Forgotten fishes: what is the future for small threatened freshwater fish? Population risk assessment for southern pygmy perch, *Nannoperca australis*

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ABSTRACT:

1. Fish species that have no commercial or recreational value are often overlooked in conservation management, despite serious threats to their long-term future. We term this the 'small threatened freshwater fishes' paradigm.
2. Population viability analysis (PVA) is a useful technique to assess threatened species and conservation management options. While the development and use of population models and population viability analysis is common in conservation, and often used for larger fishes, this has not been so for small threatened freshwater species.
3. This study uses the PVA process to develop a stochastic population model for *Nannoperca australis* (southern pygmy perch) in temperate south-eastern Australia.
4. The model was most sensitive to early life-history survival rates, for which there were no estimates from field data, compared with other model uncertainty. This study also found that the oldest age class had the highest reproductive value, providing unique support to the value of big, old, fat and fecund fish (BOFFFs) in sustaining natural populations.
5. Modelling indicated that a population in stable habitat supporting about 2000 female adults would likely to be viable, able to withstand some disturbance and possibly be used as a source population for reintroductions. In reality, however, there are few populations in the wild of sufficient size to withstand such take for translocations and hence the production of fish through hatchery means may be required.
6. This type of approach should prove useful for the conservation management of many similar species globally.

Keywords: fish, wetland, river, conservation evaluation, modelling, endangered species

INTRODUCTION

Although freshwater fishes worldwide are under serious threat, it is often the larger, recreationally or commercially important, more charismatic species that receive the most attention (Hogan, Moyle, May, Vander Zanden, & Baird, 2004; Xu, Schneider, &

Rideout, 2013). Smaller, cryptic, non-commercial species, tend to receive less attention despite being at equal or greater extinction risk (Angermeier, 1994; Olden, Hogan, & Vander Zanden, 2007). Threats to such species are likely to be higher in arid and semi-arid regions (Collares-Pereira & Cowx, 2004), as many smaller species reside in non-permanent habitats such as wetlands and ephemeral stream systems. These habitats are highly susceptible to the impacts of river regulation and altered hydrology (such as disconnection from the main river channel), the destruction of habitats associated with land clearing, grazing, salinization, and invasive species (Kingsford et al., 2011). With small fishes often restricted to spatially isolated habitats (refuge pools or wetlands) the physical and biological processes that determine fish communities (Schlosser, 1987) can be magnified and readily result in local extirpations. In particular, habitat loss and fragmentation (Arthington, Dulvy, Gladstone, & Winfield, 2016; Hanski, 2013) and predation (MacRae & Jackson, 2001) are recognized as major causes of extinction for small species and these impacts may be increased under extreme conditions such as drought (Magoulick & Kobza, 2003; Matthews & Marsh-Matthews, 2003). A review of conservation listed threatened fishes globally indicated that freshwater species tend to be smaller bodied and were affected by a range of non-fishery threats (Olden et al., 2007). A variety of fishes across a range of continents can readily be identified to fit this 'threatened small fish paradigm' (Bergey, Matthews, & Fry, 2008; Saddlier, Koehn, & Hammer, 2013; Varela-Romero, Ruiz-Compos, Yepiz-Velazquez, & Alaniz-Garcia, 2002).

Threatened species management requires an understanding of the ecology of the species of concern and the threatening processes affecting them. Some species face multiple threats: understanding the complexities of the impacts these have on a species is not straightforward (McDonald-Madden et al., 2010) but necessary to ensure management interventions are successful (Reece et al., 2013). Assessing the viability of remnant populations is important for establishing and prioritizing key management actions (Beissinger & McCullough, 2002; Possingham, Lindenmayer, & Norton, 1993). Population viability analysis (PVA: Beissinger & McCullough, 2002; Stephens, 2016) is a process for assessing the viability of a population, including the projections from a stochastic model that summarizes demographic and environmental variation and other relevant ecological and management information (e.g. removals, density-dependence, trends in habitat change) about the population in question. The construction and use of such population models is also useful for ranking management options for rare or endangered species, predicting results of recovery actions (Koehn & Todd, 2012; Morrison, Wardle, & Castley, 2016; Todd & Lintermans, 2015), identifying emerging issues, testing hypotheses and evaluating management actions before implementation (McCusker, Curtis, Lovejoy, & Mandrak, 2017; Todd & Lintermans, 2015), and guiding future research (Morrison et al., 2016).

While complex models have been developed and used in commercial fisheries management (Sainsbury, Punt, & Smith, 2000) and for larger, recreationally important fishes (Koehn & Todd, 2012), this approach has been used rarely for small threatened freshwater fish species (McCusker et al., 2017). The model development process often uses inclusive expert workshops to allow the most up to date knowledge to be included and discussed within the management framework for the species (Koehn & Todd, 2012). This ensures that the population model can be appropriately structured and supported by the available data.

Southern Australia's pygmy perches (Percichthyidae), are one such group of small (< 85mm total length), threatened, freshwater fishes that have suffered declines owing to habitat loss or degradation and altered hydrology. The Australian pygmy perches comprise a group of seven species, of which five species (Yarra pygmy perch *Nannoperca obscura*, variegated pygmy perch *Nannoperca variegata*, Oxleyan pygmy perch *Nannoperca oxleyana*, Balston's pygmy perch *Nannatherina balstoni* and the little pygmy perch *Nannoperca pygmaea*) are considered threatened at a national level (Morgan, Beatty, & Adams, 2013; Saddlier et al., 2014) with *N. obscura*, *N. variegata* and *N. oxleyana* on the International Red List of Threatened Animals (IUCN, 2016). *Nannoperca australis* (southern pygmy perch) is one of the more widespread species, but has suffered severe declines in range and abundance, and is now rare within Australia's largest river system, the Murray-Darling Basin (Lintermans, 2007), where most native fish species are in need of recovery actions (Koehn & Lintermans, 2012). *Nannoperca australis* now generally occurs within small, often isolated populations in fragmented, patchy and variable habitats. As a consequence of a major drought (1998-2010 – Murphy & Timbal, 2008) populations of *N. australis* in the region of southern New South Wales were placed under severe stress and many appear to have been lost (Pearce, 2014; Sharpe & Wilson, 2012). Consequently, there is an urgent need for conservation management actions and *N. australis* provides a valuable case study for other similar small, threatened, freshwater fishes.

The objectives of this study were to develop a stochastic population model for *N. australis* and to determine what constitutes a viable population for the species. The model was then to be used to provide guidance for the establishment of new populations, assess the impacts on donor populations and to consider other conservation management actions. In light of this application to *N. australis*, the outcomes were extended to the management of other pygmy perches and small threatened freshwater fish species generally.

METHODS

Specialist workshop on *Nannoperca australis*

Management decisions about threatened species are frequently made irrespective of the understanding and knowledge about the species of concern (Koehn & Todd, 2012; Todd & Lintermans, 2015). Models can be useful in decision making processes through combining the latest available information, knowledge and understanding (Akçakaya, Burgman, & Ginzburg, 1997; Possingham et al., 1993; Todd, Nicol, & Koehn, 2004). To establish up-to-date and relevant information for *N. australis*, a workshop was held with relevant fish ecologists and managers that allowed access to individual expertise as well as published and unpublished data and information, and to provide trust and 'ownership' in the model development.

The workshop provided a clear consensus to undertake a PVA, using life history to structure an age-based model, to make estimates of viable population size; test different population sizes for fish stocking or translocations to establish new populations; assess the impact of removal of fish from donor populations; and explore risks and catastrophic event predictions. While there were no data available from the populations of interest in southern NSW, age and fecundity data were available from *N. australis* sampled from Tasmania (Humphries, 1995) and Victoria (Morrongiello, Bond, Crook, & Wong, 2012). Only limited quantitative information on early life history (egg, larval and young of the year survival; Morrongiello et al., 2012) was available and density-dependence was thought to affect mainly adults through limitation of available habitat where juveniles would not experience similar impacts.

The major threats to *N. australis* were identified as flow modification and reduction (through flow regulation and climate change); habitat loss (wetland drainage); sedimentation; reduced connectivity; blackwater (water containing high levels of dissolved organic carbon); fire; nutrient run-off (blue-green algae); depleted oxygen; land use changes; chemicals; and impacts from introduced species. Predation occurs from introduced *Perca fluviatilis* (redfin) (Humphries, 1995; Wedderburn & Barnes, 2016), possibly trout in upland systems and eastern gambusia (*Gambusia holbrooki*) (Humphries 1995) which may nip fins and prey on eggs and larvae (Macdonald et al., 2013; Woodward & Malone, 2002). *Cyprinus carpio* is a pest alien fish species that occur in high densities, including in slow-flowing *N. australis* habitats (Koehn, Brumley, & Gehrke, 2000) and *N. australis* do not co-exist with *C. carpio* where they are present in high abundance (Pearce, 2014).

Model development for *Nannoperca australis*

Life-history analysis

Nannoperca australis has an estimated life span of up to 5 years, maturing by the end of year 1. Females produce from a few hundred to several thousand small, transparent, non-adhesive eggs (Humphries, 1995; Llewellyn, 1974), depending on age, body size, and environmental conditions (Humphries, 1995; Morrongiello et al., 2012; Woodward & Malone, 2002). Eggs are scattered over vegetation or rocks and, at 15-18 °C, take 2 – 4 days to hatch and larvae start foraging at ~5 days (Llewellyn 1974). *Nannoperca australis* at 30 mm TL are ~70 days old (Tonkin, King, & Mahoney, 2008), 45 mm at ~one year old, 52 mm at ~1.5 years old, and approach maximum size of ~85 mm at 4 years (Humphries, 1995).

Four discrete life stages can be described providing for an age-based model to be constructed where fish in the final age class do not survive beyond 4 years: eggs (2 – 4 days); larvae (3 – 5 days); juveniles (11 months); and adults (3 – 4 years). While it was plausible that some individuals may live to ≥5 years, age data available had no individuals aged 5. Males were thought not to be limiting, consequently a four age-class female-only model sufficiently encapsulates the dynamics of *N. australis* with the following age-structured projection matrix:

$$\begin{pmatrix} s_0 \times f_1 & s_0 \times f_2 & s_0 \times f_3 & s_0 \times f_4 \\ s_1 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 \\ 0 & 0 & s_3 & 0 \end{pmatrix}$$

Data assessment

The projection matrix requires estimates of age-based survival rates (s_i: i = 1 to 3), age-based fecundity (f) and survival to one year olds (s_0: a combination of egg survival, larval survival and young of the year survival).

Age data were used to generate estimates of age-specific survival, where the proportional change in age frequencies from one year to the next represents the proportion that survives. Female *N. australis* (n=148) were aged from the Macquarie River, Tasmania (Humphries, 1995) which was used to estimate age-specific survival rates.

Three studies provided fecundity data, and indicated high variability: Llewellyn (1974) for New South Wales (N = 9, mean 2261.22 ± 1085.47 SD); Humphries (1995) for Tasmania (N = 20, mean 345.30 ± 167.34 SD); and Morrongiello et al. (2012) for Victoria (N= 185, mean 460.23 ± 373.79 SD). Llewellyn (1974) suggested unusually high estimates of fecundity in comparison with the other two data sets and consequently these data were not used here. Humphries (1995) and Morrongiello et al. (2012) had counts that ranged from 65 to 2651 (mean 451.19 ± 359.82 SD) from unknown aged fish of 33 mm to 84 mm. An age-length relationship was combined with a length-fecundity relationship to establish an age-fecundity relationship for use in the model.

Density dependence

The model accounted for density-dependence by assuming a proportional decrease of all age classes by the amount the total female adult population was above the carrying capacity (Todd & Lintermans, 2015). This mechanism does not attribute any advantage to particular age (or size) classes, nor constrain the number of juveniles in the model. As a result it may not capture density-dependence mechanisms such as food limitation for larvae but applying this proportional construct to all adult fish produces sufficient negative feedback to constrain population growth and ensures recruitment to one year olds is constrained.

Stochasticity

Stochasticity in the model was incorporated using Monte Carlo simulation where random numbers were generated from distributions describing variation in population parameters representing sources of observed and random variation (Burgman, Ferson, &

Akçakaya, 1993; Todd & Lintermans, 2015). Demographic stochasticity was modelled by allowing variation in the survival and reproduction of individuals (Akçakaya, 1991) and was incorporated by using a binomial distribution to model the number of individuals surviving between consecutive time steps, and a Poisson distribution to model recruitment (Todd & Lintermans, 2015). Environmental stochasticity was modelled by randomly selecting survival and fecundity rates from specified distributions for each time step (Todd & Lintermans, 2015; Todd & Ng, 2001).

Stochastic population model

A female only *N. australis* population model can be represented by the following equations:

$$
\begin{aligned}
&N_i(t+1) = Bin\left(N_{i-1}(t), dens(t)\times s_{i-1}(t)\right), \qquad i = 2,\ldots,4\\
&N_1(t+1) = Poisson\left(dens(t)\times s_0(t)\times 0.5\times EggNum(t)\right),\\
&EggNum(t) = \sum_1^4\left(F_i(t)\times N_i(t)\right) \qquad \ldots(1)\\
&dens(t) = \begin{cases} APS\Big/\sum_1^4 N_i(t), & \text{when } \sum_1^4 N_i(t) > APS\\ 1, & \text{when } \sum_1^4 N_i(t) \le APS\end{cases}\\
&F_i(t) = \exp\left(f_c\times\left(\exp\left(l_c\times i + y_1(t)\right)\right) + y_2(t)\right)
\end{aligned}
$$

where t is an annual time interval; $N_i(t)$ is the number of fish in the i^{th} age class; $s_i(t)$ is a random variate describing environmental variation in survival rates of fish in the i^{th} age class drawn from normal distributions transformed to the unit interval (Todd & Ng, 2001) with specified means and standard deviations; $s_0(t)$, is a random variate describing environmental variation in survival from hatching to 1-year old (all survival rates are perfectly correlated); $dens(t)$ is the density-dependence factor for adults; $EggNum(t)$ the total number of eggs produced at time t; $F_i(t)$ is the fecundity rate of the i^{th} age class (all fecundity rates are perfectly correlated but not correlated with survival); $dens(t)$ is the density dependence factor at time t; APS is the average population size of adults for the system over the long term; f_c is a parameter estimated from length-fecundity data; l_c is the estimated parameter from age-length data; $y_1(t)$, and $y_2(t)$, are random variates describing environmental variation in fecundity; $Bin(n,s)$ is a random variate representing demographic variation in transition from one age class to the next with a binomial distribution $Bin(n,s) = X \sim \mathrm{Binom}(n,s)$; and $Poisson(m)$ is a random variate representing demographic variation in recruitment with a Poisson distribution $Poisson(m) = Y \sim \mathrm{Poi}(m)$.

Mathematical and sensitivity analysis

The growth rate for the projection matrix can be obtained mathematically by solving the following characteristic equation:

$$\lambda^4 - s_0 f_1 \lambda^3 - s_0 s_1 f_2 \lambda^2 - s_0 s_1 s_2 f_3 \lambda - s_0 s_1 s_2 s_3 f_4 = 0$$

Solving for λ establishes the deterministic growth rate of a population if all parameters are known. There are estimates for all parameters except s_0, the proportion of eggs that hatch and survive to become 1-year old female fish. Rearranging the characteristic equation to solve for s_0 when $\lambda = 1$ gives the proportion of eggs that survive to become 1-year old female fish necessary for a stable population.

It is important to examine the sensitivity of the model to parameter estimation (Burgman et al., 1993) and four types of perturbation analysis were considered: sensitivity analysis, measuring the absolute change in growth rate given a small change in a vital rate; elasticity analysis, measuring the proportional change in growth rate given a small change in a vital rate identifying the impact of measurement error; reproductive values, measuring the contribution of an age class to future generations and summarizing reproduction, survival and timing (Caswell, 2001); and stochastic analysis, measuring the proportional change in the growth rate given a change in the underlying distribution for each vital rate (Todd et al., 2004).

Expressions of risk – the expected minimum population size

In order to examine the consequences of potential management actions, each scenario was run for 1000 iterations over 20 time steps in the simulation software package *Essential* 2.15 (Todd & Lovelace, 2014). This was considered sufficient to sample from the parameter distributions so that a full exploration of distributional variation could be undertaken and the likelihood of extreme events assessed (Burgman et al., 1993; Todd & Lintermans, 2015). The minimum population size from each iteration or trajectory was recorded and a cumulative frequency distribution of minimum population sizes generated. This distribution represents both the chances of extinction (probability of falling to zero) and the chances of falling below some non-zero population threshold (Burgman et al., 1993: quasi-extinction risk). A method for quantifying changes in risks is to calculate the expected minimum population size (EMPS) for each model run or scenario and compare these values (McCarthy & Thompson, 2001; Todd & Lintermans, 2015). Given that one of the objectives of the study was to examine a number of management scenarios, this study reports on the following statistics for female adults: EMPS; the absolute difference in EMPS; and the percentage change in EMPS; risk of extinction; and the probability of the minimum population size (MPS) less than or equal to a specified threshold.

Scenarios

Parameter uncertainty

Parameter uncertainty, especially in the mean and variation of adult and juvenile survival rates, influences what may be interpreted as a viable population. To be certain that changes to parameter values were reflected in the output, density dependence was effectively turned off by setting the average population size (APS) to 100,000 female adults and exploring changes in parameters with an initial population size of 2000 female adults over 20 time steps (years). Fecundity was estimated from data and changing the mean and standard deviation by ±10% was used to explore sensitivity to changes in fecundity. Similarly, the mean survival rates were estimated from data and changing the mean for each age by ±10% was used to explore sensitivity to changes in survival. Variation in survival rates remain unknown, however, and so three levels of variation were used to explore uncertainty in variation in survival: 10% coefficient of variation (CV); 20% CV; and 30% CV, where the model with 20% CV in survival rates was considered the baseline model and comparisons made with it.

Viability, catastrophes, reintroductions and impacts on donor populations

To explore viability within the model framework, population growth was restricted using density dependence. The density dependence mechanism constrains the female adult population by decreasing survival proportional to APS: female adult number, if the female adult population is greater than the average population size. Provided habitat is stable (that is the average population size does not change through time), it is possible to explore the consequences of a variety of impacts on the modelled population's viability. Three alternate population constructs were used to develop an understanding of the effect that population size and density dependence have on population viability. All models were run over 20 time steps with the average initial population size for: construct 1) 500 female adults and APS = 500; construct 2) 2000 female adults and APS = 2000; and construct 3) 8000 females and APS = 8000. The consequences of catastrophes, such as recruitment failure and sudden population declines, percentage of females breeding, and the removal of adults for translocation were explored within the three constructs. Assessing reintroduction strategies were also explored by setting initial population size to zero and fish being introduced at the first time step. Density dependence plays an important role in assessing reintroduction success because habitat quality influences the ability of a reintroduced population to establish and expand (Todd & Lintermans, 2015). To examine the success of a reintroduction strategy, and using the same range of expected densities above, the minimum population size (of female adults) from each trajectory was estimated after intervals of 1 year (standard minimum population size distribution), 2 years, 5 years and 10 years after the first year of introduction. This results in a distribution of minimum population sizes for the periods 1 to 20 years, 2 to 20 years, 5 to 20 years and 10 to 20 years. The construction of the models and modelling of all scenarios was undertaken using the software package *Essential* (Todd & Lovelace, 2014).

RESULTS

Vital rates

The ratio between numbers of fish in consecutive age classes was taken as the average or mean survival rate for the *N. australis* population model: $s_1 = 0.5270$; $s_2 = 0.4872$; $s_3 = 0.0526$. It was found after examining the fecundity data from Humphries (1995) and Morrongiello et al. (2012) (Table S1), that a log-linear relationship best described the data ($R^2 = 0.64$; Figure 1a): $Fecundity = \exp(0.05068 \times Length + 3.2043)$. Similarly a log-linear relationship was used to describe the relationship between age and length ($R^2 = 0.50$; Figure 1b): $Length = \exp(0.1933 \times Age + 3.4597)$. As no ages were recorded with the fecundity data, the age-length relationship was combined with the length-fecundity relationship to establish an age-fecundity relationship:

$$F_{Age} = \exp(0.05068 \times \exp(0.1933 \times Age + 3.4597) + 3.2043) \qquad \text{...(2)}$$

It is desirable to use variation in the data to inform the model parameters describing environmental variability of fecundity. Length varies within age classes (Figure 1b) and varying one coefficient of the fitted curve, $L_{Age} = \exp(0.1933 \times Age + y_1)$: $y_1 \sim Y_1 = N(3.4597, sd_1)$, facilitated the exploration of variability in growth. Selecting $sd_1 = 0.09$ provides a reasonable description of variation in growth given age. Variation in fecundity was similarly explored, $F_{Length} = \exp(0.05068 \times Length + y_2)$: $y_2 = Y_2 \sim N(3.2043, sd_2)$. Selecting $sd_2 = 0.3$ returned estimates of fecundity with variance similar to that observed. Using the specified distributions above in equation (2) provides a variety of fecundity estimates for a given age (see Figure 1c), where fecundity parameters in equation (1) are $f_c = 0.05068$, $l_c = 0.1933$ and $y_1(t) \sim Y_1 = N(3.4597, 0.9)$ and $y_2(t) = Y_2 \sim N(3.2043, 0.3)$. In the absence of any suitable information to the contrary, survival rates were perfectly correlated with each other and independent of fecundity rates, which were also perfectly correlated with each other.

Sensitivity

Solving the characteristic equation for s_0 when $\lambda = 1$ gives the proportion of eggs that survive to become 1-year old female fish necessary for a stable population, that is s_0 = 0.0046. If $s_0 > 0.0046$ the population increases and if $s_0 < 0.0046$ the population declines (Table 1). The potential growth rate of an *N. australis* population when conditions are good is unknown, however it is expected to be > 1. Choosing s_0 = 0.0055 for the subsequent sensitivity analysis and scenario testing, generates a growth rate of 1.10 where in the absence of density dependence the population would double every 8 years.

Elasticity analysis indicated that the growth rate was most sensitive to proportional change in s_1, and the influence of vital rates declined with age (Figure 2), whereas the influence of fecundity declines slowly until age 4 (when reproductive values are maximum) highlighting the importance of the contribution of 4-year olds to future growth. Measuring the change in the growth rate given ±10% change in vital rates demonstrates that the model is most sensitive to the estimation of s_0 (±10% change in the value of s_0 produces approximately ±5% response in the growth rate; Table 2). The growth rate is more sensitive to small changes in survival than fecundity.

Parameter uncertainty

Parameter uncertainty was explored with density dependence effectively removed from the model. The baseline model used survival rates specified in Table 3 with a 20% CV for fecundity as specified in equation 2 with variation $N(3.4597, 0.09)$ and $N(3.2043, 0.3)$. The model was most sensitive to changes in s_0, with the greatest sensitivity resulting from ±10% changes to the mean, much greater than when a ±50% change in the variation was applied (Table 4). The model was much less sensitive to changes in fecundity, although again changes in the mean rates for the youngest age class produced the largest changes. The stochastic sensitivity produced greater overall changes in the model than the equivalent deterministic model (compare Tables 2 and 4: for example, +10% change in all mean parameters produces 15.92% increase in the deterministic analysis and a 39.52% increase in the stochastic analysis). This stochastic sensitivity points to the importance of accounting for it in any management scenario analysis. Further, while the model is sensitive to stochastic processes it is not overly sensitive to changes in variation.

Reintroduction strategies

The more fish released, the more likely the success of the reintroduction (Table 5). Results were similar for an average population size of 2000 and 8000, and generally better than an average population size of 500, particularly if the total release was 500 female adults or higher (Table 5). Early in the release phase (years 1 to 5) the probability of the population being small is high for small releases, however, this decreases with time, where the probability of the minimum population size being ≤ 50 female adults in the period 10 – 20 years was 0.1 for a total release of 250 female adults. This is relatively high in comparison with 0.01 for a total release of 500 female adults and 0.001 for a total release of 1000 female adults. These results are reflected in the risk curves for *N. australis* following a reintroduction or translocation (Figure 3).

Evaluation of scenarios

Three baseline cases were considered when comparing scenarios where the average population size was set at the initial population size: an initial population size of 500 female adults; an initial population size of 2000 female adults; and an initial population size of 8000 female adults (500 – EMPS = 263.79; 2000 – EMPS = 1076.03; 8000 – EMPS = 4317.51: Table 6, scenario 1). A 10% chance of recruitment failure in any given year produces a >50% decline in the EMPS compared with the three baseline cases, with non-zero probabilities of extinction and higher probabilities of being small (Table 6, scenario 2). A 20% chance of recruitment failure produces an approximately 80% decline in the EMPS compared with the baseline cases (Table 6, scenario 3). A

10% probability in any given year of an 80% decline in the female adult population produces an approximately 50% decline in the EMPS compared with the baseline cases (Table 6, scenario 4), although scenario 4 has a higher probability of being small in comparison with scenario 2 which has a marginally greater decline in EMPS (compare Pr(MPS = 0) and Pr(MPS ≤ 25)). Removals of 100 female adults for 5 years in the first 5 years of the scenario produces greater impacts when the initial population size and the average population size was small, with marginal differences between 2000 and 8000 compared with 500 (Table 6, scenario 5). Combining recruitment failure and catastrophes further reduces the EMPS (Table 6, scenario 6) and then including the removal of female adults reduces the EMPS again (Table 6, scenario 7). The removal effect, however, is ameliorated with increasing initial population size and the average population size.

DISCUSSION

This study has provided a description of the PVA process and model development for an exemplar small and threatened freshwater fish, *N. australis*, and explored both viability and uncertainty to assist with conservation management. In particular, it addressed the key threats relating to this species in isolated, non-permanent habitats such as drought (Magoulick & Kobza, 2003; Matthews & Marsh-Matthews, 2003), habitat loss and fragmentation (Hanski, 2013) and predation (MacRae & Jackson, 2001); all of which have relevance to small fish species worldwide. In contrast to larger species, where the impacts are often mostly from fishing, the wide range of threats that affect smaller species is both complex and particular to the species and location (Olden et al., 2007); hence needing individual management. The high extinction risk for such species (Angermeier, 1994; Olden et al., 2007;), especially in arid and semi-arid regions (Varela-Romero et al., 2002; Collares-Pereira & Cowx, 2004) and the need to deal with multiple threats (McDonald-Madden et al., 2010) makes the approach used in this study particularly applicable to their conservation management.

The model synthesized information gathered at an expert workshop designed to elicit knowledge, perception, issues and data, and represents the best understanding of the life cycle and ecology of the species. This is important for lesser known species (often the threatened ones) where there is a lack of readily available, published data and provides a useful case study for other similar fishes worldwide. As part of the process, this became the first study to provide valuable trait relationships (e.g. age-fecundities) and estimate vital rates for *N. australis*. The collection of similar data and information for the development and use of population models for the other, more threatened members of the genus *Nannoperca*, and related *Nannatherina*, to guide the conservation management and recovery actions for their populations in other parts of Australia would be most beneficial.

Reducing the risk of extinction through the establishment of additional populations is a common conservation tool for freshwater fishes (Soorae, 2008; Todd & Lintermans, 2015). The model was used to inform management strategies for establishing new populations through sourcing donor fish either from translocation or captive breeding. In particular, it was used to determine what constitutes a viable population for the species, to provide guidance for the establishment of new populations and to assess the impacts on donor populations (Sheller, Fagan, & Unmack, 2006). The exploration of reintroduction scenarios presented in this study indicated that if the site of reintroduction is assessed as being able to support a larger rather than a smaller population, then releasing 500 female adults (1000 adults for an even sex ratio) over a 5-year period would probably be successful, although releasing 1000 female adults would be likely to achieve success in a shorter period of time. This assumes that none of the vital rates would be influenced by the capture and release process, or a captive breeding programme (see Morrongiello, Bond, Crook, & Wong, 2011b for an example of depressed size-dependent fecundity in captivity). Although not presented in this study, the model could also be used to examine possible capture and release impacts on the success of a reintroduction. Alternative reintroduction strategies can be readily explored, particularly as the only strategy examined in this study was the release of female adults over a 5-year period. The availability of donor adult fish may not come to hand in a consistent manner; if and when a translocation is ready to be implemented the model can be used to explicitly model the release strategy for assessing the likelihood of success.

The viability of a population was investigated through the inclusion of plausible threatening natural processes, such as floods causing a sudden population decline or recruitment failure. The modelling outcomes indicate, unsurprisingly, that the larger the population the greater the capacity to withstand a significant population loss or occasional poor recruitment. A population in stable habitat supporting about 2000 female adults is likely to be viable, able to withstand some disturbance and possibly be used as a source population for reintroductions. Even when removals were included to assess the impact on a donor population, the larger the population the more robust it is expected to be to disturbances. Although more abundant populations will assist both population resilience and recovery, assessment of scenarios that include the likelihood of recruitment failures or catastrophic events is important for this species in its inherently variable and vulnerable habitats. A reduction in the likelihood of such events is essential for this species, and measures may include the need for regular use of environmental water allocations to maintain recruitment success and prevent population loss during drought periods (see Wedderburn, Barnes, & Hillyard, 2014). Unfortunately, *N. australis* has a high susceptibility to drought, rating second most vulnerable on scores of resistance and resilience of 15 south-eastern Australian fish species (Crook et al., 2010,). Furthermore, the high variation among populations in genetic structure (Cook, Bunn, & Hughes, 2007) and life history traits (Morrongiello et al., 2012) mean that careful consideration needs to be given to the selection of donor populations to ensure they are compatible with recipients and possess the required traits to be successful. In reality, however, there are few populations of *N. australis* in the wild of sufficient size to withstand such take from translocations and hence the production of fish through hatchery means may be required. The production of fish and stocking of populations is common for larger species (Koehn & Todd, 2012), and with the provision of suitable facilities is considered a feasible recovery option for *N. australis.*

Some important uncertainties arose during model development, mainly relating to the appropriate parameterization of early life-history survival, s_0, and hence population growth rate, and the level of variation in survival rates. As these empirical data were unavailable, a more theoretical and explorative approach was required. Such a lack of knowledge or data is not uncommon for rare or threatened species. This study has explored the consequence of uncertainty in survival rates through both deterministic and stochastic sensitivity, and illustrated that the model remains sensitive to estimates of survival in the first year of life, s_0. The sensitivity analysis indicated that knowing survival rates is more important than knowing the variation surrounding them. Despite adult survival rates being estimated using data from another population in a very different ecological setting (healthy population, good habitat; Humphries, 1995), they are likely to be representative of the species generally and could be considered to be the 'best' example of what survival rates would be in the wild. It is interesting that the reproductive value increases in the last age-class which is atypical for most large fish species, where it is more usual to see the reproductive value decline with age after reaching a maximum before the final age-class. These results therefore corroborate a growing awareness of the value of bigger, older and more fecund females to population persistence (Hixon, Johnson, & Sogard, 2014).

Although the ecological knowledge for *N. australis* is generally well established, some aspects do remain uncertain. For example, it would have been preferable to use data collected from the populations of interest, rather than from other sites. Destructive sampling to collect such data (especially for ageing fish) is not a viable option for small populations of threatened species. Other areas of uncertainty could also be explored, particularly the most appropriate way to characterize habitat constraints through density-dependence. In addition, there is uncertainty around the strength of recruitment, and it is recommended that some populations be monitored annually to inform this process. The key habitat requirements of *N. australis* are not well established but they need to be defined in order to select suitable sites for the establishment of new populations. The best sites for new populations will probably be determined by the mix of alien species present as *N. australis* is known to be highly sensitive to the presence of alien species (Pearce, 2014). Some definitive physico-chemical tolerance ranges (e.g. temperature, dissolved oxygen) have also not been quantified for *N. australis* and this information is important for establishing environmental 'triggers' to enable managers to address critical condition thresholds (Morrongiello, 2011b).

Rivers, ephemeral streams and especially wetlands in south-eastern Australia, have been severely affected by significant drought ('millennium drought' 1998–2010) (Kingsford et al., 2011; Murphy & Timbal, 2008). This has focused some attention on the issue of climate change for all Australian freshwater fishes with trends of increased temperatures and reduced rainfall predicted to further threaten vulnerable freshwater environments (Koehn, Hobday, Pratchett, & Gillanders, 2011; Morrongiello et al., 2011a). Globally, climate change and drought are altering fish communities (Daufresne & Boet, 2007; Frederico, Olden, & Zuanon, 2016), with vulnerable species disappearing from some river basins (Matthews & Marsh-Matthews, 2003; Morgan, Beatty, Allen, Keleher, & Moore, 2014). As *N. australis* is a short-lived species with poor dispersal ability, the fragmented and patchy nature of suitable remaining habitat across the landscape, and variability of this habitat between seasons and years, makes it extremely vulnerable to extirpation. Consideration needs to be given to the protection of refuge pools during periods of low flows (Hammer, Piller, & Sortino, 2009; Magoulick & Kobza 2003) to reduce the chance of poor water quality (McNeil & Closs, 2007) and catastrophic population failure. Concomitantly, loss of habitat linkages caused by prolonged dry periods and reduced flooding (likely to result from continuing climate change) will greatly limit habitat recolonization (Knight & Arthington, 2008) as well as population connectivity that maintains gene flow (Cook et al., 2007). Given the low numbers of *N. australis* in the Murray-Darling Basin, there is a greater reliance on the reintroduction of this species as a method to manage the conservation risk and re-establish populations. There are limited data for the other pygmy perches; however, if *N. australis* is representative of this group of fishes, it is likely that this method would be appropriate for the other related species and to many similar small-bodied species generally. It is important to note though, that while the focus of reintroduction may be at a local scale, planning for conservation management should be undertaken at a large scale (Maire et al., 2015) even for small-bodied species.

The issues facing the conservation of *N. australis* fits the 'small threatened freshwater fishes' paradigm and are common to many species throughout the world. It was considered that the threats to *N. australis*, combined with limited dispersal ability and short life-span, greatly reduced the ability to recolonize new habitats and makes this species particularly vulnerable to localized extinctions. The collaborative process outlined in this paper provides a useful framework for collating key knowledge, identifying levels of uncertainty, and then developing population models to assist management. The model can evaluate the viability and risks to populations, assist with the establishment of new populations and set priorities for conservation management actions. The application of this approach to other small, threatened freshwater fish species would greatly assist the conservation management of this group of forgotten fishes.

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Table 1. A range of growth rates (λ) for given s_0.

s_0	λ
0.004	0.9326
0.004578	1.0000
0.005	1.0477
0.0055	1.1029
0.006	1.1570

Table 2. Sensitivity analysis of the characteristic polynomial expressed as changes in the vital rates in terms of percentage change and the associated growth rate λ.

Parameter	-10%	λ	+10%	λ
s_0	-5.51	1.0421	5.38	1.1623
s_1	-3.17	1.0680	3.00	1.1361
s_2	-1.39	1.0876	1.34	1.1177
s_3	-0.11	1.1017	0.11	1.1042
All survival rates	-10.00	0.9926	10.00	1.2132
F_1	-2.33	1.0773	2.40	1.1294
F_2	-1.73	1.0839	1.70	1.1217
F_3	-1.28	1.0889	1.23	1.1166
F_4	-0.11	1.1017	0.11	1.1042
All fecundity	-5.51	1.0421	5.38	1.1623
All vital rates	-14.96	0.9379	15.92	1.2785

Table 3. A range of estimated standard deviations for given specific survival rates.

Survival Parameter	Survival Mean	10% CV	20% CV	30% CV
s_0	0.0055	0.0005	0.0010	0.0015
s_1	0.5270	0.0527	0.1054	0.1581
s_2	0.4872	0.0487	0.0974	0.1462
s_3	0.0526	0.0053	0.0106	0.0158

CV – coefficient of variation

Table 4. Stochastic sensitivity analysis of changes to vital rate distributions used in the *Nannoperca australis* model

	Mean						Standard deviation					
Parameter	-10%	Diff[a]	-10%%Δ[b]	+10%	Diff	+10%%Δ	Decrease[c]	Diff	%Δ	Increase[d]	Diff	%Δ
s_0	1325.25	-454.56	-25.54	2096.38	316.57	17.79	1961.99	182.19	10.24	1581.87	-197.93	-11.12
s_1	1543.13	-236.68	-13.30	1962.80	182.99	10.28	1890.92	111.11	6.24	1656.22	-123.59	-6.94
s_2	1683.77	-96.04	-5.40	1866.62	86.82	4.88	1831.79	51.98	2.92	1727.31	-52.50	-2.95
s_3	1772.89	-6.92	-0.39	1785.96	6.15	0.35	1781.10	1.29	0.07	1780.27	0.46	0.03
All Surv	852.98	-926.83	-52.07	2274.82	495.01	27.81	2070.30	290.49	16.32	1393.04	-386.77	-21.73
F_1	1596.60	-183.21	-10.29	1943.35	163.54	9.19	1787.17	7.36	0.41	1771.23	-8.58	-0.48
F_2	1643.42	-136.38	-7.66	1898.19	118.38	6.65	1787.78	7.97	0.45	1773.89	-5.92	-0.33
F_3	1680.15	-99.66	-5.60	1866.68	86.88	4.88	1786.35	6.55	0.37	1772.94	-6.86	-0.39
F_4	1771.00	-8.81	-0.49	1787.84	8.04	0.45	1781.71	1.91	0.11	1780.67	0.86	0.05
All Fec	1299.79	-480.02	-26.97	2108.92	329.11	18.49	1802.19	22.38	1.26	1757.94	-21.86	-1.23
All Params	392.23	-1387.58	-77.96	2483.22	703.41	39.52	2092.39	312.59	17.56	1378.22	-401.59	-22.56

[a] Diff – the difference between the expected minimum populations size recorded for the baseline scenario without density dependence, 1779.81, and the expected minimum population size recorded for the specified parameter change.
[b] %Δ – percentage change
[c, d] Decrease relates to a change from a 20% coefficient of variation (CV) to a 10% CV or an increase to a 30% CV exploring uncertainty in variation in survival whereas decrease/increase relates to a 10% decrease or a 10% increase in the variation of fecundity.

Table 5. Evaluation of reintroduction scenarios for *Nannoperca australis* with different final average population sizes.

		Results evaluated from 1 to 20 years			Results evaluated from 2 to 20 years			Results evaluated from 5 to 20 years			Results evaluated from 10 to 20 years		
Released[a]	APS[b]	EMPS[c]	Pr(MPS≤25)[d]	Pr(MPS≤50)	EMPS	Pr(MPS≤25)	Pr(MPS≤50)	EMPS	Pr(MPS≤25)	Pr(MPS≤50)	EMPS	Pr(MPS≤25)	Pr(MPS≤50)
250	500	16.378	0.968	1.000	35.887	0.189	0.897	96.224	0.024	0.128	163.715	0.023	0.100
	2000	16.378	0.968	1.000	35.887	0.189	0.897	96.602	0.024	0.128	179.587	0.023	0.100
	8000	16.378	0.968	1.000	35.887	0.189	0.897	96.602	0.024	0.128	179.610	0.023	0.100
500	500	32.624	0.194	0.984	72.392	0.000	0.128	180.648	0.000	0.010	245.168	0.000	0.010
	2000	32.624	0.194	0.984	72.466	0.000	0.127	189.797	0.000	0.009	332.506	0.000	0.009
	8000	32.624	0.194	0.984	72.466	0.000	0.127	189.797	0.000	0.009	335.212	0.000	0.009

1000	500	65.447	0.003	0.174	142.948	0.000	0.001	271.644	0.000	0.001	295.727	0.000	0.001
	2000	65.447	0.003	0.174	144.964	0.000	0.001	383.891	0.000	0.001	652.429	0.000	0.001
	8000	65.447	0.003	0.174	144.964	0.000	0.001	383.891	0.000	0.001	707.362	0.000	0.001

[a] The total number of female adult fish released from year 1 to 5, i.e. 250 ~ 50 female adults for 5 years.
[b] APS – average population size
[c] EMPS – expected minimum population size
[d] Pr(MPS≤XX) – probability that the minimum population size is less than or equal to XX

Table 6. Evaluation of scenarios for *Nannoperca australis*

		IPS + APS = 500			IPS + APS = 2000			IPS + APS = 8000		
Scenario*		EMPS	Pr(MPS=0)	Pr(MPS≤25)	EMPS	Pr(MPS=0)	Pr(MPS≤25)	EMPS	Pr(MPS=0)	Pr(MPS≤25)
1	Baseline	263.79	0.000	0.003	1076.03	0.000	0.000	4317.51	0.000	0.000
2	RF 0.1	125.92	0.018	0.129	496.88	0.004	0.044	1985.25	0.001	0.007
3	RF 0.2	53.26	0.120	0.482	218.25	0.044	0.217	839.69	0.034	0.114
4	Cat 0.1	131.50	0.024	0.199	541.35	0.004	0.053	2190.17	0.000	0.010
5	Rem	119.27	0.000	0.052	964.66	0.000	0.000	4221.59	0.000	0.000
6	2 + 4	61.51	0.092	0.454	251.12	0.032	0.235	1004.97	0.014	0.089
7	6 + 5	26.23	0.238	0.71	198.87	0.079	0.321	950.10	0.024	0.120

* Scenario: 1 Baseline survival rates from Table 5 with 20% coefficient of variation, fecundity eqn 2 with variation specified; 2 10% probability of recruitment failure (RF) in any given time step; 3 20% probability of recruitment failure (RF) in any given time step; 4 10% probability of 80% population crash (Cat) in any given time step; removal of 100 adults per time step for the first five time steps; 6 the combination of scenarios 2 and 4; and 7 the combination of scenario 6 with removals (scenario 5).
IPS – initial population size; APS – average population size; EMPS – expected minimum population size; Pr – propbability; MPS – minimum population size

Figure 1. Combining length-fecundity data with age–length data to establish an age–fecundity relationship for *Nannoperca australis*: a) ln(fecundity) versus length data and regression line; b) ln(length) versus age data and regression line; c) generated age–fecundity data from the inferred age–fecundity relationship, 10000 samples, with combined regressions of eq. (2).

Figure 2. *Nannoperca australis* sensitivity analysis when $s_0 = 0.0055$.

Figure 3. Risk curves for the probability of small population size in *Nannoperca australis* following a reintroduction or translocation into habitat with an average population size of 500 female adults. In total, 250 female adults were released over 5 years.