



Large-scale serial replacement of invasive tench (*Tinca tinca*) by invasive carp (*Cyprinus carpio*) in the presence of redfin perch (*Perca fluviatilis*) in the Murray-Darling River system, Australia

Matthew P. Hill · Peter Caley · Ivor Stuart · Richard P. Duncan · David M. Forsyth

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Abstract Ecosystems worldwide are increasingly being invaded by multiple species, and the rate of biological invasion is accelerating, leading to more interactions among invasive species. One such interaction that has received little attention is the phenomenon of ‘serial replacement’ or ‘over-invasion’, where an established invasive species is supplanted by a second invasive species. Understanding this interaction is important as controlling the second species could inadvertently lead to an increase in the abundance of the first species. We used a hierarchical state-space

model to analyse changes in annual abundances (commercial catch-per-unit-effort) of three invasive fish species, tench (*Tinca tinca*), common carp (*Cyprinus carpio*) and redfin perch (*Perca fluviatilis*), in the Murray-Darling River system (MDRS), Australia between 1954–2002. Tench were present at low abundances until the mid-1970 s, before declining to the point of no commercial catch post-1989. This rapid decline coincided with a significant increase in carp abundance, suggesting that carp may have driven the tench decline through habitat modification (particularly the destruction of aquatic plants), consistent with findings from European studies that show the disappearance of tench from ponds with intensive carp farming. Redfin perch populations, were inferred to be much less impacted by the invading carp population. While carp were present in the MDRS for the duration of the study, the rapid increase in carp abundance in the early 1970 s coincided with the introduction of a specific genetic lineage—the “Boolarra strain”. Our analysis provides compelling evidence of serial replacement of long-established tench by invading common carp triggered by the introduction of a novel carp strain.

M. P. Hill · P. Caley (✉)
CSIRO Data61, GPO Box 1700, Black Mountain,
ACT 2600, Australia
e-mail: peter.caley@csiro.au

I. Stuart
Gulbali Institute for Agriculture, Water and Environment,
Charles Sturt University, P.O. Box 789, Albury,
NSW 2640, Australia

R. P. Duncan
Centre for Conservation Ecology and Genetics, Institute
for Applied Ecology, University of Canberra, Canberra,
ACT 2617, Australia

D. M. Forsyth
Arthur Rylah Institute for Environmental Research,
Heidelberg, VIC 3084, Australia

D. M. Forsyth
School of Biological, Earth and Environmental Sciences,
University of New South Wales, Sydney, NSW 2052,
Australia

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Introduction

The impacts of invasive species have commonly been assessed in terms of changes to native biota (Simberloff et al., 2013; Gallardo et al., 2016) but interactions between invaders can alter their respective population dynamics and in turn the composition of broader ecological communities (Didham et al. 2005). Interactions between co-occurring invasive species have usually been viewed as ranging from additive (i.e. species have independent impacts (Jackson et al. 2014)) to facilitative (i.e. sympatric non-indigenous species enhance each others invasiveness, possibly leading to invasional melt-down (Simberloff and Von Holle, 1999, Simberloff, 2006)). One interaction between invasive species that has received relatively little attention is the replacement of an established invasive species by a second invasive species, termed ‘serial replacement’ or ‘over-invasion’ (Russell et al. 2014). Serial replacement (Lohrer and Whitlatch 2002) describes a process of negative effects from one invader on another leading to one species out-competing the other and significantly reducing or replacing it within a community, sometimes leading to extirpation (Jackson et al., 2014; Rauschert and Shea, 2017; Lohrer and Whitlatch, 2002).

For serial replacement to occur, there are two requirements. Firstly, that one invasive species is more ‘dominant’ than the other (e.g. through functional response (Wasserman et al. 2016), or some form of ecosystem engineering to provide a competitive advantage (Gonzalez et al. 2008)), and secondly, that the dominant species arrives after the first, ‘subordinate’ invasive species. While invasive species may compete and interfere with one another (Rauschert and Shea 2017), serial replacement occurs when the population of the incumbent invasive species is extirpated. Theory predicts that serial replacement is most likely to occur as a competitive outcome among species sharing similar niches (Russell et al. 2014). Indeed, examples of serial replacement may involve congeners, for example competitive displacement of invasive *Rattus exulans* populations on islands by subsequent invasions of exotic *R. rattus* and *R. norvegicus* (Russell et al. 2014). Additionally, high niche overlap that results in one species driving a diet change in the other may also result in replacement, such as seen with Asian shore crabs replacing European green crabs in rocky intertidal habitats (Lohrer and Whitlatch 2002; Griffen et al.

2008; Baillie and Grabowski 2019). Understanding serial replacement is important because, where it has occurred, efforts to control the dominant species may have the unintended consequence of facilitating the subordinated species to increase in abundance.

The major two rivers (Murray and Darling) of the Murray-Darling River System (MDRS) in Australia total 5,280 km in overall length, and have been invaded by multiple non-native invasive fish species long (i.e. decades) ago (Lintermans and Murray-Darling Basin Commission 2007; García-Díaz et al. 2018). One such species is tench (*Tinca tinca* (L. 1758); Tincidae), a globally invasive species (Avlijaš et al. 2018) that was introduced to the MDRS in 1876 and became common in slow-flowing water with a muddy bottom (Lintermans and Murray-Darling Basin Commission 2007). Common carp (*Cyprinus carpio* L. 1758) are a Cyprinid that occupy the same trophic level as tench and are also a highly successful invasive species globally (Vilizzi et al. 2015). Common carp were first introduced to the MDRS in the mid-1800 s (Koehn 2004), but it was not until after the more vigorous fast-growing European ‘Boolarra’ strain was introduced in the early 1960 s that the population began to grow rapidly (Davis et al. 1999; Koehn et al. 2000; Rowland 2020). Common carp can spawn in the main channel of rivers (King et al. 2003), but overbank flows provide access to optimal spawning and recruitment conditions in floodplain habitats (Koehn et al. 2000; Stuart and Jones 2006). Large-scale flooding in 1974 and 1975 likely facilitated the spread and increase of the Boolarra strain of common carp into the Riverina, Murrumbidgee, Lachlan and Darling catchments of the Murray-Darling Basin (Forsyth et al. 2013). Carp have subsequently become the dominant fish species in the MDRS, often dominating the fish biomass (Koehn 2004; Stuart et al. 2021). The increasing abundance of carp coincided with tench declining from being a commonly-caught commercial species to being seldom caught (Reid et al. 1997; Lintermans and Murray-Darling Basin Commission 2007; Rowe et al. 2007; Reynolds 1976). The negative effects of high carp biomass on aquatic plants (Fanson et al. 2024), and the high suspended sediment loads caused by their ‘mumblin’ feeding habit generating suspended sediments (De Moor and Bruton 1988), can result in the disappearance of tench in ponds in which carp are raised intensively (Adámek et al. 2003). Further,

tench and carp have a potentially high diet overlap (Britton et al. 2018; Adámek et al. 2003), suggesting that in some systems resource competition between these species could be biologically important.

Classical population models (i.e., with logistic-type population growth and accounting for carrying capacity) have been used to explore serial replacement (Russell et al. 2014; Rauschert and Shea 2017). However, fitting population models to real abundance data to formally demonstrate the process of serial replacement has not been undertaken. Such an approach requires a long-term time series of abundances spanning before and after the arrival of the second species. As systematic counts of invasive species are not often undertaken, other data sources may provide avenues to investigate serial replacement over a long time period. Catch-per-unit-effort (CPUE) data, such as that commonly collected in fisheries, can be a useful source of information for inferring changes in abundance of invasive species populations over time (e.g. Forsyth et al. 2013, 2018).

Environmental variation can also influence species abundances independent of interspecific competition (Porzig et al. 2016). In the MDRS, fish abundance varies in response to flow variation (Humphries et al. 2008). If changes in flow regimes in the MDRS have caused changes to the fish community we might expect correlated responses across different fish species. In addition to carp and tench, another non-native species, redfin perch (*Perca fluviatilis* L. 1758) is abundant across the MDRS. The redfin perch is a pelagic carnivore (Wedderburn et al. 2014) that was introduced to the MDRS in 1861 (Lintermans and Murray-Darling Basin Commission 2007). While the distribution of redfin perch within the MDRS overlaps tench and carp (Lintermans and Murray-Darling Basin Commission 2007), in contrast to tench, it did not undergo a noticeable sustained decline in abundance following the increase of carp during the 1970 s (Reynolds 1976). If serial replacement of tench has occurred, we would expect correlated responses only between carp and tench, with redfin relatively unaffected.

Here our objective is to determine whether serial replacement of tench by carp has occurred in the MDRS by simultaneously modelling the population dynamics of these three invasive species. By including three species and an environmental covariate, we aim to demonstrate that the decline in abundance

of tench is due to the presence of carp, and that this decline relates to an interaction with carp (but not between redfin perch and carp), or whether the dynamics could be due to river flow (i.e., environmental variation unrelated to interspecific competition). Understanding the interaction between tench and carp is important because there is a proposal to introduce a biological control agent to Australia to control carp (McColl et al. 2016, 2017; McColl and Sunarto 2020), and if there has been serial replacement of tench by carp then the abundance of the former could increase if the latter is controlled to low abundances.

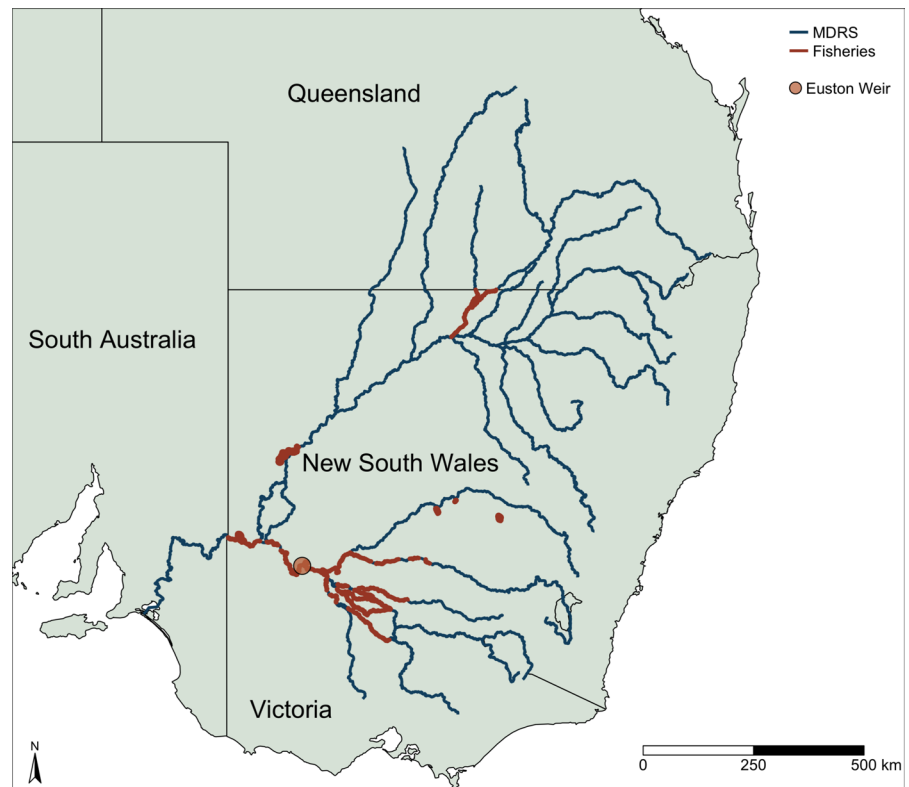
Methods

Data

The catch-per-unit-effort data used to model the population dynamics of tench, carp and redfin perch were from the New South Wales (NSW) inland commercial fishery spanning from 1954–2002. The fishery was centered around the mid-Murray River, in the Wakool and Edward rivers, also in the Darling River upstream to the Menindee Lakes and in the Lachlan River system (Fig. 1; Reid et al. 1997). The data consisted of annual commercial catch (kg of species) and effort (days fished). The fishing methods included gill-nets (maximum length 27.5 m, minimum mesh size of 130 mm) in backwaters and drum nets (1.25 m diameter, minimum mesh size of 130 mm, with wings up to 3 m long) in flowing waters. The dimensions of these nets was set under the Fisheries Management Act (1994) and changed very little over the life of the fishery (Reid et al. 1997). For more information on how these data were collected, see Reid et al. (1997) and Forsyth et al. (2013). There was considerable market demand for carp, tench and redfin as table fish and, with the exception of redfin, also as bait for marine rock lobsters (Reynolds 1976).

Limitations of the data were that fishing effort data collected before 1978 records were restricted to number of fishers per month, whereas records from 1978–1995 includes number of days fished (Reid et al. 1997). We therefore calculated CPUE as kilograms of fish divided by number of fishers per annum. Number of fishers data for the years 1956 and 1983 were unavailable and therefore both years

Fig. 1 Major waterways of the Murray-Darling River System (MDRS), eastern Australia. Data from the waterways shown in red (all within New South Wales) were used in our analyses. The location of the mid-Murray River gauge at the Euston weir is indicated by an orange circle



were treated as missing. There are also spatial grouping of catches (i.e. fish from various regions were included under a single record; Gilligan (2005)). In the northern rivers, such as the Paroo and Warrego systems, there were long periods of low (or no) flows, which means that they were fished infrequently, and by a small number of fishers (Reid et al. 1997). We emphasise that these CPUE data reflect the catchable adult population and not the entire population present (Forsyth et al. 2013).

The MDRS is characterised by highly variable and unpredictable rainfall and run-off, and hence river flows are also highly variable (Balcombe et al. 2011). Overbank flows typically generate substantial increases in the abundance of juvenile carp (King et al. 2003; Koehn et al. 2017) and strong cohort effects in the carp population (Stuart and Jones 2006). In contrast, high flows are thought to have relatively little effect on the abundances of tench because they breed in late spring or summer when flow events have passed (Avlijaš et al. 2018). Redfin perch spawn in lakes and rivers but are not known to increase in abundance following floodplain inundation (Čech

et al. 2009). Annual river flow data (gigalitres per annum) were obtained from the mid-Murray Euston gauge (Fig. 1) (see Forsyth et al. (2013) for details) and are assumed to be representative of flows throughout the MDRS fishery. To make parameter estimates easier to interpret (see Model details Section below), we redefined our flow response measure as the divergence from the long term mean (i.e. the total data included in our models) (Hobbs and Hooten 2015).

Population dynamic modelling

General approach

Longitudinal monitoring data can be used to jointly model the effects of environmental effects, intra- and inter-species interactions on the abundance of a species of interest (e.g. Dennis and Otten 2000). Putting this type of model into a Bayesian state-space modelling framework enables the two sources of variation in a time series of abundance to be differentiated: the biological (“process”) variation, and measurement

(“observation”) error in the observations (e.g. Newman et al. 2014). This modelling approach enables inter-specific effects to be estimated using the latent population estimates, providing insights that are not self-evident from observation data.

The state process typically estimates $N(t)$ as the true population size at time t , $\lambda(t)$ as the finite population growth rate between t and $t + 1$ (with equivalent exponential growth rate $r(t) = \log(\lambda(t))$), with environmental stochasticity affecting the population growth rate modelled as log-normally distributed with variance σ_w^2 . The observation process incorporates a population count (data) as $y(t)$, and residual variation (the observation error) also modelled as log-normally distributed with variance σ_v^2 . Environmental covariates can also be included to examine their effect on demographic parameters.

This approach produces yearly population estimates based on the observations of all three non-native species simultaneously, allowing for interactions between species to be quantified in a probabilistic framework. The results then enable prediction of population trends in the absence and presence of competitors, to quantify the interaction strength between species.

Model details

We choose a Gompertz-type population growth model for all three species that can incorporate environmental covariates, agonistic interactions, and density-dependence. We do not fit a population growth model that includes a constant carrying capacity (e.g. a Ricker type), as in such a variable environment it is hard to justify a constant carrying capacity (McLeod 1997).

Our final model is as follows. Let:

$N_C(t)$ = the true index of the abundance of carp in year t ,

$N_R(t)$ = the true index of the abundance of redfin in year t ,

$N_T(t)$ = the true index of the abundance of tench in year t ,

$y_C(t)$ = measured index (CPUE) of the abundance of carp in year t ,

$y_R(t)$ = measured index (CPUE) of the abundance of redfin in year t ,

$y_T(t)$ = measured index (CPUE) of the abundance of tench in year t ,

ρ_C = exponential rate of increase of carp during average river flow,

ρ_T = exponential rate of increase of tench during average river flow in the absence of carp,

ρ_R = exponential rate of increase of redfin during average river flow in the absence of carp,

ϕ_C = coefficient for the effect of flow anomaly on carp rate of increase (r_C),

ϕ_R = coefficient for the effect of flow anomaly on redfin rate of increase (r_R),

ϕ_T = coefficient for the effect of flow anomaly on tench rate of increase (r_T),

β_C = coefficient for carp density-dependence,

β_R = coefficient for redfin density-dependence,

β_T = coefficient for tench density-dependence,

α_{CR} = coefficient for possible antagonistic impact of carp on redfin,

α_{CT} = coefficient for possible antagonistic impact of carp on tench, and

$D(t)$ = the difference between recorded flow and mean flow in year t , on a logarithmic (base 10) scale, and

$S(t)$ = multiplicative factor allowing for changed vigour arising from the introduction of the Boolarra carp strain such that:

$$S(t) = \begin{cases} 1 & \text{if } t \leq 1969 \\ \lambda & \text{if } t > 1970 \end{cases} \quad (1)$$

The true carp population is modelled as growing exponentially with log-normal process noise:

$$\log(N_C(t+1)) = \log(N_C(t)) + r_C(t). \quad (2)$$

The exponential rate of increase in year t is linearly related to the anomaly in river flow in the previous year and the logarithm of carp abundance (density-dependence) (Eqn. 3). Here, ρ_C can be interpreted as the rate of increase of the population under average flow conditions (i.e. $D_t = 0$) when abundance is low such that intraspecific density-dependence is negligible. With the Gompertz-type growth (Eqn. 3) this will occur when the population size is one unit (i.e. $N_C(t) = 1$ and hence $\log(N_C(t)) = 0$). For an example of a similar approach see Hobbs and Hooten (2015). Process noise around population growth is log-normally distributed (as r_t is already on a logarithmic scale). Specifically:

$$r_C(t) = S(t)(\rho_C + \phi_C D(t)) + \beta_C \log(N_C(t)) + W_C, \text{ where } W_C \sim N(0, \sigma_{W_C}^2). \quad (3)$$

Population growth of redfin and tench are also assumed to be Gompertz-type with log-normal process noise (after Eqn. 2), however the models for the exponential rate of increase of tench (Eqn. 4) and redfin (not shown) contains an additional term to capture the potential agonistic effect of carp:

$$r_T(t) = \rho_T + \phi_T D_t + \beta_T \log(N_T(t)) + \alpha_{CT} \log(N_C(t)) + W_T, \text{ where } W_T \sim N(0, \sigma_{W_T}^2). \quad (4)$$

Again, ρ_T and ρ_R can be interpreted as the rate of increase of the population under average flow conditions (i.e. $D_t = 0$), negligible intraspecific density-dependence and additionally negligible interspecific effects arising from the carp population. Finally, the total observed catch-per-unit-effort for all species is assumed to have log-normal observation error. That is:

$$\log(y(t)) = \log(N(t)) + V, \text{ where } V \sim N(0, \sigma_V^2). \quad (5)$$

The observation error was modelled separately for each species (i.e. with $\sigma_V = \sigma_{V_C}$, $\sigma_V = \sigma_{V_T}$ or $\sigma_V = \sigma_{V_R}$).

On the treatment of zeros

The tench data are notable for observations of zero CPUE. Some of these zeros, particularly during the later years of the time series, are quite possibly true zeros (i.e. no tench were present hence none caught). Some of the earlier zeros, however, are more likely to be either a situation of “no tench recorded” as opposed to “no tench being caught”, or that the abundance of tench is below what can be termed the “level of detection.” This could occur if the population of tench was sparse enough that it did not overlap spatially with fishing effort. The usual approach of adding 1 (or a suitably small number) to zero counts when analysing data on a logarithmic scale can introduce problems. First, some of the data are true zeros, whilst some are “lazy reporting” zeros — treating them as the same introduces a non-trivial number of

observations of the tench population not changing (remembering that analyses are being undertaken on a logarithmic scale, hence small numbers still have influence on parameter estimation). We prefer the approach of treating the zero tench CPUE data points as missing (specifically NA or “Not available”), for which the Bayesian approach can naturally accommodate, but to additionally to model the NAs as being below the level of detection. This was done by modelling detection as a function of the unobserved true tench abundance using the complementary log-log function:

$$\text{cloglog}(p(t)) = \log(d) + \log(N_T(t)) \quad (6)$$

where d is the per unit of catch effort detection rate. A binary variable for whether any tench were caught ($z = 1$) or not ($z = 0$) was then included within the model as $Z(t) \sim \text{Bernoulli}(p(t))$.

Model fitting

We used JAGS version 4.3 (Plummer et al. 2003), accessed in R through the `rjags` (Plummer 2019) and `jagsUI` (Kellner 2024) packages. Values for prior distribution are shown in Table 1. For priors on variances, following Gelman (2006) we used a uniform prior on the scale of the standard deviation. For the sampler to achieve convergence for the parameters of interest, it was necessary to bound them within reasonable limits (Table 1). Model convergence was examined using the R package `mcmcplots` (Curtis 2018), including the convergence diagnostic of Gelman and Rubin (1992) that calculates potential scale reduction factors. We found that three chains of 100,000 iterations, following an initial burn in of 10,000 were sufficient to result in R -values for parameters of interest (λ , ρ_T , ρ_C , ρ_R , ϕ_T , ϕ_C , ϕ_R , β_T , β_C , β_R , α_{CR} , α_{CT} , d) to be ≤ 1.1 . We further calculated the Bayesian p -values based on the posterior predictive distribution of the goodness-of-fit statistic (Gelman et al. 2013) based on the modelled values of carp, tench and redfin. We note that this method is subject to criticism, though still used by respected practitioners (e.g. Hobbs and Hooten 2015, p. 203).

We report parameter estimates as medians (unless otherwise stated) and their 95% credibility intervals (CIs) from the posterior distributions sampled.

Table 1 Model parameters, their description and statistical prior values (including rationale). Subscripts *C*, *T* and *R* refer to “carp”, “tench” and “redfin”, respectively

Parameter(s)	Description	Prior value	Rationale
λ	Multiplicative factor for change in rate of increase associated with Boolarra strain	Uniform(0,10)	Assumed > 0 and less than a 10-fold effect.
ρ_C, ρ_T, ρ_R	Exponential rate of population increase (long-term) during average flow year and low abundance	TruncNorm($\mu=0, \sigma=100, a=-5, b=5$)	Largely uninformative within biological bounds.
ϕ_C, ϕ_T, ϕ_R	Effect of flow anomaly on r_C, r_T and r_R	TruncNorm($\mu=0, \sigma=100, a=-2, b=2$)	Largely uninformative within bounds.
$\beta_C, \beta_T, \beta_R$	Density-dependence coefficient (Gompertz-type)	TruncNorm($\mu=0, \sigma=100, a=-2, b=2$)	Largely uninformative within bounds.
α_{CT}, α_{CR}	Agonistic term for effect of carp abundance on tench or redfin rate of increase	TruncNorm($\mu=0, \sigma=100, a=-2, b=2$)	Largely uninformative within bounds.
$\sigma_{V_C}, \sigma_{V_T}, \sigma_{V_R}$	Standard deviation of log-normal observation error.	Uniform(0,10)	Largely uninformative within bounds.
$\sigma_{W_C}, \sigma_{W_T}, \sigma_{W_R}$	Standard deviation of log-normal process noise.	Uniform(0,10)	Largely uninformative.
d	Rate of encounter of fishery with tench	Uniform(0.0001,10)	Largely uninformative.

The R code and data set required to run the model are provided as Supplementary Material.

Results

Data scope

When the time series began in 1954, tench, redfin and carp were all present in the MDRS (Fig. 2a, 2b, 2c). Carp, however, were at relatively low abundances until 1973, after which the “Boolarra strain” increased rapidly such that they greatly exceeded the abundances of tench and redfin within several years (Fig. 2 b). Tench declined steadily from the mid-1970 s, with the last recorded commercial catch in 1989 (Fig. 2a). Compared to tench, redfin abundances changed little following the increase in the abundance of carp, with the species still commercially caught when our time series ended in 2002 (Fig. 2c). Though not factored into our model, the decline in redfin abundance during the early 1980 s (Fig. 2c) is thought to have been caused in part by outbreaks of epizootic hematopoietic necrosis virus (EHNV) (Langdon et al. 1986). Annual river flow (Fig. 2d), as measured at Euston on the Murray River, averaged

8,058 GL (range: 1,751–43,664 GL). There were two extreme flood events, in 1955 and 1975, and several multi-year periods where river flow was well below the mean value, particularly in the 1960 s, 1980 s and from 1997–2002.

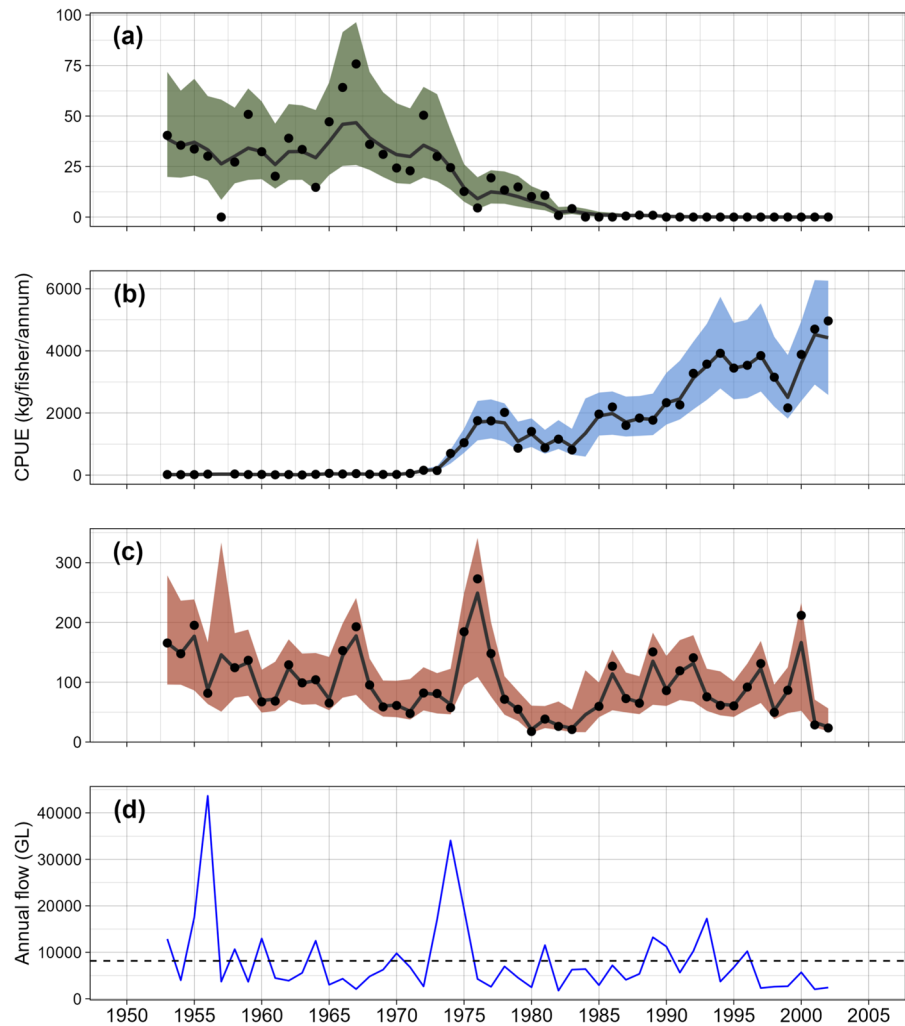
Model fit

Trace plots for the parameters of interest indicated that the Markov chains had converged adequately (i.e. R values all < 1.05, see Table 2 in Appendices). The Bayesian p-values for the modelled abundances of carp (0.73), tench (0.75) and redfin (0.62) indicated that the models provided good approximations of the observed data (see Fig. 8 in Appendices).

Modelled changes in the abundances of tench, redfin and carp

Our model reproduced the observed changes in the abundance of tench, redfin and carp well (Fig. 2). The posterior predictive value for the median abundance of tench tended to zero at the end of the observation period, driven by the estimated agonistic (i.e.

Fig. 2 Observed and modelled abundances (CPUE) for (a) tench, (b) carp and (c) redfin, and annual river flow (gigalitres per annum) (d), in the Murray-Darling River System, 1954–2002. For CPUE, filled circles are observed values, solid lines are medians of posterior modelled population trajectories, and shading indicates 95% credibility intervals. Note that the abundance scales differ for the three species. The dashed line in (d) indicates the mean annual flow



negative) interaction from the large and increasing carp population (Fig. 2). This is in agreement with the observed data of zero catch of tench.

Parameter estimates

Effect of Boolarra strain on carp rate of increase

The introduction of the Boolarra lineage was associated with a near three-fold increase in the rate of increase of the carp population ($\hat{\lambda} = 2.6$, 95% C.I. 1.95–3.58, $P(\lambda > 0) = 1.00$) (Fig. 3a). The result of this was to increase the rate of increase of carp

under average flow conditions and minimal density-dependence (one unit of carp CPUE) from 0.65 yr^{-1} (95% C.I. $0.30\text{--}1.05 \text{ yr}^{-1}$) to 1.65 yr^{-1} (95% C.I. $0.87\text{--}2.50 \text{ yr}^{-1}$) (Fig. 3b).

River flow

River flow had a strong positive effect on the rate of increase of carp once the Boolarra strain was introduced ($\hat{\lambda}\phi_C = 0.45$, 95% C.I. $-0.01\text{--}0.91$, $P(\lambda\phi_C > 0) = 0.97$) (Fig. 4a), with the effect becoming particularly noticeable during the series of wet years during the 1970 s when carp abundance

increased strongly (Fig. 2a). There was also substantial support for a positive effect of river flow on redfin ($\hat{\phi}_R = 0.33$, 95% C.I. -0.23 – 0.87 , $P(\phi_R > 0) = 0.88$) (Fig. 4c) and a negative effect on tench ($\hat{\phi}_T = -0.45$, 95% C.I. -1.34 – 0.24 , $P(\phi_T < 0) = 0.88$) (Fig. 4b).

Intraspecific density dependence

Both carp ($\hat{\beta}_C = -0.21$, 95% C.I. -0.32 – 0.10 , $P(\beta_C < 0) = 1$) and redfin ($\hat{\beta}_R = -0.52$, 95% C.I. -0.86 – 0.22 , $P(\beta_R < 0) = 1$) were inferred to undergo strong negative density-dependence (Figs. 5a and 5c). In contrast, the tench population was inferred

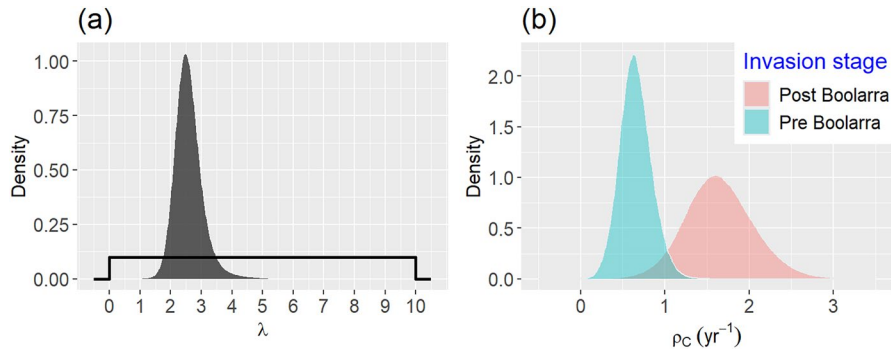


Fig. 3 Posterior distributions for (a) the multiplicative effect of the introduction of the “Boolarra strain” of carp (λ) on density-independent rates of population increase of the carp population, where the shaded histogram represents the poste-

rior distribution for λ , overlaid on the Uniform(0,10) prior distribution, and (b) The rate of increase of the carp population prior to and following the release of the Boolarra strain under average flow conditions and low carp abundance

Fig. 4 Posterior distributions for the effect of flow deviation (ϕ s) on rates of increase of (a) carp, (b) tench, and (c) redfin. Note that in the case of carp the distribution is scaled by the posterior distribution for λ (the effect of Boolarra lineage introduction)

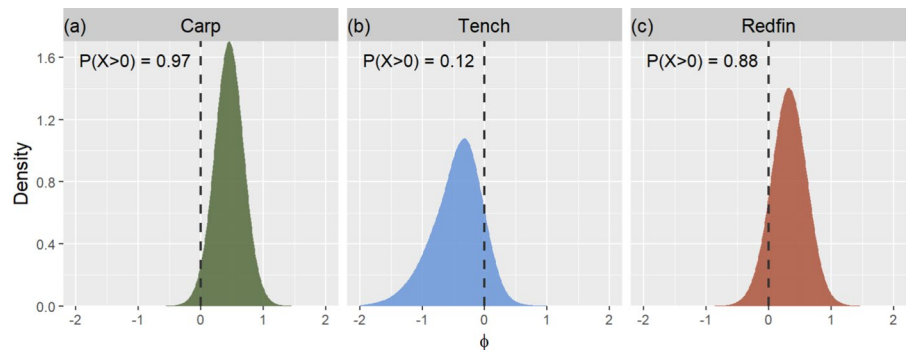


Fig. 5 Posterior distributions for the effect of density dependence (β s) on rates of increase of (a) carp, (b) tench, and (c) redfin

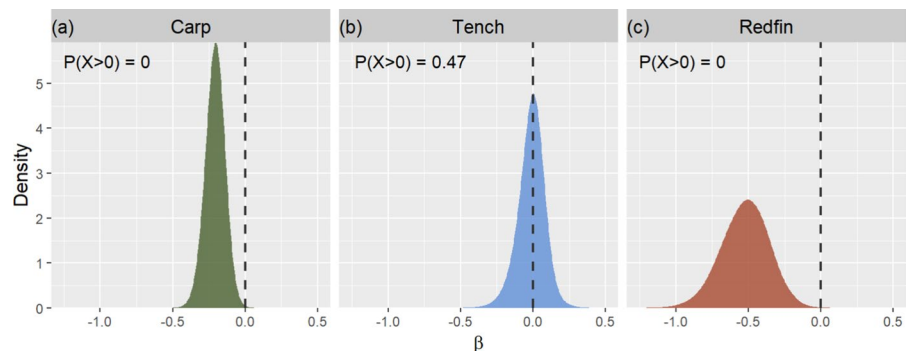
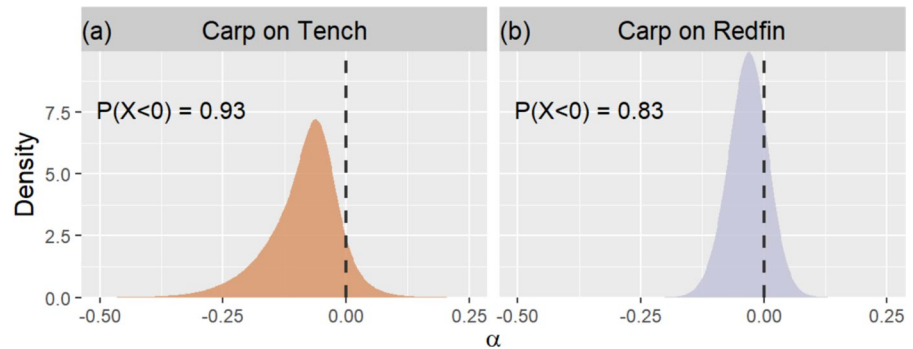


Fig. 6 Posterior distributions for the effect of carp on the rates of increase of (a) tench and (b) redfin



to experience no intraspecific density dependence (Fig. 5b).

Interspecific agonistic effects of carp

The estimated relationship between the abundance of carp and the rate of increase of tench was strongly negative ($\widehat{\alpha}_{CT} = -0.09$, 95% C.I. -0.26 – 0.03 , $P(\alpha_{CT} < 0) = 0.93$) (Fig. 6a). For the interaction between carp and redfin the size of the negative interaction was smaller and less certain ($\widehat{\alpha}_{CR} = -0.03$, 95% C.I. -0.11 – 0.04 , $P(\alpha_{CR} < 0) = 0.83$). That said, the mean cpue for redfin post-1978 (a somewhat arbitrary time point post major flooding and the establishment of Boolarra strain of carp) was 32.3% lower than before, noting that this doesn't account for the positive effects of the 1955 and 1974 floods nor the post-1978 arrival impact on redfin of EHNV.

Population growth rates during average flow in absence of competition and/or intraspecific density-dependence

During average flow conditions and at low abundance (i.e. at one unit of abundance, the density-dependent term in Eq. 3 equals zero), carp abundance post Boolarra strain introduction was predicted to increase strongly (Fig. 7a). For tench, with the interference term attributable to carp additionally set to zero in Eq. 4 the rate of increase was much lower with less vigour (Fig. 7b). Indeed, it is not certain that tench populations would recover strongly in the absence of carp, because tench appeared to prefer lower-than-average flow years (Fig. 4b). In contrast, redfin populations were predicted to increase strongly (Fig. 7c), arising from the lack of both intraspecific competition and interspecific effects of carp (Fig. 7c).

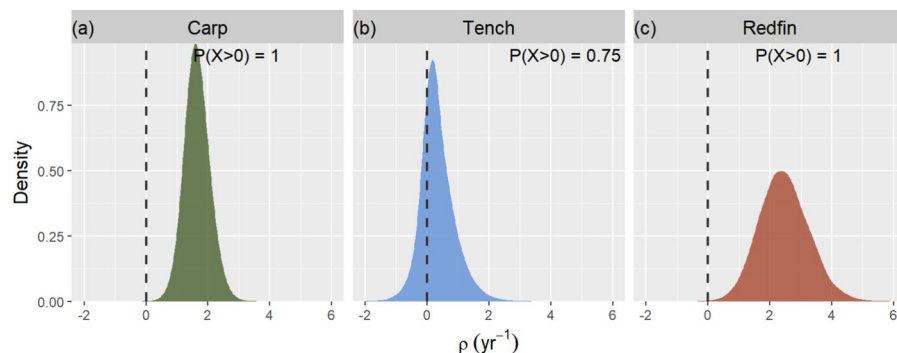


Fig. 7 Posterior distributions for the rate of increase (ρ) of (a) carp, (b) tench and (c) redfin under average flow conditions in the previous year, negligible intraspecific competition, and in

the case of redfin and tench, negligible carp abundance. Note that for carp the value is scaled upwards by the value of λ (effect of Boolarra lineage introduction)

Discussion

Our analysis provides compelling evidence for rapid and large-scale serial replacement of invasive tench by invasive common carp in Australia's Murray-Darling Basin. These results are from a rare example of a long time-series (i.e., 1954–2002) dataset collected before and after the arrival of a new invader. The decline of tench was concomitant with the increasing abundance of the Boolarra strain of common carp after the floods of 1974–75, leading to extinction of the commercial tench fishery by 1990. Our quantification of the much greater population vigour of the carp population following the introduction of the Boolarra strain is a first. After incorporating the effects of river flow on fish population dynamics, our models revealed a large negative effect of common carp abundance on tench abundance. There appeared to be a smaller and less certain effect of common carp on redfin perch abundances, which is consistent with the literature (Weber and Brown 2011), and because these two species have less dietary overlap (redfin are pelagic carnivores) than common carp and tench which are benthic omnivores and carnivores, respectively. Concluding no effect of carp on redfin, however, would be inconsistent with the idea that environmental changes/flows might have caused widespread changes to the fish community.

The decline in tench catch within the NSW commercial fishery coincident with the spread of the Boolarra carp strain was also noted further downstream in the lower Murray River in South Australia. Specifically, in the commercial catch records, there was another precipitous decline in tench catch from 250,000 kg in 1972–73 to 1,000 kg in 1975–76 which coincided with the escape, spread and huge biomass increase of Boolarra strain carp in 1969–70 (Reynolds 1976)(see Fig. 9 in Appendices). Tench were last reported from the commercial fishery in 1982 and are now exceedingly rare in the lower Murray River having been completely replaced by carp whose abundance remains very high (Davies et al. 2008; Todd et al. 2024).

The decline of tench in South Australia led to Reynolds (1976) proposing that the most likely mechanisms for common carp replacement in the MDRS were food and habitat competition, habitat modification, eutrophication, and predation. These mechanisms are non-exclusive. There are no comparative

data on the diets of tench and carp in the MDRS (in part because tench are now rarely caught there; Lintermans and Murray-Darling Basin Commission (2007)), but both species occupy the same trophic level and are considered 'benthic carnivores and benthic omnivores, respectively' (Lintermans and Murray-Darling Basin Commission 2007). Several European studies have documented high overlap in the diets of tench and carp (Adámek et al. 2003; Guo et al. 2017; Britton et al. 2018). In the MDRS, tench inhabit sites with abundant aquatic plants where they feed on macroinvertebrates (Lintermans and Murray-Darling Basin Commission 2007), while high carp biomass has reduced the biomass of aquatic plants across eastern Australia by -36% (Fanson et al. 2024). High carp biomass has also significantly increased (+63%) the turbidity of inland rivers (Fanson et al. 2024), which could reduce the suitability of a site for tench either directly (e.g., through effects on respiration) and/or indirectly (e.g., through negative effects on aquatic plant biomass). Excretion and bioturbation by high biomasses of carp can alter nutrient dynamics, sometimes leading to eutrophication (Matsuzaki et al. 2007). Eutrophication of ponds by intensively-stocked common carp was suggested to be the most likely mechanism for the decline (and sometimes extinction) of tench in European ponds (Adámek et al. 2003). In Lake Naivasha (Kenya) the invasive largemouth bass (*Micropterus salmoides*) was replaced by common carp, with the postulated mechanism 'sub-optimal foraging conditions' caused by habitat modification and eutrophication (Britton et al. 2010). A decline in 'littoral habitat health' was the primary cause of decline in Poland's commercial tench fishery (Skrzypczak and Mamcarz 2006). Predation of tench eggs and older life-history stages by carp has not been documented, but deserves investigation. Common carp prey on redfin perch eggs, which are generally not palatable to other fish due to a gelatinous layer surrounding them (Rowe et al. 2007), so it is likely that carp also prey on tench eggs.

In addition to carp replacing tench in the NSW and South Australian Murray system, another clear example of the speed of the replacement process comes from the upper Murray River at Lake Mulwala, where tench comprised 44% of fish caught in 1978, but decreased to 0 by 1981/82 (Rowland 2020). In the same time period, carp had increased from 1% to 57%, suggesting that carp displaced tench in five

years (Rowland 2020). In doing so, carp also replaced tench as a diet item for Murray cod (*Maccullochella peelii*, (Mitchell, 1838)) (Rowland 2020). In addition to the ecosystem changes caused by carp in the MDRS, there are significant reproductive differences that could have contributed to the serial replacement of tench by carp. Male and female carp attain sexual maturity at 1.5 and 2.7 years, respectively, but male and female tench mature at 4 and 5 years, respectively (Alaş and Solak 2004; Brown et al. 2005). Female carp can also be an order of magnitude more fecund than tench (Yilmaz, 2002; Alaş and Solak, 2004; Sivakumaran et al., 2003). The timing of breeding also differs, with carp beginning to breed in late winter, and tench in late spring or early summer (Koehn et al. 2000; Avlijaš et al. 2018). This difference gives carp earlier access to resources (Conallin et al. 2011). Female carp can also breed multiple times (and even batch spawn ovaries) over a longer annual period, from late winter to early autumn (Smith and Walker 2004). Hence, in favourable conditions carp could increase faster than tench.

Consistent with the propensity of common carp to utilise inundated river flood plains for large-scale spawning and recruitment (Stuart and Jones 2006), our models revealed a large positive effect of river flow on the rate of increase of carp. In contrast, the effects of river flow on the rates of increase of tench (negative) and redfin (positive) were much weaker. Tench and redfin both inhabit slow-flowing waters with a high biomass of aquatic plants (Lintermans and Murray-Darling Basin Commission 2007), conditions that would occur when river flows are low.

In contrast to tench, redfin perch abundances were estimated to be less affected by increasing common carp abundances. Redfin perch occupy a different trophic level and are pelagic carnivores, feeding on decapods, insects, zooplankton and small fish (Lintermans and Murray-Darling Basin Commission 2007). European studies suggest that redfin compete with common carp for approximately half of available food items, with particularly strong competition between adult fish for chironomid larvae (Adámek et al. 2004). Redfin perch likely occupy a niche that does not completely overlap with common carp, enabling these species to co-exist.

Our 50-year time series of annual CPUE abundances for three invasive fish species, spanning 1953–2002, enabled us to fit Bayesian state-space

models to estimate the effects of a second invader (carp) on two incumbent invaders (tench and redfin perch). A key advantage of state-space models is that they enable process variation to be separated from observation error. The data used to parameterise the models had several limitations. First, fishing occurred over many reaches of the MDRS within NSW (Fig. 1), but data were not consistently reported by reach for our timeframe of interest. Hence, the observed data could not be used to investigate spatial variation in fish population dynamics. Second, commercial fishing effort (i.e. days fished) was unavailable prior to 1978, and catches among regions were often grouped. As fishing methods have remained very similar across this time (Reid et al. 1997), we suggest that relating the kilograms of fish caught to the number of fishers is a reasonable assumption to make. Third, we included only one environmental variable, river flow, in our models. Another environmental variable that could have been important is floodplain inundation (see above), but suitable data for this variable were unavailable for our 50-year timeframe of interest. River flow is an appropriate variable because it determines the strength of abiotic and biotic processes that are important for ecological communities in the MDRS (Overton et al. 2009). Fourth, the interactions described here are latent processes (i.e., unobserved or unobservable) so there are some assumptions when linking these parameters to ecological processes such as competition. Despite these limitations, Bayesian state-space models provide a powerful means of quantifying serial replacement, particularly if environmental variation could confound observed changes in abundances.

There is a proposal to attempt to reduce carp abundance in Australia by releasing cyprinid herpesvirus 3 (CyHV-3) to act as a biological control agent (McColl et al. 2016, 2017; McColl and Sunarto 2020). Despite the apparent efficacy of the virus in some situations, there are a range of concerns for the release of the virus, from co-evolution and non-target effects (although these appear unlikely), low efficacy of the virus due to fecundity and resistance (Mintram et al. 2021), through to indirect ecological ramifications (including creating anoxic water conditions following death of the fish) (Kopf et al. 2019). It is hoped that release of the CyHV-3 will reduce carp abundances in the MDRS such that the negative impacts of this species on water turbidity, aquatic plant biomass and

native fish abundances are reversed (McColl et al. 2014, 2016). Our analysis indicates that a very substantial reduction in carp abundance would be needed for a non-desirable recovery of tench populations to become a possibility. We note that the predicted low rate of tench increase in the absence of carp would be factoring in habitat degradation arising from carp that may be ameliorated following their control. We also note, however, that even if this was to occur that the maximum abundance of tench was several orders of magnitude less than that attained by the Boolarra strain of carp. It therefore seems highly unlikely that tench would ever attain the historical maximum biomass that carp have. Nevertheless, the scenario that biocontrol of carp might not generate all of the proposed benefits due to competitive release of one or more invasive species should be considered.

Conclusions

Here we have demonstrated widespread serial replacement of one invasive species by another. Population models parameterised with 50-years of annual abundance and river flow data revealed that the invasion of Australia's Murray-Darling River System by the Boolarra strain of common carp led to serial replacement of the incumbent tench. This study is one of the few examples to use such a long term dataset spanning both pre- and post-invasion of a new invasive species to demonstrate both the impact within the new invasive species of successive introductions increasing population vigour, and the serial replacement at a large scale. The most likely mechanisms for carp replacing tench in the Murray-Darling River System are food competition (tench are benthic carnivores and carp benthic omnivores), habitat competition and destruction of aquatic macrophytes used by tench for spawning, eutrophication, and possibly predation. In contrast, there was less effect of carp on the invasive redfin perch, a pelagic predator. High

river flows favoured common carp more than tench, likely because overbank flows create optimal spawning and recruitment conditions for carp on inundated river floodplains. Our study identifies the potential for unintended consequences arising from the control of an invasive species if it has serially replaced or is suppressing the establishment of another.

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Author Contributions DF and IS conceived the study. MH wrote the first draft with input from all authors. MH and PC undertook the analysis. All authors read and approved the final manuscript.

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Availability of data and materials The data and complete code to run the models used in this study is provided as Supplementary Material.

Code availability The data and complete code to run the models used in this study is provided as Supplementary Material.

Declarations

Conflict of interest None to report.

Ethics approval Not applicable.

Consent to participate Not applicable.

Appendix 1: Model evaluation

See Fig. 8.

Fig. 8 Bayesian posterior predictive checks for (a) carp, (b) tench and (c) redfin

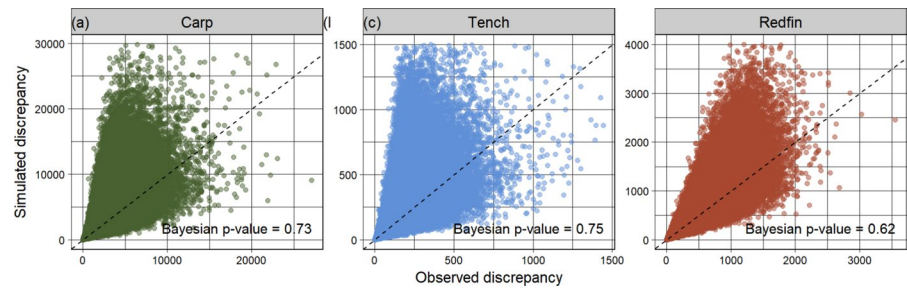


Table 2 Parameter, mean, standard deviation, 95 %Credibility Interval (C.I), the probability it differs from zero in either direction and the associated Gelman and Rubin's R statistic

Parameter	Mean	Std. Dev.	Median (95% C.I.)	$\Pr(X > 0)$	R
λ	2.58	0.407	1.95–3.58	1	1
ρ_C	0.652	0.188	0.302–1.05	1	1.01
$\lambda\rho_C$	1.65	0.409	0.871–2.49	1	1.01
ρ_R	2.46	0.802	0.975–4.12	0.999	1
ρ_T	0.335	0.543	–0.623–1.6	0.747	1
ϕ_C	0.178	0.0954	–0.00388–0.375	0.973	1
$\lambda\phi_C$	0.451	0.232	–0.00994–0.908	0.973	1
ϕ_R	0.326	0.281	–0.232–0.871	0.879	1
ϕ_T	–0.445	0.401	–1.34–0.243	0.883	1
β_C	–0.208	0.0559	–0.324–0.102	1	1.01
β_R	–0.523	0.162	–0.855–0.22	1	1
β_T	–0.0119	0.0851	–0.202–0.143	0.53	1.01
α_{CR}	–0.0326	0.0359	–0.106–0.0364	0.826	1
α_{CT}	–0.0857	0.0706	–0.256–0.0329	0.933	1
d	1.2	0.78	0.341–3.26	1	1

Appendix 2: Parameter estimates

See Table 2.

Appendix 3: Details from previous work

An unpublished report (Reynolds 1976) documents commercial fish catch in the Murray River within South Australia over a 20-year period. Data for tench, carp and redfin are redrawn in Fig. 9.

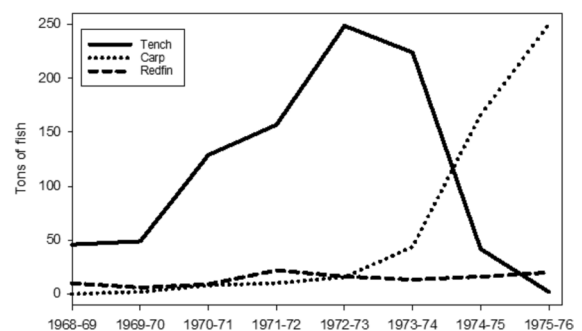


Fig. 9 Relationship between commercial fishery catches tench, carp and redfin perch in the lower Murray River. Redrawn from Figure 1 of Reynolds (1976)

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