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# Climate change decouples marine and freshwater habitats of a threatened migratory fish

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## Abstract

**Aim:** To assess how climate change may decouple the ecosystems used by a migratory fish, and how decoupling influences priorities for stream restoration.

**Location:** Australia.

**Methods:** We modelled changes in habitat suitability under climate change in both riverine and marine habitats for a threatened diadromous species, the Australian Grayling *Prototroctes maraena*, using niche models. The loss of riverine habitats for Grayling was compared with or without considering the impact of climate change on adjacent marine habitats. We also asked whether considering marine climate change changed the locations where removing dams had the greatest benefit for Grayling conservation.

**Results:** Climate change is expected to cause local extinction in both marine and river habitats regardless of whether dams are retained or removed at the trailing edge of the Grayling's range (north-eastern). Decoupling of habitats was most apparent in the eastern and south-eastern portion of the Grayling's range, where ocean warming may cause a decline in the suitability of marine habitats for larvae, while many freshwater habitats retained suitable habitat for adults. Removing dams to restore connectivity between ocean and freshwater habitats was predicted to have the greatest benefit for Grayling in southern portions of their range. Under climate change, the priorities for barrier removal gradually shift towards dams at higher elevation because of increasing suitability of freshwater habitats at higher elevations.

**Main conclusions:** Our study highlights the importance of assessing climate range shifts in multiple ecosystems for migratory species and can help inform priorities for stream restoration under a changing climate.

## KEYWORDS

climate change, freshwater ecosystem, global warming, marine ecosystem, migration, threatened species

## 1 | INTRODUCTION

Climate change is expected to have a significant impact on biodiversity world-wide, with responses already observed at many levels including shifts in the distribution of many species, their phenology and their

population dynamics (Settele et al., 2014). The rate and direction of isotherm shifts through space (i.e., climate velocity) have been analysed across ecosystems (Burrows et al., 2011; Loarie et al., 2009) to assess possible rates and directions of species-range shifts (Burrows et al., 2014; Pinsky, Worm, Fogarty, Sarmiento, & Levin, 2013). While

shifting distributions have been observed and predicted in terrestrial (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011), marine (Poloczanska et al., 2013) and freshwater (Comte, Buisson, Daufresne, & Grenouillet, 2013) ecosystems, the rates of range shift vary among species and ecosystems (Sorte, Williams, & Carlton, 2010). Observed range shifts have been faster in marine systems than those of terrestrial systems because marine populations more fully occupy the extent of their thermal tolerance ranges than terrestrial populations (Sorte et al., 2010; Sunday, Bates, & Dulvy, 2012). Therefore, differences in the rate of climate change across marine, freshwater and terrestrial ecosystems might decouple the habitats used by migratory species and threaten their persistence (Saunders et al., 2016).

Climate change, in particular global warming, generally causes the distributions of marine fish to shift to higher latitudes and deeper waters (Pinsky et al., 2013; Poloczanska et al., 2013), and freshwater fish to shift to higher altitudes and latitudes (Comte et al., 2013). However, anthropogenic barriers can make upstream habitats unavailable to fish despite the apparent presence of suitable habitat (Bond, Thomson, Reich, & Stein, 2011; Comte & Grenouillet, 2015). Here, we argue that ignoring the dependence of diadromous species on both freshwater and marine habitats, and the impacts due to anthropogenic barriers on connectivity will underestimate their perceived vulnerability to climate change.

Migratory species may be particularly vulnerable to extinction under climate change because they will be affected by change in both the ecosystems they inhabit and their migration routes (Robinson et al., 2009; Runge, Martin, Possingham, Willis, & Fuller, 2014). Diadromous fish, which migrate between marine and freshwater ecosystems (McDowall, 1988), exemplify the risk climate change poses to migratory species. The populations of many diadromous fish have undergone a dramatic decline world-wide due to habitat loss, overfishing, invasive species, pollution and climate change (Costa-Dias, Sousa, LobónCerviá, & Laffaille, 2009; Limburg & Waldman, 2009; Mota, Rochard, & Antunes, 2016). Further climate change may lead to a disconnection between the marine and freshwater habitats required by diadromous fish because the climate velocity has been higher in the ocean than on land at the same latitudes during the past 50 years (1960–2009) (Burrows et al., 2011). However, most studies have focused on changes of diadromous species' distributions in either riverine (e.g., Lassalle, Bégue, Beaulaton, and Rochard (2008); Lassalle and Rochard (2009); Bond et al. (2011)) or marine habitats (e.g., Lynch et al. (2014)) in spite of both habitats being required to complete their life cycles. Studies suggest that the combined effect of climate change in both freshwater and marine environments threatens the persistence of diadromous fish populations such as Atlantic salmon *Salmo salar* (Piou & Prévost, 2013) and anguillid eels *Anguilla spp* (Jacoby et al., 2015; Kettle, Asbjørn Vøllestad, & Wibig, 2011). Therefore, assessing and integrating the impacts across habitats and life stages are keys for the conservation of diadromous fish (McDowall, 1992).

The Australian Grayling *Prototroctes maraena* is a diadromous fish endemic to the coastal rivers of south-eastern Australia. Adult fish migrate to lower reaches of a river to spawn during autumn and winter with increased river flows (Amtstaetter, O'Connor, & Pickworth, 2016;

Koster, Dawson, & Crook, 2013). After 4–6 months at sea, juveniles migrate upstream to freshwater habitats to grow and mature (Berra, 1982; Crook, Macdonald, O'Connor, & Barry, 2006). Since European settlement, Grayling has undergone severe population declines and is now protected by state and federal legislations, as well as being on the IUCN Red List as Near Threatened (Backhouse, Jackson, & O'Connor, 2008b). Anthropogenic barriers, river regulation, habitat degradation, invasive species and climate change are considered as primary threats for Grayling (Backhouse, Jackson, & O'Connor, 2008a). Barriers that prevent migration lead to the local extinction of upstream populations (McDowall, 1993) because obligatory migrants like Australian Grayling can only persist in habitats connected to the sea (Backhouse et al., 2008a). The persistence of the Australian Grayling is particularly significant because after the extinction of New Zealand Grayling *P. oxyrhynchus* in 1930, it is the only member of the *Prototroctes* genus remaining (McDowall, 2006).

In this study, we use niche models to assess the vulnerability of Australian Grayling to future climate change due to shifts in the suitability of both freshwater and marine habitats. We compared the loss of riverine habitats for Grayling with or without considering the impact of climate change on adjacent marine nursery habitats. The location of anthropogenic barriers was also incorporated to evaluate what impact their removal might have on habitat availability, and how priorities for dam removal might change under climate change.

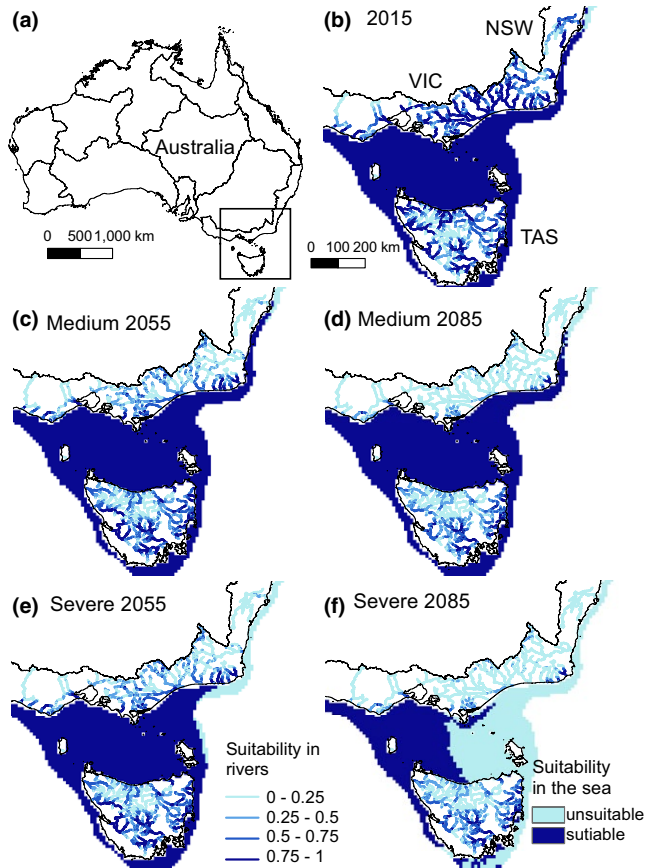
## 2 | METHODS

### 2.1 | Occurrence records and environmental data

Occurrence data for Australian Grayling in freshwater habitats were collected from the Australian Museum, New South Wales Department of Primary Industries and Victorian Biodiversity Atlas, and additional records from the Atlas of Living Australia database (<http://www.ala.org.au>; i.e., Museum Victoria, West Australian Museum, Queen Victoria Museum and Art Gallery, Tasmanian Museum and Art Gallery, and Queensland Museum). Records prior to 1975 were discarded to match the climatic baseline. In total, 241 records of Australian Grayling from 241 subcatchments were used to train the niche model. Data were spread across all the major coastal catchments of the Grayling's currently known distribution in south-eastern Australia (Figure 1).

Environmental data for building the freshwater habitat model were structured to reflect the hydrological network of rivers based on the National Catchment and Stream Environment Database V.1.1.3, part of the Australian Hydrological Geospatial Fabric (Stein, Hutchinson, & Stein, 2014). Downscaled climate and hydrological parameters were provided by James et al. (2013) with additional recent climate data from the eMAST portal (Whitley et al., 2014). Future climate conditions were projected from a seven-GCM (Global Climate Model) ensemble that performed well in south-eastern Australia (Fordham, Wigley, & Brook, 2011) as a "best estimation" of future freshwater habitat distribution.

For marine habitats, downscaled Australian coastal water temperature for current condition was extracted from Oliver and



**FIGURE 1** Study region (a) and projections of current (b) and future (c, e: 2055 and d, f: 2085) suitable habitats for Australian Grayling under Representative Concentration Pathways 8.5. Global climate model (GCM) for freshwater habitats is a seven-GCM ensemble, and GCMs for marine habitats are HadGEM2-ES (c, d: Medium) and FGOALS-s2 (e, f: Severe). Habitat suitability is shown as continuous probabilities of occurrence between 0 and 1 in rivers and binary variables (suitable vs. unsuitable) in the sea. NSW: New South Wales, VIC: Victoria and TAS: Tasmania

Holbrook (2014). We used a different set of GCMs for the marine realm because the connection between predicted land surface temperature and adjacent sea surface temperature is weak in the extra-tropics (28°N/S to the poles), and there is little agreement among projections from different GCMs of extra-tropical sea surface temperature (Tyrrell, Dommenges, Frauen, Wales, & Rezny, 2015; Wang, Dommenges, & Frauen, 2015). Therefore, two GCM projections from Earth System Grid Federation (ESGF) were used to span the range of possibilities from medium (HadGEM2-ES) to severe (FGOALS-s2) ocean warming of the Grayling's marine habitat. Only winter (austral winter: May to October) sea surface temperature were extracted because Australian Grayling larvae occupied marine nursery habitats during winter to spring (Shenton, Hart, & Chan, 2011) and the ocean warming was projected differently across seasons in south-eastern Australian (Koehn, Hobday, Pratchett, & Gillanders, 2011). Representative Concentration Pathways (RCP) 8.5 was used to explore the worst-case greenhouse gases emission scenario for 2055 and 2085. We chose these

years to represent possible results in the middle and the end of this century. These years also meant our results were comparable to other climate change studies in Australian ecosystems (James et al., 2013) and government reports (Climate change in Australia, Projections for Australia's NRM regions, CSIRO and Bureau of Meteorology, 2015).

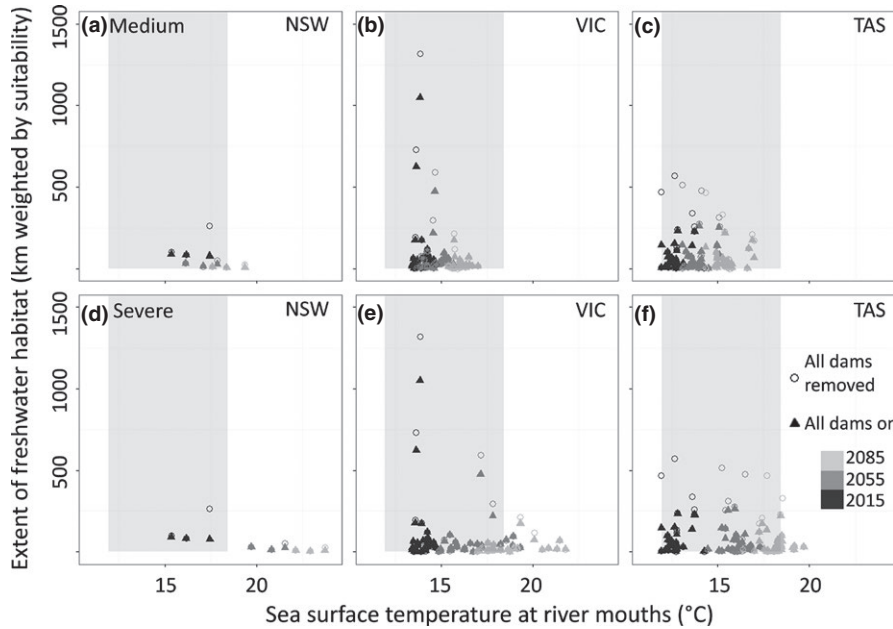
## 2.2 | Modelling suitable habitat

We applied two different methods to model the distributions of suitable habitat in freshwater and marine ecosystems. For freshwater habitat, a range of climatic, hydrological and topographic variables potentially important to the distribution of diadromous fish were considered in model testing (e.g., Leathwick, Elith, Chadderton, Rowe, and Hastie (2008), Lassalle and Rochard (2009), & Bond et al. (2011)). After removing correlated factors, complementary predictor variables were selected through forward selection using Akaike information criteria (Warren & Seifert, 2011). Selected variables for modelling Australian Grayling included minimum air temperature, precipitation seasonality, mean annual flow, slope, maximum distance upstream and distance to outlet. Given we could not reliably infer absences (Guillera-Arroita, Lahoz-Monfort, & Elith, 2014), freshwater habitat suitability was modelled using an ensemble of five presence-only algorithms (GAM, GLM, GBM, MARS, MAXENT) that were fitted in R (R Core Team, 2015) using the packages *dismo* (Hijmans, Phillips, Leathwick, & Elith, 2013) and *biomod2* (Thuiller, Lafourcade, Engler, & Araújo, 2009), and weighted using the True Skills Statistic (Allouche, Tsoar, & Kadmon, 2006). This produced continuous probabilities of occurrence (habitat suitability) under given climate scenarios. Our modelling covered the full distribution of this species. For presentation of results, we divided the range into northern, central and southern sections that align with state boundaries and hence the different management jurisdictions.

We used current and projected coastal water temperature to represent the potential range shift of suitable habitats in the sea because sea surface temperature has been recognized as a main driver for distribution shifts in marine species (Poloczanska et al., 2013; Sunday et al., 2012). Furthermore, narrower thermal windows of larval fish (Pörtner & Farrell, 2008) may constrain their distribution within the suitable temperature range. Thus, the range of mean winter coastal water temperature which covers all river mouths with adult fish recorded upstream was used to represent a suitable temperature range for larvae as no distribution data for Australian Grayling larvae are available. Binary outputs have been produced to represent suitable (projected temperature is within current temperature range) vs. unsuitable (projected temperature is outside current temperature range) habitats in the sea for each climate scenario.

## 2.3 | Assessing habitat change by climate change and dams

We focused on the potential habitat shifts in sixty-three "important rivers" that have been identified as crucial to long-term population



**FIGURE 2** The extent of predicted riverine habitat with (filled triangles) or without (hollowed circles) dams versus predicted sea surface temperatures from two Global Climate Models (HadGEM2-ES/Medium: a–c; FGOALS-s2/Severe: d–f) in New South Wales (NSW, three important rivers, a and d), Victorian (VIC, thirty-one rivers, b and e) and Tasmanian (TAS, twenty-nine rivers, c and f) rivers. The shaded area indicates the temperature range of coastal waters from the current distribution of Grayling, and each point indicates a single river

persistence in the National Recovery Plan for the Australian Grayling (Backhouse et al., 2008a). The northern, central and southern sections of the Australian Grayling range included three important rivers in New South Wales (NSW), 31 in Victoria (VIC) and 29 in Tasmania (TAS). Although headwaters of the Snowy River are within New South Wales, the river was assigned to the central section (Victoria) because its estuary is further south. The extent of suitable habitats was calculated as the sum of river segment lengths (Stein et al., 2014) weighted by the projected habitat suitability in each climate and management scenario (dam removal in this study).

The extent of suitable freshwater habitat was calculated

1. under current conditions and following climate change in 2055 and 2085,
2. with and without dams, and
3. with and without considering climate change in coastal waters.

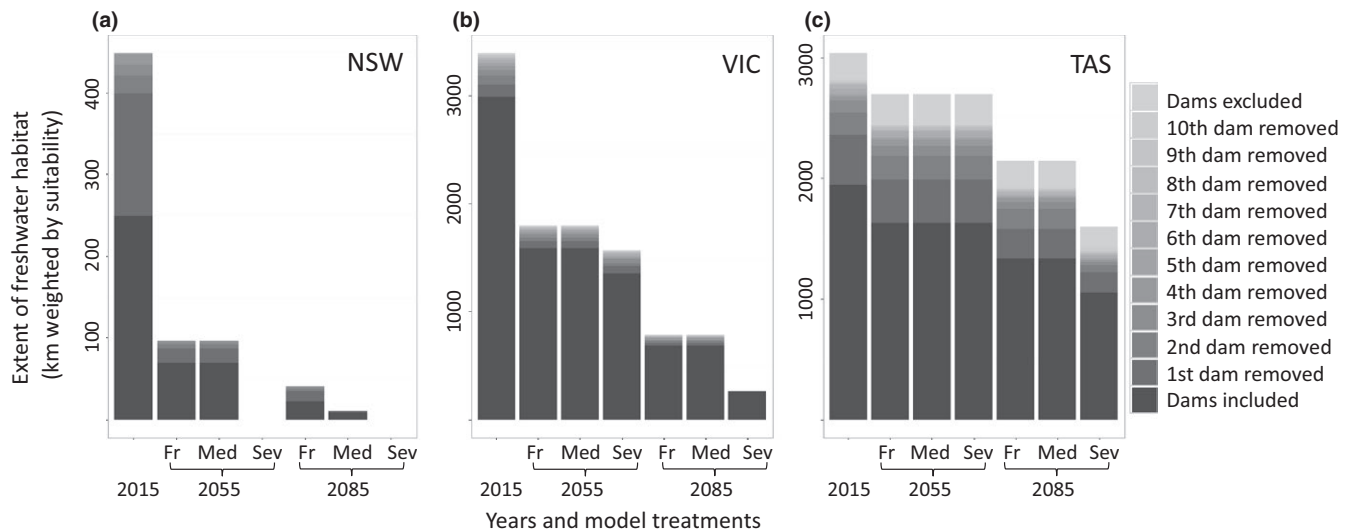
We assessed the impact of lost freshwater connectivity on habitat extent by comparing totals for standard projections that neglect dams (“Dams excluded”), and totals after suitability was reset to zero for all streams and rivers upstream of a dam (“Dams included”). We assessed habitat gain by gradually removing the top ten dams (five for New South Wales because there are only five dams among important rivers in this state) that blocked most upstream habitat (length weighted by suitability) following the steps below. First, we calculated the extent of suitable habitat between every dam and headwater or another upstream dam. Then, we gradually removed dams that blocked access to the most upstream habitat (i.e., greatest gains in suitable habitat extent after removal). Due to the obligatory marine larval stage of Australian Grayling (Backhouse et al., 2008a), only the removal of dams that had no other barriers downstream were considered for each move. The removal of any upstream dam within a series of dams will be considered after downstream dam was removed in a previous decision. Finally, we calculated

potential habitat loss of all upstream freshwater habitats if downstream coastal water temperature was considered unsuitable, and assessed how this affects dams which were in the top ten priorities. Only the top ten dams (five for New South Wales) in each state were evaluated because our main goal was to reveal the influence of climate change on conservation plans instead of designing specific prioritization plans. We calculated habitat size changes using graph metrics to incorporate river hydrographic network (Saunders et al., 2016) by R package *igraph* (Csardi & Nepusz, 2006).

### 3 | RESULTS

#### 3.1 | Habitat suitability in rivers and the sea

We predicted the extent of suitable habitat for Australian Grayling will decline dramatically throughout its range by 2085 (Figures 1–3). The suitability of freshwater habitat was predicted to decline in New South Wales (northern portion of the range), and some areas of central Victoria (central portion of the range, Figure 1). In Tasmania (southern portion of the range), we predict both habitat losses and gains locally but a minor loss in total (Figures 1, 2c,f and 3c). The impact of climate change on marine habitats varied among GCMs and states (Figures 1 and 2). While a mild warming from the north was found with HadGEM2-ES (medium) in 2055 and 2085, the water temperature in coastal New South Wales, eastern Victoria and north-eastern Tasmania might become less suitable for larval fish in 2085 subject to the FGOALS-s2 (severe) projections. The southerly shift of suitable marine habitats was predicted to occur more rapidly than freshwater habitats in New South Wales (Figure 1). Decoupling between marine and freshwater habitats might occur in New South Wales under both medium and severe marine warming projections (Figures 1, 2a,d and 3a), and in Victoria (Figures 1, 2e and 3b) and Tasmania (Figures 1, 2f and 3c) under severe ocean warming.



**FIGURE 3** The extent of predicted riverine habitat for sequentially removing dams in order of new habitat made available in (a) New South Wales (5 dams total), (b) Victoria (10 dams total) and (c) Tasmania (10 dams total) under current (2015), 2055 and 2085 climate conditions without considering ocean warming (Fr: climate range shift modelled in freshwater only), or with a medium (Med: HadGEM2-ES) or a severe (Sev: FGOALS-s2) ocean warming

### 3.2 | Priorities of dam removal under climate change

Dams had a significant impact on the extent of suitable freshwater habitat in New South Wales under current climate conditions (blocked 44.5% of total habitat) and in Tasmania under current or future climate conditions (blocked 34–36% of total habitat) (Figure 3). Climate change in both riverine and marine habitats influenced the highest priority dams for removal, especially in Victoria (Figure 4b). Under moderate ocean warming, the removal of upstream dams became more important because of the upward shifts in suitable habitat (hollowed arrow in Figure 4b). However, severe ocean warming from the east (Tasman Sea) made the removal of dams in central or western Victoria more important (arrows in Figure 4b). None of the dams in New South Wales were a removal priority for maintaining Grayling's habitat connectivity, because both freshwater and marine habitats were projected to become unsuitable under climate change (Figures 3a and 4a). The distribution of freshwater habitats and hence priorities for dam removal in Tasmania remained relatively stable under medium ocean warming (Figure 4c), but more severe warming in the north-east increased the importance of removing dams from south-western Tasmania (arrows in Figure 4c).

## 4 | DISCUSSION

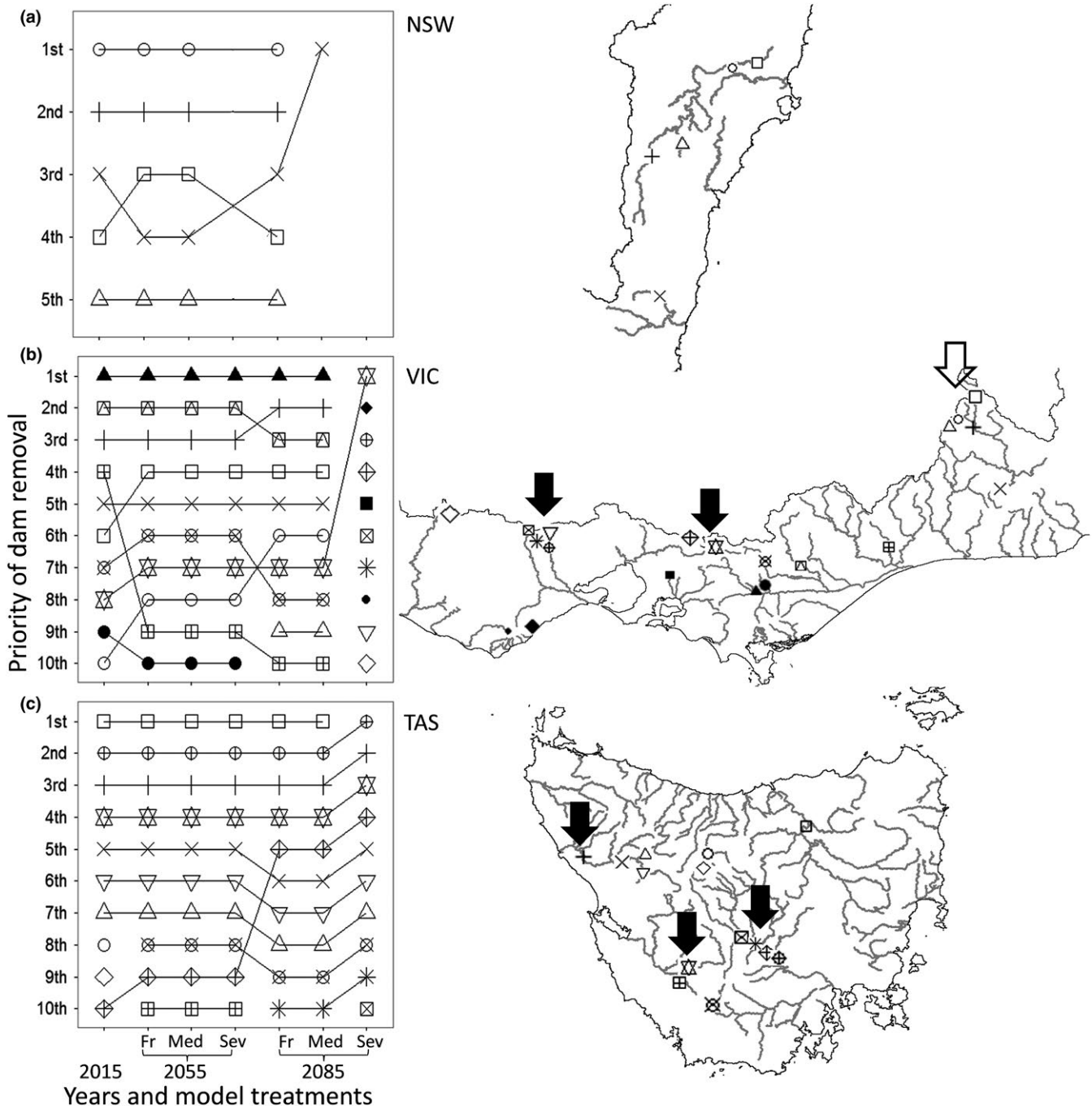
The mismatch in timing between migration and resource availability among habitats is relatively well studied (Rijnsdorp, Peck, Engelhard, Möllmann, & Pinnegar, 2009; Robinson et al., 2009), compared to the decoupling of critical habitats under climate change (Wauchope et al., 2016). Our results revealed that ignoring the differences in the rate of climatic change and species' sensitivity within separate habitats could result in ineffective restoration plans for conserving

species that require multiple connected habitats to complete their life cycle. Furthermore, changing the spatial distribution of suitable habitats in different ecosystems might interact with anthropogenic disturbances, like dams. Therefore, the impact of climate change on intersystems connectivity should be taken into consideration for conservation planning (Álvarez-Romero et al., 2011; Saunders et al., 2016).

For Australian Grayling, our results indicated that north-eastern (trailing edge) populations are likely to experience dramatic declines or even local extinction based on the projected decrease in suitability of both freshwater and marine habitats. In addition, the extent of suitable habitats was more stable in south-western populations, but anthropogenic barriers reduced the accessible habitats. Climate change could be the major threat to the persistence of Grayling in New South Wales and Victoria, but anthropogenic barriers will continue to be the most important constraint in Tasmania.

The increasing temperature of marine nursery habitats could compromise the viability of local populations in adjacent river catchments. Studies indicate that early life stages of fish are more vulnerable to climate change (Pörtner & Farrell, 2008; Rijnsdorp et al., 2009) and the stress experienced during early stages may have long-term negative impacts on individual fitness and population dynamics (Morrongiello, Walsh, Gray, Stocks, & Crook, 2014; O'Connor & Cooke, 2015). Significant warming in coastal waters and lower river flows in south-eastern Australia might also impact the primary production in coastal waters (Booth, Bond, & Macreadie, 2011; Hobday & Lough, 2011; Koehn et al., 2011). In addition, the intensification of Eastern Australian Current has caused southwards shifts of many marine species by increasing water temperature and transporting pelagic larva further south (Booth et al., 2011; Wilson et al., 2016). As the warming in Tasman Sea is consistently projected by different GCMs (Hobday & Lough, 2011) and the rate of observed ocean warming is 3–4 times





**FIGURE 4** Plot of priority dams for removal in (a) New South Wales, (b) Victoria and (c) Tasmania under current (2015), 2055 and 2085 climate conditions without considering ocean warming (Fr: freshwater only), or with a medium (Med: HadGEM2-ES) or a severe (Sev: FGOALS-s2) ocean warming. Symbols on the maps represent dams and match to symbols on the line charts. Line charts show shifts in the rank priorities of dams over time and under different ocean warming models. Arrows show the upward (hollowed) and west- or southward (solid) shifts of dams for remove through time

higher than global average (Hobday & Pecl, 2014), this potential decoupling might impact species migration and energy flows between coastal and marine systems in eastern Australia.

Genetic studies suggest that diadromous fish may have greater dispersal ability than freshwater fish because they can move between river catchments through marine life stage (Chenoweth & Hughes, 1997; Schmidt, Crook, O'Connor, & Hughes, 2011). However, barriers

between freshwater and marine habitats can severely constrain their dispersal ability (Lassalle, Crouzet, & Rochard, 2009; Leathwick et al., 2008). Similar to our results, suitable habitats for freshwater fish have been predicted to shift upward along altitudinal gradients and poleward in Australia (Bond et al., 2011) and globally (Comte et al., 2013). The expansion of suitable habitat from lower to further upstream reaches may occur for some diadromous fish (Bond et al., 2011).

However, barriers along rivers could make these novel habitats still inaccessible for fish (Lassalle & Rochard, 2009).

#### 4.1 | Implication for conservation management

Multiple methods have been suggested to prioritise anthropogenic barrier removal for restoring river connectivity (Hermoso, Januchowski-Hartley, & Linke, 2015; Kemp & O'Hanley, 2010). The prioritization of barrier removal may become more critical because climate change and economic development will likely increase competition for water resources between human society and other species (Vörösmarty, Green, Salisbury, & Lammers, 2000). Currently, removing anthropogenic barriers and building fish passages on weirs have been implemented in this region under Australian Grayling National Recovering Plan (Backhouse et al., 2008a,b). Barrier survey was also completed in New South Wales for prioritizing future barrier removal plans. While the changes in local climate and hydrological characteristics by climate change can be important for barrier removal and river restoration (Palmer et al., 2009), we suggest that the future distribution of suitable habitats for protected species should also be taken into consideration. Incorporating socio-economical cost of dam removal and estimating future water need in human society could further improve prioritization.

There are numerous sources of uncertainty when predicting species' future distribution (Buisson, Thuiller, Casajus, Lek, & Grenouillet, 2010; Bush & Hoskins, in press), and these can be roughly divided into three parts; climate uncertainties, methodological uncertainties, and biotic uncertainties (Pacifi et al., 2015). We use ensembles of GCMs and modelling algorithms to balance the variation among climate projections and species distribution modelling methods (Fordham et al., 2011; Pacifi et al., 2015), and identify more likely outcomes but nonetheless stress the importance of including projection uncertainty in conservation planning (Carvalho, Brito, Crespo, Watts, & Possingham, 2011). Further, biotic uncertainties arise partly from the assumption that species' current distribution is in equilibrium with surrounding environmental variables and these relationships are consistent under future climate conditions might not be realistic (Pacifi et al., 2015). While correlative models estimate realized niche, using mechanistic models that consider species traits may improve our understanding about how fundamental niche and population dynamics change after climate change (Rougier et al., 2015). Other constraints such as biotic interactions or non-climatic stressors can provide a more realistic view to assess future distribution (Franklin, 2013). For example, as introduced salmonids contribute to the decline of Australian Grayling and other galaxioids (McDowall, 2006), future distribution shifts of exotic species could change the predation or competition pressure on native species. In addition, land use change and water abstraction plans can also impact the future distribution of Australian Grayling (Backhouse et al., 2008a).

Besides changing the distribution of suitable habitats, climate change can also impact connectivity between freshwater and marine habitats by changing hydrology and increasing the intensity of human water use such as water abstraction (Gillanders et al., 2011; Jaeger,

Olden, & Pelland, 2014; Saunders et al., 2016). Decreased annual runoff and increased temperature are projected in south-eastern Australia catchments (Morrongiello et al., 2011), and both factors can severely lower spawning and recruitment success of Australian Grayling (Shenton et al., 2011). Thus, maintaining natural flow regimes in the "important rivers" during autumn and spring to secure reproduction success, and restoring riparian vegetation to mitigate warming temperature are likely to be critical to conserve this threatened species (Amtstaetter et al., 2016; Shenton, Hart, & Chan, 2014; Shenton et al., 2011).

#### 4.2 | Future directions and conclusion

While we modelled the distribution of suitable habitats only, models that have the ability to simulate both population dynamics and the distribution of migratory fish under climate change have been developed (e.g., GR3D in Rougier et al. (2015)). However, their complexity and data requirements make them less suitable for poorly studied species. Meta-analysis has shown previous works disproportionately focused on the impact of climate change on migratory birds and some fishes in Northern Hemisphere such as salmonids while neglecting other animal groups (Comte et al., 2013; Robinson et al., 2009). Conservation plans based on anadromous (i.e., adults live in saltwater habitats but migrate to freshwater for reproduction) salmonids may not be effective for species with different migration types such as amphidromy (i.e., adults live in freshwater, but early life stages are in saltwater habitats, e.g., Australian Grayling), catadromy (i.e., adults live in freshwater but migrate to saltwater habitats for reproduction, e.g., freshwater eels) or potamodromy (i.e., fish migrates among different freshwater habitats, e.g., lake sturgeon) (McDowall, 1999). Furthermore, biotic interactions such as competition and predation by introduced salmonids can also impact the distribution of Grayling as discussed above, multispecies models (e.g., joint species distribution models in Pollock et al. (2014)) may provide more comprehensive information for conservation plans.

The number of studies that incorporate the impact of climate change into spatial conservation prioritization has increased over the past decade (Jones, Watson, Possingham, & Klein, 2016). While the impact of climate change on species distribution is recognized, considering climate change can help to achieve persistence of target species under changing climate by prioritizing conservation actions for future distribution, climate refugia and connectivity as in ours and other studies (e.g., Schmitz et al. 2015, Jones et al. 2016, and Iwamura, Fuller, and Possingham 2014).

In conclusion, we predicted that climate change will decouple connections between the habitats Grayling need to complete their life cycles. Thus, climate-driven decoupling of habitats threatens the persistence of Grayling and influences the most effective places to restore freshwater connections by removing barriers. We suggest that decoupling of connections among habitats might become an issue more generally for migratory species facing rapid climate change within their ranges. While the loss or degradation in one habitat can influence the population dynamic in another habitat (O'Connor &

Cooke, 2015), integrating impacts throughout species' life history can improve the effectiveness of conservation actions.

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## AUTHOR CONTRIBUTIONS

H.Y.L., C.J.B., S.L., and H.P.P. conceived the ideas; A.B. and H.Y.L. collected and analysed the data; H.Y.L. led the writing of the manuscript with C.J.B., A.B., S.L., and H.P.P.; all authors contributed to the final version of the manuscript.

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## BIOSKETCH

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