



Identifying species at risk from climate change: Traits predict the drought vulnerability of freshwater fishes



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ABSTRACT

Trait analysis has potential to identify species that are vulnerable to climate change, but its predictive strength has not been adequately examined. Conditions during the recent 'Millennium Drought' in Australia's Murray-Darling Basin resembled the projected future climate of the region and provided an opportunity to test the ability of traits to predict population responses to a warmer and drier environment. I used data from a large-scale monitoring program to assess how 14 dietary, life-history and physiological-tolerance traits related to changes in occurrence and abundance of 39 of the basin's freshwater fish species. Species that fared worse under prolonged drought were significantly more likely to have an invertivorous rather than omnivorous diet, a low age at sexual maturity, a small maximum body size, a low spawning temperature, a long spawning season, low fecundity, demersal rather than planktonic eggs, and a low upper thermal limit. Rankings of drought vulnerability of fish species derived from correlations between population changes and traits showed good agreement with a previous assessment of inter-specific variation in resistance to drought, and were corroborated by independent observations of drought responses for some species. Trait analysis should have wide application to identifying species at risk from climate change, provided that sufficient traits are assessed and that adequate consideration is given to variation in trait-vulnerability relationships among different groups of organisms, geographic regions and types of ecosystems.

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1. Introduction

Evidence that climate change threatens many species with extinction continues to grow (Warren et al., 2011; Bellard et al., 2012). Assessment of biological traits (e.g. physiological tolerances, life history attributes, dietary and habitat requirements and dispersal ability) may help to identify the species at greatest risk, given that such characteristics often correlate with current conservation status (e.g. Purvis et al., 2000; Anderson et al., 2011). However, it is uncertain whether trait analysis has the requisite prognostic strength to underpin practical conservation decisions (Angert et al., 2011).

One way to test the power of traits to predict vulnerability to expected climate change is to see whether they explain population responses to climatic fluctuations of the past. Such an approach can be taken for south-eastern Australia by considering the period 1997–2009, when the region suffered a succession of severe rainfall deficits and record high temperatures (Leblanc et al., 2012). This 'Millennium Drought' or 'Big Dry' impacted severely on both aquatic and terrestrial ecosystems, especially in the Murray-Dar-

ling Basin (Bond et al., 2008; Kingsford et al., 2011). A return to wetter conditions in mid-2010 provided a respite, but probably only a temporary one because global climate models project a warming and drying trend for the region in the longer term (Leblanc et al., 2012). Species' reactions to the Millennium Drought may therefore foreshadow their responses to future climate change, providing clues to how those responses may be dictated by traits.

Here, I test the extent to which characteristics of freshwater fish species in the Murray-Darling Basin explained their population changes as the Millennium Drought unfolded. Drought stresses or kills freshwater fishes through physical changes such as rises in water temperature, lack of hydrological cues for reproduction and complete drying of water bodies, chemical changes such as increases in salinity and decreases in dissolved oxygen, and biological changes such as greater exposure to parasites, pathogens and predators (Magoulick and Kobza, 2003; Bond et al., 2008). Once droughts break, fish assemblages usually recover over a few weeks, months or years (Matthews and Marsh-Matthews, 2003), but barriers to movement from refuges can prevent re-colonization (Griswold et al., 1982). Droughts can also facilitate the establishment of alien species (Bêche et al., 2009; Boix et al., 2010) and exacerbate impacts of water abstraction (Wedderburn et al., 2012). Expected increases in drought severity and intensity due to global warming

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(Dai, 2011) can only compound the worldwide pressure that harvesting, pollution, river impoundment, water abstraction, introduced species, habitat loss and habitat degradation have already placed on freshwater fishes (Bruton, 1995; Xenopoulos et al., 2005; Clausen and York, 2008).

Freshwater fishes are a focus of biodiversity conservation in the Murray-Darling Basin because many species have declined dramatically in distribution or abundance and several are formally listed as threatened either internationally, nationally, or within individual Australian states (Koehn and Lintermans, 2012). Previous research has estimated the vulnerability of Murray-Darling fishes to either drought or projected climate change by reviewing relevant literature and soliciting expert opinion (Crook et al., 2010), developing conceptual models of likely mechanisms of climate-change impacts (Balcombe et al., 2011), and species distribution modelling (Bond et al., 2011). These studies provide extensive insight into the potential for beneficial and adverse impacts but do not cover all Murray-Darling species, have not been tested against empirical observations of population changes, and sometimes differ in the fates that they imply for particular species. Consequently, there is scope to extend and refine our understanding of the vulnerabilities of Murray-Darling fishes.

In this study, my aims were to (1) test the capacity of traits to predict changes in freshwater fish populations during severe and prolonged drought, (2) develop a trait-based method of ranking species according to drought sensitivity, and (3) develop directions for future refinement of trait-based vulnerability assessment in general. I analysed fish catch data from a basin-wide monitoring program in order to relate changes in distribution and abundance to inter-specific variation in traits that I assessed via an extensive literature review. I then used relationships between traits and population changes to assign rankings of relative drought vulnerability for Murray-Darling freshwater fish species. Finally, I evaluated these rankings by comparing them with previous assessments of the sensitivities of fish species to drought and projected climate change.

2. Methods

2.1. Study area

The Murray-Darling Basin (Fig. 1) covers 1,061,469 km² of south-eastern Australia between the latitudes of 24 and 38°S. It includes Australia's three longest rivers, the Darling (2740 km), the Murray (2530 km) and the Murrumbidgee (1690 km), as well as many smaller streams and wetlands. Elevation ranges from 2228 m on Mount Kosciuszko to sea level at the mouth of the Murray River. Most of the basin is arid or semi-arid and consequently it has a low annual average discharge relative to its area: 4700 GL, which would rise to 12200 GL if water diversion were absent (CSIRO, 2008). The basin is a prime agricultural region, including about 65% of Australia's total area of irrigated crops and pastures and about 39% of the national value of agricultural production (ABS, 2008). Its fish fauna includes about 70 freshwater, estuarine, marine and diadromous fish species, including a dozen introduced from outside of Australia (Hardy et al., 2011).

2.2. Data sources

Fish distributional and abundance data came from the Sustainable Rivers Audit (SRA), which has sampled rivers (but not reservoirs, natural lakes or wetlands) across the entire Murray-Darling Basin since 2004 (Davies et al., 2010). The data comprised the number of individuals of each species caught at each survey site on each sampling occasion between November 2004 and June

2010. In this period 839 sites were sampled (Fig. 1): 695 on one occasion and 144 on two occasions with an intervening period of about 3 years. Sampling sites were selected by a stratified random process wherein the basin was divided into geographical zones and sites were chosen randomly from a defined stream network within each zone, but with restrictions on the proximity of sites to one another. Sampling was spread over all calendar months except July, August, September and October. Fish were collected in box traps and with either boat-mounted, bank-mounted or backpack electro-fishing gear, depending on site characteristics, and recorded if longer than 15 mm.

I searched over 1000 journal papers, technical reports, books, theses and on-line data bases for information on traits of freshwater fish species recorded from the Murray-Darling Basin (Appendix A). I considered 14 traits relating to diet, life history and physiological tolerance (Table 1), which I chose for their diversity, ability to be expressed numerically, and likelihood that values could be obtained for most species. Ideally, trait data would have been confined to populations in natural environments within the Murray-Darling Basin, but obtaining adequate information required including data from beyond the basin and from artificial environments such as aquaculture ponds and aquaria. However, I used data from research outside of Australia only when I could not find sufficient information in Australian studies. I also favoured primary sources, i.e. accounts of original research, over secondary sources such as fish identification guides. When data on a particular trait and species differed among sources, or when a range of values was reported, I usually calculated averages. However, for those traits that were expressed as maxima and minima (e.g. adult size as maximum body length), I took the most extreme value unless it appeared anomalous.

Total consistency was not possible for some traits when using data from multiple sources. For adult size I used the largest body length reported for each species whether total, fork or standard. For heat tolerance I accepted any estimate of upper thermal limit including the highest temperature at which a species had been observed in the field or a laboratory endpoint such as critical thermal maximum or EC₅₀. This diversity of measurements introduced some unwanted variability but it was minor relative to variation among species. To standardise and simplify dietary data I calculated the percentage of digestive tract contents represented by five major food categories – algae, detritus, living plants, invertebrates and fish – ignoring other items and unidentified material. I used any sources that allowed digestive tract contents to be apportioned by approximate volume or weight of different components, and calculated within-study averages per species if a study reported data separately for different localities, habitats, sampling periods or fish size classes.

In a few cases where I could not find the necessary information in the literature, I assigned trait values to a species by adopting those of a relative, provided that the trait concerned appeared conservative within a genus or family. For example, because *Galaxias olidus* has been reported to feed almost exclusively on invertebrates, I assumed the same would be true of other small species of *Galaxias* for which I lacked adequate dietary data.

2.3. Statistical analysis

Under the SRA sampling design a rotating third of the basin is sampled for fish each year so that the entire basin is sampled each triennium. I therefore compared the catch of each species between the first complete sampling round (2004–2007) and the second (2007–2010), in terms of both prevalence and abundance. I expressed prevalence as the percentage of sampling sites in which each species was recorded in round 1 (P_1) and round 2 (P_2) and calculated both the absolute change in prevalence ($\Delta P_a = P_2 - P_1$) and

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