pollution for significant lengths of river below water storages. As a result, increased temperatures are likely to ameliorate some of these impacts and thus increase the abundance and range of species such as trout cod, Murray cod, yellowbelly and silver perch (Table 2). Given the lack of connectivity of this highly modified and regulated river with off-channel and floodplain habitats, any further reductions to flow will mean fewer floodplain connections and further degradation of fish such as yellowbelly, silver perch, Australian smelt, flat headed gudgeons, un-specked hardyheads and pygmy perch that use floodplains and associated waterbodies (Table 1). Less floodplain inundation will also have an impact on riparian vegetation, especially river red gum. This will have longer-term effects on the habitat use and food resources of native fish. However, fewer floodplain connections may have an impact on common carp recruitment because inundated floodplains provide a significant source of carp recruits in the MDB (Crook and Gillanders 2006).

Southern rivers

The southern rivers of the MDB that feed into the mid- and lower Murray (Fig. 5) are mostly regulated with storages on all but the Ovens River (Table 2). The likely reduced flows and reductions in flood frequency will have an impact on in-channel and floodplain habitats. Although weirs are likely to maintain refuge pools in regulated river reaches, overall flow reductions may exacerbate the loss of longitudinal and lateral connectivity. With less flow, there is also likely to be less macrophyte habitat, leading to fewer small-bodied species such as pygmy perch, carp

Table 2. Overall changes in fish assemblage in 10 regions, owing to the effects of climate change and relevant hydrological variation from water-resources development (WRD)
Assemblage changes are predicted from the potential impacts on individual species given in Table 1

Region	Relevant WRD changes	Fish-assemblage change
Northern uplands	Highly regulated headwaters of dryland rivers. Changes to flow seasonality as a result of flow management in storages. Cold-water pollution downstream of some storages.	Some localised increases in Murray cod and river blackfish below storages, as a result of partial mitigation of cold-water pollution. Highly regulated rivers so potential range expansion by high temperature-tolerant generalists such as yellowbelly, eel-tailed catfish and bony bream will be negated by further flow reductions in an already highly disturbed region. Increased stream temperatures are likely to reduce distribution and abundance of river blackfish
Eastern uplands	Highly regulated headwaters of dryland rivers. Cold-water pollution downstream of some storages.	As for northern uplands.
Southern uplands	Mixture of regulated and unregulated rivers. Headwaters are largely unregulated.	Reduced range and abundance of river and two-spined blackfish because of increased temperatures. Exotic trout will be reduced in distribution and abundance as a result of higher stream temperatures, thereby leading to increases in species vulnerable to competition and predation by trout such as mountain galaxiids, two-spined and river blackfish.
Alpine	Mixture of unregulated and regulated headwaters of the upper Murray and Murrumbidgee Rivers.	Little change apart from the reduced range for cold-tolerant species, e.g. two-spined and river blackfish. Potential reduction of Macquarie perch because of impacts on spawning season and food availability. Localised increases in mountain galaxiids, two-spined and river blackfish where trout declines with increased temperature.
Darling tributaries	These are the lowland sections of the northern Darling tributaries, with some headwater storages, low-level weirs and abstraction for irrigation.	Decrease in Murray cod abundance because of fewer refuge pools and increased temperature. Some increase in generalist species such as yellowbelly, carp gudgeons and bony bream in response to fewer Murray cod individuals. Potential increase in exotic fish as a result of increased temperature; encroachment by lignum may also facilitate the spread of exotics.
Dryland	Unregulated rivers with no major water abstraction; largely low weir barriers.	Fish assemblages will remain largely intact. These represent highly variable systems, with the fish assemblages comprising ecological generalists. Increase in temperature will probably reduce Murray cod populations only. Further flow reductions may reduce species that undergo spawning migrations, such as Hyrtl's tandan. Potential increase in exotic fish populations in response to increased temperature; encroachment by lignum may also facilitate this.

Darling lowland	The major WRD impacts in this region are the high abstractions for irrigation. There are also several low-level weirs throughout. The river is highly regulated below Menindee Lakes.	Further reductions to flow will further affect the remnant fish assemblages. Likely reduction in refuge pools combined with increased temperature will reduce Murray cod populations. In such a regulated region, bony bream will most likely increase in response to higher algal productivity with higher temperatures. Potential increase in exotic fish populations in response to increased temperature; encroachment by lignum may also facilitate this.
Murray	Highly regulated riverine system, with large numbers of weirs and locks. Flows are highly modified by storages. Cold-water pollution relevant in the upper reaches below storages.	Potential increase of several species affected by cold-water pollution in reaches close to the main storages, including trout cod, Murray cod and yellowbelly. The highly modified flow regimes and lack of connectivity with floodplains will potentially cause further reduction in species that use floodplains, including, yellowbelly, silver perch, Australian smelt, pygmy perch and flat-headed gudgeons. Loss of floodplain and wetland vegetation will have an impact on all natives; small-bodied species in wetlands (e.g flat-headed gudgeons and pygmy perch) and large-bodied riverine species, such as Murray cod and yellowbelly, will be affected because of loss of river red gums from riverine habitats.
Southern rivers	Mostly regulated rivers, with varying types of storages. Ovens River remains the only unregulated system.	Reduction of several small-bodied species because of reduced flows resulting in fewer refuge pools (Australian smelt, pygmy perch) and less macrophyte habitat (pygmy perch, flat-headed gudgeons). Potential impacts on larger-bodied fish (e.g. Murray cod) via impacts on riparian woodlands (e.g. river red gum). Reduced range and abundance of two-spined and river blackfish and trout cod because of increased temperatures.
Lower Murray	Highly regulated riverine systems, with major locks and weirs.	Fish assemblages already degraded from a highly regulated and disconnected system. Riverine species unlikely to be any further degraded because the major issue is the lack of longitudinal and lateral connectivity, which will remain. Increased temperatures and reduced flow may, however, affect smaller wetland species such as Murray–Darling rainbowfish, flat-headed gudgeons and pygmy perch because of increased salinity, loss of macrophytes and fewer refugia. Generalists, such as carp gudgeons, are likely to increase in distribution; however, where macrophytes are lost, there may be localised reductions in abundance. Further impacts on river red gum woodlands will affect all fish species through lower carbon inputs and less structural woody habitat.

gudgeons and flat headed gudgeons as they become more vulnerable to predation (Table 2). In headwater streams, increased temperatures will drive an upstream contraction of cold water-tolerant species such as river and two-spined blackfish and trout cod. Again, barrier effects may impede such movements in more developed catchments.

Lower Murray

The lower Murray region represents the termination of the Murray–Darling system (Fig. 5) and is highly regulated via locks and weirs (Table 2). Consequently, the assemblages of riverine fish are already highly degraded and subtle changes to either temperature or flow will probably not result in much impact (Table 2). Nonetheless, increased water temperatures combined with less flow, and thus less lateral connectivity, are likely to further affect the already degraded habitats for wetland fish species such as pygmy perch, flat headed gudgeons, un-specked hardyheads and Murray–Darling rainbowfish because of loss of macrophytes and increased salinity (Table 1). Given the high temperature tolerance of gambusia, it is likely to flourish in these wetland habitats and further affect small-bodied native fish species. Further declines in river red gum woodlands will also have flow-on effects to the riverine fish assemblages because of reduced structural woody habitat, carbon inputs and food resources. Given the raft of impacts already known for this region, the future looks bleak for several species that are restricted in distribution and abundance, including river blackfish, purple-spotted gudgeon (*Mogurnda adspersa*) and Murray hardyhead (*Craterocephalus fluviatilis*).

Conclusions

Most of the regions of the MDB contain highly altered river systems. The Lower Murray region is characterised by weirs and locks that constrain longitudinal connectivity throughout the river and lateral connectivity with associated floodplains. In the northern uplands, reaches show significant effects of thermal pollution and flow regulation from water storages, again leading to riverine systems that have been largely altered. As such, the fish assemblages of the MDB are highly degraded and unlikely to improve significantly under current management regimes. Climate change will further stress these already ‘degraded’ fish assemblages. However, in some regions the change will be limited given the already degraded environment, whereas in others there could be an improvement for native fish, given that temperature increase is likely to at least partially ameliorate some of the effects of thermal pollution and increase stress on resident exotic taxa.

The effects of climate change on fish assemblages should not be considered in isolation from existing water-resource development in any river catchment, especially in heavily altered systems such as the MDB, where historical levels of water-resource use exceed the likely impacts of climate change. In this respect, future management plans that aim to improve the condition of rivers in the MDB must consider both the added pressure of climate change as well as the current stress associated with agricultural and human water use.

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