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Occupancy modelling confirms the first extirpation of a freshwater fish from one of the world's largest river systems

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Abstract

1. Numerous human-induced changes to freshwater ecosystems are implicated in the loss of biodiversity, including fish extinctions. Dams and weirs have profoundly altered the ecological character of the Murray–Darling Basin (MDB), one of the world's largest river systems, which discharges at the mouth of the River Murray in South Australia.
2. These impacts are evident in the Ramsar-listed final reaches of the river, where regulation, drought, and flow reductions over recent decades have led to the collapse of freshwater fish populations, including Yarra pygmy perch (*Nannoperca obscura*), which is Endangered on the International Union for Conservation of Nature Red List of Threatened Species.
3. *Nannoperca obscura* occurs in several major catchments in south-eastern Australia, but the genetically unique population in the MDB only inhabits wetlands near the terminus of the River Murray where wild populations were last recorded in 2008 approaching the end of a prolonged drought.
4. This study involved repeated surveys targeting *N. obscura* to evaluate its occupancy in the MDB while accounting for imperfect detection. The surveys failed to find *N. obscura* despite regular detection of the closely related southern pygmy perch (*Nannoperca australis*), which provides a proxy for the congener.
5. This study presents strong evidence that *N. obscura* is absent in the survey region, thereby inferring the first freshwater fish extirpation from the MDB. The outcomes of this study should prompt responses required to aid the species' population recovery and present a reliable approach to confirm the status of freshwater fishes for conservation management.

KEYWORDS

detection probability, ecological specialist, endangered species, IUCN red list, Percichthyidae, species loss

1 | INTRODUCTION

Species extirpations and extinctions are occurring at an unprecedented rate, and freshwater fishes are particularly vulnerable (Ceballos et al., 2015; Darwall & Freyhof, 2016). For example, 28% of freshwater fish species assessed for the International Union for

Conservation of Nature (IUCN) Red List of Threatened Species are deemed threatened with extinction (Tickner et al., 2020), with 90 species already Extinct or Extinct in the Wild (World Wide Fund, 2021). Changes to freshwater systems resulting from interacting factors, including flow alteration, channelization, alien species, and climate change, are implicated in the loss of freshwater

biodiversity, including fish extinctions (Dudgeon et al., 2006; Darwall & Freyhof, 2016). Further, there is an apparent trade-off between biodiversity protection and the perceived needs of modern society resulting from the competing demands of water for agriculture and the environment in regulated rivers (Grafton et al., 2011; McShane et al., 2011). It is increasingly important, therefore, to understand the nature of conservation trade-offs as human demand on fresh water grows. This will require accurate and defensible measures of species declines or losses.

Accurately determining the population status of a rare species is often difficult given its scarcity in the environment being subsampled. Most wildlife monitoring programmes fail to account for imperfect detection (i.e. false absences) of rare species, however, thereby leading to inaccurate estimates of occupancy (Watson, 2017). This limitation has been increasingly addressed in recent decades, whereby imperfect detection is measured to estimate occupancy accurately by modelling presence/absence data from repeated surveys (Mackenzie et al., 2018), yet this approach is apparently lacking in monitoring programmes targeting rare freshwater fishes. For example, in one of the world's largest river systems, the Murray–Darling Basin (MDB) in south-eastern Australia, few fish monitoring programmes account for imperfect detection, despite the findings being used to make important management decisions (e.g. environmental flows; Gwinn et al., 2016). Therefore, a study design should consider imperfect detection to confirm the presence or absence of a rare freshwater fish – often a threatened species.

Yarra pygmy perch (Percichthyidae: *Nannoperca obscura*) is a rare, small-bodied fish (<8 cm long) in the MDB, where more than 50 native freshwater fish species are recorded (Murray–Darling Basin Authority, 2020). It is Endangered on the IUCN Red List of Threatened Species due to population decline and apparent extirpations (Hammer, Wedderburn & van Weenan, 2009; Whiterod et al., 2019). It occurs in other catchments in south-eastern Australia, but the genetically unique population in the MDB only inhabits wetlands associated with a single freshwater lake in a Ramsar-listed site at the terminus of the system (Hammer, Wedderburn & van Weenan, 2009; Brauer et al., 2013). River regulation and critical water shortages during a prolonged drought from 1997 to 2010 resulted in broad-scale drying and loss of the species' remnant habitat whereby wild populations were last recorded in 2008 (Wedderburn, Hammer & Bice, 2012). Beforehand, 200 individuals were rescued in 2008 for captive breeding (Hammer et al., 2013), but annual monitoring using repeated fyke net surveys (i.e. accounting for probability of detection) has failed to detect the species since 2015 after several reintroduction attempts (Wedderburn, 2018). To date, there is no commitment toward a large-scale reintroduction programme for *N. obscura*, largely because of uncertainty regarding its extirpation in the system following failed reintroductions.

This study evaluated the status of *N. obscura* in its entire range in the MDB to make inferences about its possible extirpation from the system. To strengthen inference, repeated surveys were conducted to account for imperfect detection by estimating the detection probability for all fish species using occupancy models. The primary

aim was to provide a defensible description of the status of *N. obscura*. A secondary aim was to examine relationships between freshwater fishes and their habitat, with an emphasis on congeneric southern pygmy perch (*Nannoperca australis*). Given the close taxonomic, morphological, and similar distribution of the two congeners, the findings may provide insight regarding the rarity of *N. obscura* to inform responses required to aid its population recovery in the MDB. This study also presents a scientifically defensible approach to confirm the status of other rare freshwater fish threatened with extinction.

2 | METHODS

2.1 | Sampling

Thirty-two sites were selected for sampling to encompass the contemporary range of *N. obscura* (i.e. following river regulation in the 1930s; Hammer, Wedderburn & van Weenan, 2009). The impacts of the prolonged drought were basinwide, so there is no likelihood of the species occupying any other region of the highly altered river system (Hammer, Wedderburn & van Weenan, 2009; Wedderburn, Hammer & Bice, 2012). Sampling was undertaken at 18 sites where the species was formerly detected prior to 2008 (Bice, Whiterod & Zampatti, 2014; Wedderburn & Hammer, 2003), six sites where reintroductions had occurred between 2011 and 2015 (Bice, Whiterod & Zampatti, 2014; Wedderburn et al., 2020), and eight new sites of favourable conditions. All sites were connected at the time of sampling. The sites were in the islands region of south-west Lake Alexandrina, the lower reaches of the Mount Lofty Ranges, and the Goolwa Channel (Figure 1). Essentially, surveys were conducted in all water bodies within the entire range of *N. obscura* in the MDB that were suitable for the species and other sites that held potential. Each site was surveyed three times between November 5 and December 14, 2018.

Surveys at each site (~30 m long × 5–10 m wide) occurred within 3 days of each other, but usually over three consecutive days. Three 6 m single-leader fyke nets (5 mm half mesh) were set at least 10 m apart overnight at all sites on the three occasions and placed perpendicular to the bank or angled when in narrow channels. Grids (50 mm) at the entrances of nets excluded turtles and fish that might harm other fish, but were not expected to affect their ability to capture fish <250 mm long. Fish were identified to species and counted. *Nannoperca australis* and the alien European perch (*Perca fluviatilis*) were measured to distinguish between juvenile and adult fish in the models (see later) to gain resolution and to account for the different ontogenetic diets or other ecological dynamics. Fish sampling was conducted in accordance with the Animal Ethics policy of the University of Adelaide (approval S-2018-094), the National Parks and Wildlife Act 1972 (Permit to Undertake Scientific Research: Q26018–8), and the Fisheries Management Act 2007 (permits MP0105 and ME9903009).

Electrical conductivity (EC, $\mu\text{S cm}^{-1}$), pH, and water temperature ($^{\circ}\text{C}$) were recorded using a TPS WP-81 meter (TPS Pty Ltd, Brendale,

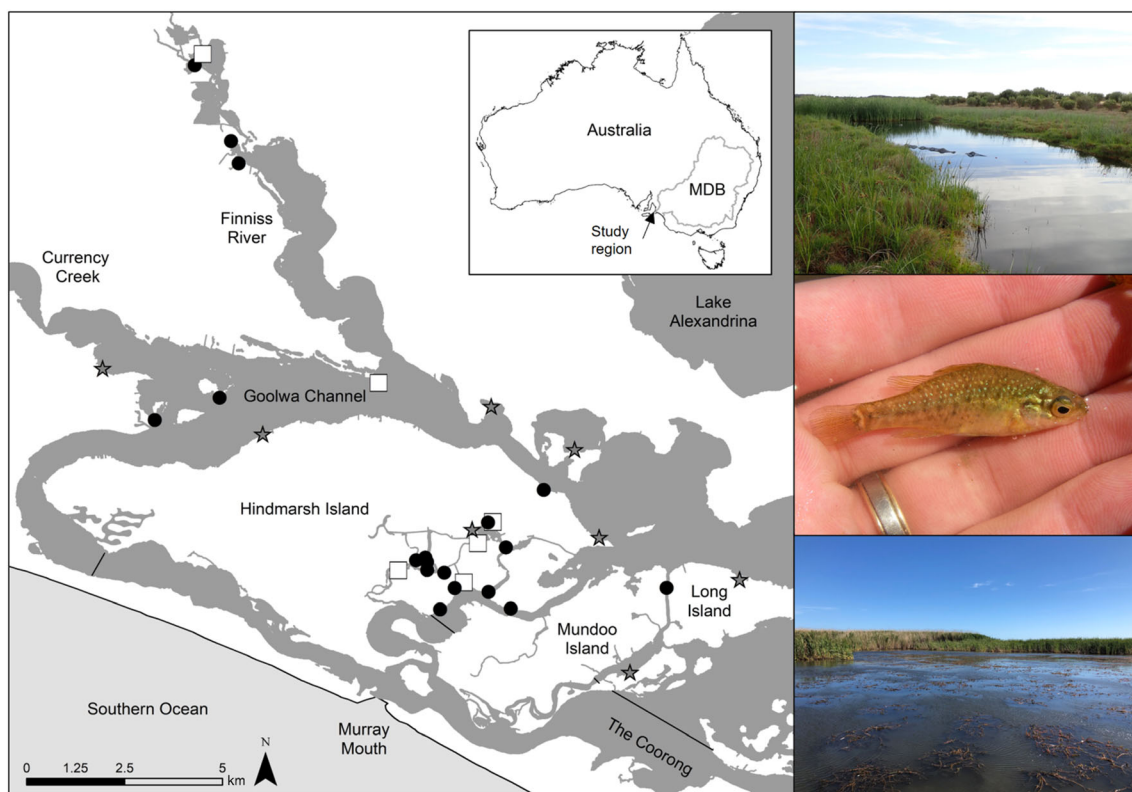


FIGURE 1 Study region at the terminus of the Murray–Darling Basin (MDB) in south-eastern Australia showing the 32 sites (black dots) surveyed three times in November–December 2018 across the entire range of Yarra pygmy perch (*Nannoperca obscura*). Sites where the species was formerly detected are indicated by black circles, reintroduction sites are indicated by white squares, and new sites with favourable conditions are indicated by grey stars. Barrages are indicated by black lines. Photographs show *N. obscura* and its representative habitat

QLD, Australia), and Secchi depth (cm) was measured within the site. Other microhabitat variables were recorded, chosen based on their potential importance to threatened fish populations: average water depth (five measures approximately 1 m apart, beginning 1 m from the bank, or five measures equally spaced if in a narrow channel) and macrophyte cover (estimated percentage of aquatic plants covering the site).

2.2 | Occupancy detection

In an occupancy study, the extent of a species' habitation in its natural range (in the present context, the proportion of survey sites where the species is detected) is determined while taking into account false absences (i.e. imperfect detection) in sampling by conducting repeated surveys (Mackenzie et al., 2018). The optimal number of repeated surveys of an occupancy study can be based on the results of a pilot study, on studies carried out for the same or similar species in comparable circumstances, or on expert opinion (Guillera-Aroita, Ridout & Morgan, 2010; Mackenzie et al., 2018). In the case of *N. obscura*, no occupancy data were available to account for imperfect detection. To derive the optimal number of repeated surveys to be carried out at each sampling site in the present study, results of Wedderburn (2018) for congeneric *N. australis* were used to

determine the optimum number of repeated surveys required within the constraints of available resources as derived from Guillera-Aroita, Ridout & Morgan (2010). These results indicated that three repeated surveys were required to reliably detect *Nannoperca* in an occupancy study within the constraints of available funding.

Probabilities of each fish species' occupancy and detection were estimated with a single-season model with constant P and a single-season model with survey-specific P using the program PRESENCE 2.13.6 (Hines, 2006). Both models treated the data as three surveys represented by the three days of sampling, and the survey-specific model was fitted to test (by Akaike's information criterion (AIC) with a delta value of 2) whether differences occurred at the survey level as a result of heterogeneity across sampling events. Overall, for each species, the following were estimated: (i) naive occupancy – the proportion of sites surveyed where the species was detected at least once and used to estimate occupancy probability without correcting for detection probability; (ii) occupancy probability – the proportion of survey sites where the species occurs; and (iii) detection probability – the proportion of total abundance of a species captured when it is present.

Sampling fulfilled the necessary assumptions for an occupancy model (Mackenzie et al., 2018): (i) fish have adequate time to recover after each survey, and therefore the detection of species and the detection histories at each site are independent; (ii) surveys are

repeated within a short period of time to meet the closure assumption (e.g. eliminate issues of seasonal migration); (iii) fish species are identified correctly; and (iv) the probability of occupancy is constant across sites because the surveys target obligate habitats of the regional wetland fishes. In the last case, the measured microhabitat variables were within the known preferences of the wetland fishes, so they were omitted from the occupancy models. Microhabitat values were included as covariates to describe overall fish–microhabitat relationships, with an emphasis on *N. australis* as a proxy of habitat suitability for *N. obscura*.

2.3 | Fish–microhabitat relationships

Constrained quadratic ordination (CQO; Yee, 2015) was used to analyse fish–microhabitat relationships. In CQO, which has been applied successfully in fish ecology (Vilizzi, Stakenas & Copp, 2012), a site \times species data matrix is related to a site \times microhabitat (variables) data matrix and the output is an ordination diagram. In the latter, the x-axis represents the latent variable, which in the present case will be a vector consisting of a linear combination of the microhabitat variables (or descriptors), whereas the y-axis plots the probability of occupancy of the species. With CQO, an optimal linear combination of the microhabitat variables (which are ‘condensed’ into the latent variable) is estimated and the species data are regressed on the latent variable axis using a quadratic (response) curve fitted to each species. Each response curve in the ordination diagram represents the distributional range of the species across the microhabitat gradient (i.e. the latent variable), so that the relative position of the curve along the gradient indicates the use or preference by the species for a certain range of the microhabitat variables summarized into the gradient and determined by the species’ probability of occupancy. The optimum is the value along the microhabitat gradient at which the highest probability of occupancy for that species is recorded, and the maximum is the highest probability of occupancy at a certain value of the gradient.

Four CQO models in total were fitted to presence/absence data for *N. australis* (young-of-the-year (YOY) and adults), owing to its relatedness to *N. obscura*, and the other freshwater specialist, Murray hardyhead (*Craterocephalus fluviatilis*) (also for reasons of model convergence), relative to the following fish groups adapted from Potter et al. (2015) and Whiterod, Hammer & Vilizzi (2015) (Table 1):

1. Alien (freshwater generalists) — goldfish (*Carassius auratus*), common carp (*Cyprinus carpio*), eastern mosquitofish (*Gambusia holbrooki*), oriental weatherloach (*Misgurnus anguillicaudatus*), and *P. fluviatilis* (YOY and adults).
2. Diadromous species — common galaxias (*Galaxias maculatus*) and congolli (*Pseudaphritis urvillii*).
3. Solely estuarine species — smallmouth hardyhead (*Atherinosoma microstoma*), western blue-spot goby (*Pseudogobius olorum*), and lagoon goby (*Tasmanogobius lasti*).

4. Freshwater generalists — unspecked hardyhead (*Craterocephalus fulvus*), carp gudgeon (*Hypseleotris* spp.), golden perch (*Macquaria ambigua*), bony herring (*Nematalosa erebi*), dwarf flathead gudgeon (*Philypnodon macrostomus*), and Australian smelt (*Retropinna semoni*).

Notably, for model convergence, the flathead gudgeon (*Philypnodon grandiceps*) was excluded from the freshwater generalists group as it did not achieve an optimum along the environmental gradient. The marine migrant group was also excluded from analysis as a result of low catch numbers of only two species. The use of separate models was dictated by the maximum suggested limit of ≤ 12 species for successful fitting of CQO (Yee, 2015), but also for improved visualization of the species interrelationships. The latent variable consisted of the six microhabitat descriptors: EC, pH, Secchi depth, temperature, depth, and macrophyte cover. Fitting of CQO models was under a binomial likelihood function of rank 1, with three non-linear degrees of freedom, equal tolerances, and following choice of the ‘best’ 100 models (Yee, 2015). Model implementation was in R x64 v3.6.3 (R Development Core Team, 2019) using library VGAM v1.1–4 (Yee, 2015).

3 | RESULTS

In total, 32,563 fish were captured during this study, consisting of 16 native and five alien species (Table 1). Notably, *N. obscura* was absent in all samples collected. Samples were numerically dominated by *P. fluviatilis*, which occurred at all but one site. Similarly, *P. grandiceps*, *G. maculatus*, *N. erebi*, *C. fulvus*, and *N. australis* were observed in high numbers. The least abundant species (recorded in fewer than four samples) were the marine migrant yellow-eye mullet (*Aldrichetta forsteri*) and sandy sprat (*Hyperlophus vittatus*) and the alien *M. anguillicaudatus* (the first detection of this species in the region). Habitat condition at the 32 sites (Appendix A) was within the expected values for wetlands fringing Lake Alexandrina during late spring and early summer (Wedderburn & Hammer, 2003; Wedderburn, 2018).

For all species, a simple single-season model with constant *P* successfully described probabilities of occupancy and detection relative to a simple single-season model with survey-specific *P* ($\Delta AIC < 2$). Predicted occupancy and detection probabilities varied among species (Table 1). Both occupancy and detection were high (i.e. > 0.7) for alien *C. carpio* and *P. fluviatilis*, for the freshwater generalists *C. fulvus*, *Hypseleotris* spp., *N. erebi*, *P. grandiceps*, *P. macrostomus*, and for the two diadromous fishes. *Nannoperca australis* had higher estimated occupancy and detection relative to *C. fluviatilis*, and these estimates for the former species were lower for the YOY relative to the adults.

The probability of occupancy of *N. australis* (hereafter, YOY and adults) along the microhabitat gradient was always distinct from that of the other species (groups), which were associated in all cases with higher pH and macrophyte cover. In contrast, the occupancy of the other freshwater specialist, *C. fluviatilis*, overlapped with that of the other species in almost all cases (Table 2). Specifically, *N. australis*

TABLE 1 Fish species recorded at the terminus of the Murray–Darling Basin in south-eastern Australia in three repeated surveys of 32 sites in November–December 2018. The following is provided for each species: raw abundance *n*, total number of sites where each species was detected, total detections, and probability of occupancy (naïve, estimated (Est.), SE, lower confidence interval (LCI), upper confidence interval (UCI)) and detection

Species	Common name	Code	Fish group	n	Sites	Total	Occupancy				Detection				
							Naïve	Est.	SE	LCI	UCI	Est.	SE	LCI	UCI
<i>Nannoperca obscura</i>	Yarra pygmy perch	NanObs	FS	0	0	0	—	—	—	—	—	—	—	—	—
<i>Nannoperca australis</i>	Southern pygmy perch	NanAus	FS	776	12	52	0.375	0.389	0.090	0.233	0.571	0.669	0.088	0.482	0.815
YOY		NanAusY	FS	687	8	21	0.250	0.327	0.120	0.144	0.585	0.382	0.133	0.170	0.650
adult		NanAusA	FS	89	10	43	0.313	0.320	0.084	0.181	0.501	0.717	0.090	0.516	0.857
<i>Aldrichetta forsteri</i>	Yellow-eye mullet	AldFor	MM	4	2	4	—	—	—	—	—	—	—	—	—
<i>Atherinosoma microstoma</i>	Smallmouth hardyhead	AthMic	ES	165	8	20	0.250	0.378	0.160	0.138	0.697	0.303	0.132	0.113	0.598
<i>Carassius auratus</i>	Goldfish	CarAur	AFG	135	22	68	0.688	0.717	0.087	0.522	0.855	0.653	0.066	0.516	0.770
<i>Craterocephalus fluviatilis</i>	Murray hardyhead	CraFlu	FS	37	6	14	0.188	0.219	0.087	0.094	0.431	0.475	0.148	0.221	0.744
<i>Craterocephalus fulvus</i>	Unspecked hardyhead	CraSite	FG	600	23	115	0.719	0.724	0.080	0.544	0.852	0.806	0.050	0.690	0.886
<i>Cyprinus carpio</i>	Common carp	CypCar	AFG	427	29	144	0.906	0.911	0.052	0.745	0.973	0.823	0.043	0.724	0.892
<i>Galaxias maculatus</i>	Common galaxias	GalMac	DI	3,755	32	230	1.000	1.000	0.000	1.000	0.000	0.948	0.023	0.881	0.978
<i>Gambusia holbrooki</i>	Eastern mosquitofish	GamHol	AFG	185	13	39	0.406	0.443	0.098	0.267	0.634	0.565	0.094	0.379	0.733
<i>Hyperlophus vittatus</i>	Sandy sprat	HypVit	MM	4	1	2	—	—	—	—	—	—	—	—	—
<i>Hypseleotris</i> spp.	Carp gudgeon (complex)	HypSpp	FG	370	31	130	0.969	0.975	0.031	0.757	0.998	0.812	0.042	0.715	0.881
<i>Macquaria ambigua</i>	Golden perch	MacAmb	FG	30	12	26	0.375	0.536	0.166	0.238	0.810	0.331	0.109	0.159	0.564
<i>Misgurnus anguillicaudatus</i>	Oriental weatherloach	MisAng	AFG	5	3	5	0.094	0.110	0.064	0.033	0.309	0.475	0.209	0.149	0.824
<i>Nematalosa erebi</i>	Bony herring	NemEre	FG	1,280	25	150	0.781	0.782	0.073	0.607	0.892	0.920	0.032	0.832	0.964
<i>Perca fluviatilis</i>	European perch	PerFlu	AFG	9,795	31	248	0.969	0.969	0.031	0.809	0.996	0.968	0.018	0.905	0.990
YOY		PerFluY	AFG	8,210	27	168	0.844	0.844	0.064	0.675	0.934	0.913	0.032	0.828	0.958
adult		PerFluA	AFG	1,585	31	234	—	0.969	0.031	0.809	0.996	0.968	0.018	0.905	0.990
<i>Philypnodon grandiceps</i>	Flathead gudgeon	PhiGra	FG	3,330	30	250	0.938	0.938	0.043	0.782	0.984	0.978	0.016	0.915	0.994
<i>Philypnodon macrostomus</i>	Dwarf flathead gudgeon	PhiMac	FG	269	30	124	0.938	0.948	0.044	0.763	0.990	0.781	0.046	0.677	0.858
<i>Pseudaphritis urvillii</i>	Congolli	PseUrv	DI	22	4	12	0.969	0.970	0.031	0.800	0.996	0.880	0.034	0.795	0.933
<i>Pseudogobius olorum</i>	Western blue-spot goby	PseOlo	ES	484	31	179	0.125	0.141	0.069	0.051	0.333	0.518	0.176	0.212	0.811
<i>Retropinna semoni</i>	Australian smelt	RetSem	FG	240	25	86	0.781	0.816	0.079	0.613	0.925	0.651	0.062	0.522	0.761
<i>Tasmanogobius lasti</i>	Lagoon goby	TasLas	ES	79	14	34	0.438	0.486	0.103	0.297	0.679	0.536	0.093	0.357	0.706

Note: Fish groups—adapted from Potter et al. (2015) and Whiterod, Hammer & Vilizzi (2015).

Abbreviations: AFG, (alien) freshwater generalist; DI, diadromous; ES, estuarine; FG, freshwater generalist; FS, freshwater specialist; MM, marine migrant; YOY, young-of-the-year.

TABLE 2 Constrained quadratic ordination (CQO) results for the occupancy of the freshwater specialists southern pygmy perch (*Nannoperca australis*), including young-of-the-year (YOY) and adult separately, and Murray hardyhead (*Craterocephalus fluviatilis*) relative to the four most abundant groups recorded in the study (see Table 1)

			Latent variable					
Component	Optimum	Maximum	EC	pH	Secchi	Temp.	Depth	Cover
Alien (freshwater generalists)			−0.010	0.318	−0.186	0.138	0.026	0.266
N. australis								
YOY	−2.275	0.600						
adult	−2.819	0.924						
C. fluviatilis	0.518	0.125						
Cyprinus carpio	−0.867	0.584						
Gambusia holbrooki	1.534	0.923						
Misgurnus anguillicaudatus	−1.150	0.400						
Perca fluviatilis								
YOY	2.268	0.350						
adult	3.729	1.000						
Diadromous								
N. australis								
YOY	−3.320	0.965	0.023	0.201	−0.177	0.012	0.021	0.167
adult	−4.548	1.000						
C. fluviatilis	1.394	0.231						
Galaxias maculatus	2.375	0.998						
Pseudaphritis urvillii	3.973	1.000						
Estuarine			−0.266	0.945	0.101	−0.457	−0.092	0.350
N. australis								
YOY	−1.453	0.275						
adult	−1.134	0.409						
C. fluviatilis	0.863	0.175						
Atherinosoma microstoma	−0.970	0.204						
Pseudogobius olorum	−0.297	0.112						
Tasmanogobius lasti	0.613	0.386						
Freshwater generalists			0.026	0.394	−0.269	0.121	−0.153	0.529
N. australis								
YOY	−1.717	0.340						
adult	−1.840	0.582						
C. fluviatilis	0.688	0.144						
Craterocephalus fulvus	2.071	0.940						
Hypseleotris spp.	−0.040	0.831						
Macquaria ambigua	1.426	0.365						
Nematalosa erebi	4.217	1.000						
Philypnodon macrostomus	0.151	0.786						
Retropinna semoni	0.777	0.656						

Note: For each CQO model, the optimum and maximum scores for each species are provided together with scores for microhabitat variables (descriptors) condensed into the latent variable. Negative scores correspond to a higher value of the descriptor on the left-hand side of the x-axis of the CQO plot; positive scores to a higher value of the descriptor on the right-hand side of the x-axis (see Figure 2).

Abbreviation: EC, electrical conductivity.

showed a preference for higher Secchi depth relative to the alien (freshwater generalists) group, among which *P. fluviatilis* (YOY and adult) and, to a lesser extent, *M. anguillicaudatus* and *C. carpio* were

mainly associated with higher pH and macrophyte cover (Figure 2a). This separation was even more distinct relative to the diadromous species, with similar corresponding microhabitat associations as

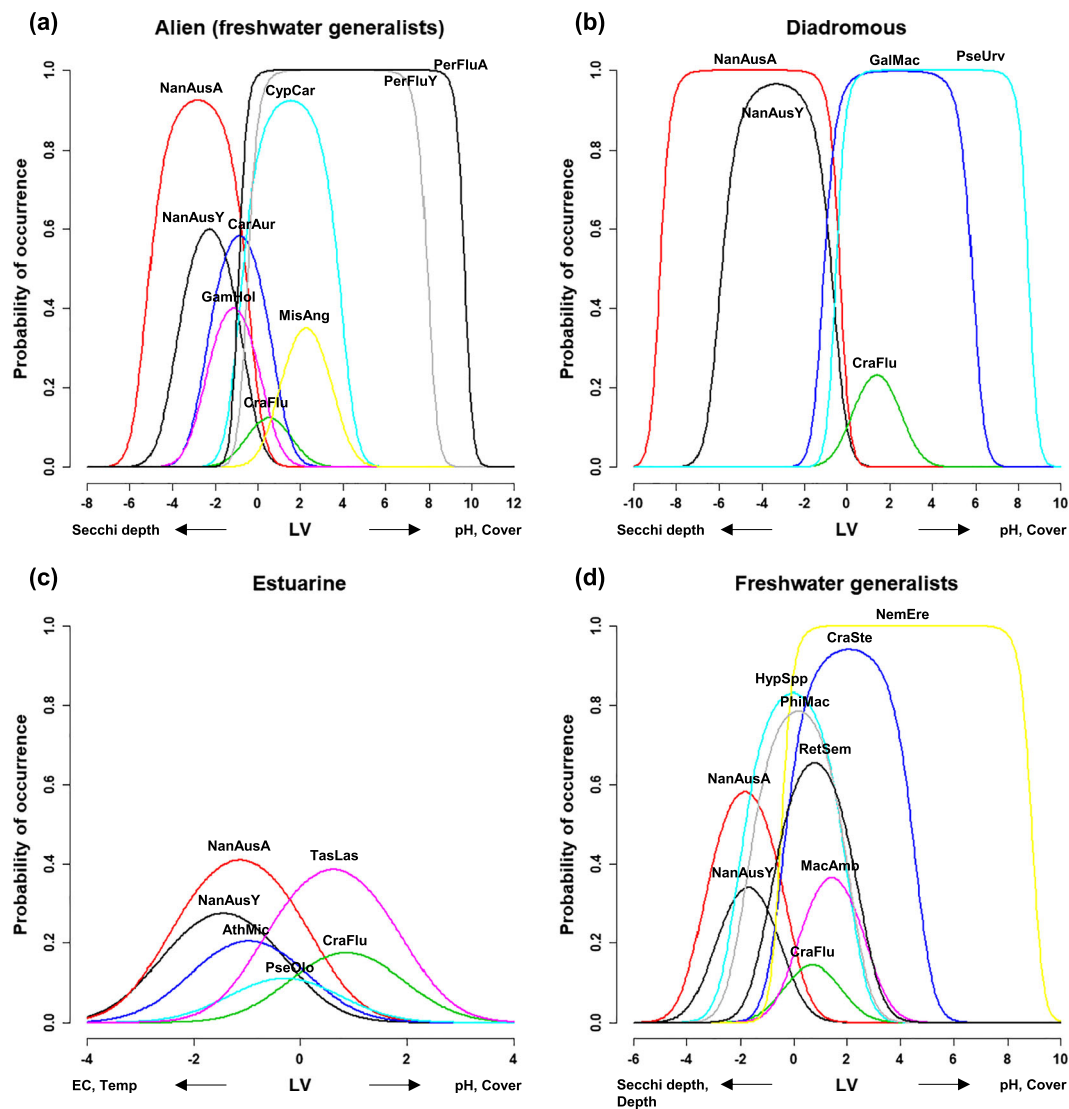


FIGURE 2 Constrained quadratic ordination plots for the freshwater specialists, young-of-the-year (YOY) and adult southern pygmy perch (*Nannoperca australis*) and Murray hardyhead (*Craterocephalus fluviatilis*), relative to (a) alien (freshwater generalists), (b) diadromous, (c) estuarine species, and (d) freshwater generalists (see Table 1, also for abbreviations). The level of relationships with the main microhabitat features is provided on the negative and positive boundaries of the latent variable (LV) x-axis describing microhabitat (see also Table 2). EC, electrical conductivity

already noted herein (Figure 2b). *Nannoperca australis* occurred in association with higher EC and temperature relative to the estuarine species, among which only *A. microstoma* showed an overlap (Figure 2c). Together with Secchi depth, depth was a second microhabitat descriptor for the species' occupancy relative to the (native) freshwater generalists, among which *N. erebi* occupied the larger range (Figure 2d).

4 | DISCUSSION

Accurately documenting the loss of populations and species to inform conservation is critical, but this becomes problematic as non-detection rarely confirms absence. The globally Endangered

N. obscura was considered extirpated from the MDB at the height of drought in 2008 (Hammer et al., 2013), and wild fish have not been detected since (Wedderburn, 2018). In this study, occupancy modelling using repeated surveys was used to infer a high likelihood of extirpation of *N. obscura* from the 1,061,000 km² MDB. This finding confirms the first extirpation of a freshwater fish species from one of the world's largest river systems. Despite the persistence of *N. obscura* in other smaller catchments in south-eastern Australia, the loss of the MDB population has important conservation implications (cf. escalation from Vulnerable to Endangered; Whiterod et al., 2019), which should be considered for management of threatened fishes in other major river systems.

Nannoperca obscura has a naturally restricted range across the lower reach of the MDB, where it represents an evolutionary

lineage distinct from other catchments. The present study targeted sites within its entire range in the MDB (Hammer, Wedderburn & van Weenan, 2009). The initial loss of the species from this restricted range in 2008 was foreseeable because it corresponded to a complete loss of its obligate habitat during critical water shortages associated with prolonged drought (Wedderburn, Hammer & Bice, 2012). Extirpated fish have the capacity for population recovery through migration from nearby populations or with deliberate translocation (Cochran-Biederman et al., 2015). The genetically distinct MDB population of *N. obscura* only occurred in the study region, so natural recolonization is unfeasible. Past reintroductions of *N. obscura* derived from the original stock achieved short-term persistence (i.e. months; Bice, Whiterod & Zampatti, 2014) despite the return of suitable habitat, but factors that influenced reintroduction success are at present unresolved (Wedderburn et al., 2020). Failure to recolonize may be a consequence of insufficient fish being released (i.e. 6,750 fish at six sites), low adaptive ability (cf. low genetic diversity; Beheregaray et al., 2021; Brauer et al., 2013), or competition and predation from alien species that have occupied the region for decades (e.g. *P. fluviatilis*; Wedderburn & Barnes, 2016).

The findings for *N. australis*, which also was extirpated from the study region during the prolonged drought, are relevant to its congener *N. obscura* given their ecological similarities (Woodward & Malone, 2002). Occupancy of *N. australis* was moderate during the current study, despite its low relative abundance, which suggests success of the reintroductions conducted in 2011–2012. Indeed, genomic research has confirmed that the current population is derived from reintroduced fish (Beheregaray et al., 2021). In addition, natural recolonization is apparent in wetlands in the lower reaches of a key tributary, probably as a result of fish immigrating from upstream where populations survived during drought (Whiterod, Hammer & Vilizzi, 2015). As the species are closely related and cohabited in comparable abundances before the consequences of drought (Wedderburn & Hammer, 2003), the detections and recovery observed for *N. australis* provide further evidence that population recovery of *N. obscura* has failed.

The recovery of the riverine environment in the MDB following drought, the population recovery of *N. australis*, and the micro-habitat assessment in the present study suggest that environmental conditions now are suitable for *N. obscura* throughout its former range. *Nannoperca australis* was detected at 12 of 32 sites in the present study, and modelling accounting for imperfect detection predicted that the true value for occupancy may be higher. The most pronounced difference for *N. australis* (YOY and adult fish) relative to other fishes was an apparent preference for sites with higher Secchi depth. This was the case at deeper sites, where water transparency generally was over half that of water depth. These characteristics apparently enable the establishment of moderate abundances of complex submerged aquatic plants required by *Nannoperca* species for feeding, spawning, and cover from predators (Llewellyn, 1974; Woodward & Malone, 2002; Wedderburn et al., 2020). As *N. obscura* was not detected in this study, despite the availability of suitable

habitat, the restoration of *N. obscura* in the MDB must now rely on reintroductions.

A reintroduction programme must be underpinned by a sustained commitment to species recovery. Consistent with overarching guidelines (IUCN/SSC, 2013), the programme must link to a robust and flexible strategy with clear goals and objectives, appropriate production and releases, and informed genetic management. For example, genetic rescue is increasingly used in conservation and is warranted to overcome low genetic diversity (e.g. inbreeding depression) and adaptive potential in backup populations of *N. obscura* (cf. Fitzpatrick et al., 2020; Hoffmann, Miller & Weeks, 2021). It will require assisted colonization across unique lineages, so careful deliberation will be necessary. Furthermore, a fundamental aspect of the reintroduction programme is research to resolve uncertainty regarding factors that influence success (Wedderburn et al., 2020). The survey methodology established in the present study, combined with other techniques, such as environmental DNA that has been applied to the region previously (Shaw et al., 2016), can form the basis for assessing the reintroduction objectives. The demonstrated successful reintroduction of similarly imperilled small-bodied fish species in the region, such as *N. australis* (Beheregaray et al., 2021) and *C. fluviatilis* (Thiele et al., 2020), and elsewhere (e.g. Oregon chub *Oregonichthys crameri*; DeHaan et al., 2016), should serve as motivation for the restoration of *N. obscura* in the MDB.

The MDB is a large floodplain system of high conservation risk owing to the consequences of regulation and over-abstraction of water during the last century, which have exacerbated the impacts of droughts (van Dijk et al., 2013). For example, there have been extensive reductions in native wildlife (Walker, 1985), including regional losses of some species, yet there is no documented freshwater fish extirpation from the MDB. The documented extirpation of *N. obscura* in this study foretells the freshwater biodiversity crisis in the MDB and worldwide (Harrison et al., 2018; Lintermans et al., 2020). Several other freshwater fish are approaching extinction in the MDB, including flathead galaxias (*Galaxias rostratus*), *C. fluviatilis*, and stocky galaxias (*Galaxias tantangara*) — all are Critically Endangered on the IUCN Red List of Threatened Species, and all suitable habitat for other fish species may be lost by the end of this century (Galego de Oliveira et al., 2019). Similarly, freshwater crayfish (Furse & Coughran, 2011), freshwater mammals (e.g. platypus: Bino, Kingsford & Wintle, 2019), freshwater turtles (Van Dyke et al., 2019), and waterbirds (Kingsford, Bino & Porter, 2017) are at heightened risk of extirpation from the MDB. In addition to taxon-specific recovery recommendations (Koehn et al., 2020), basin-wide water reform is at present being implemented in an effort to divert the system away from looming ecological collapse (e.g. the Basin Plan; Murray–Darling Basin Authority, 2012). In addition, a National Recovery Plan for *N. obscura* was produced a decade ago but has generated little recovery action for the MDB population (Saddler & Hammer, 2010). The loss of *N. obscura* signifies a critical moment when management intervention is urgently required to maintain

biodiversity in the MDB, which should be noted by authorities managing other regulated rivers (Tickner et al., 2020).

Wildlife monitoring programmes increasingly consider the probability of detection for most biotic groups, yet examples for fish are notably sparse worldwide (Mackenzie et al., 2018). This is surprising given the various complexities of aquatic habitats that can affect detection in fish surveys (Mollenhauer, Mouser & Brewer, 2018). This has implications for managing rare fish, including inaccuracies in assessing patterns in the distribution and abundance of populations (Gwinn et al., 2019), which can lead to flawed management decisions; for example, determining water extraction limits (Haynes et al., 2013) and conservation assessments (Pregler et al., 2015). Moreover, fish surveys that account for imperfect detection provide statistically robust baselines for tracking population changes over time (Guillera-Aroita, Ridout & Morgan, 2010; Mackenzie et al., 2018). For example, monitoring that follows reintroductions of *N. obscura* to the wild can use the present study as a baseline to obtain a high degree of certainty regarding recovery, or otherwise, of the population as a direct result of management interventions, thereby demonstrating an approach to fish monitoring that can be applied to other river systems.

In conclusion, this study provides strong evidence for the extirpation of *N. obscura* from the MDB using an assessment that accounts for imperfect detection. This study also highlights an approach that can provide a high level of confidence for planning in conservation management of other species. There is now a pressing need to re-establish self-sustaining populations of *N. obscura* within its contemporary range. This will require careful management of the remaining ex-situ populations needed to facilitate future reintroduction. If reintroductions are implemented and adequate water for the environment is available, the methodology and data used here will be beneficial in monitoring the population recovery of *N. obscura* in the MDB with high statistical power through repeated surveys. It is imperative to acknowledge that the first freshwater fish extirpation warrants a commitment to conserve freshwater biodiversity across the MDB and provides a warning that should be heeded worldwide.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest that could be perceived as prejudicing the impartiality of the research reported.

DATA AVAILABILITY STATEMENT

Author elects to not share data.

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