Biological Conservation 254 (2021) 108942

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Continental threat: How many common carp (*Cyprinus carpio*) are there in Australia?

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ARTICLE INFO

Keywords:
Common carp
Cyprinus carpio
Invasive species
Density
Biomass
Pest management

ABSTRACT

Common carp (*Cyprinus carpio*) are one of the world's most destructive vertebrate pests. In Australia, they dominate many aquatic ecosystems causing a severe threat to aquatic plants, invertebrates, water quality, native fish and social amenity. The Australian Government is considering release of cyprinid herpesvirus-3 (CyHV-3) as a control measure and consequently a robust, continental-scale estimate of the carp population and biomass is essential to inform planning and risk management. Here, we pioneer a novel model-based approach to provide the first estimate of carp density (no/ha) and biomass density (kg/ha) at river reach/waterbody, basin and continental scales. We built a spatial layer of rivers and waterbodies, classified aquatic habitats and calculated the area of each throughout the range of carp in Australia. We then developed a database of fishery-independent electrofishing catch-per-unit-effort (CPUE) for habitat types, containing catch information for 574,145 carp caught at 4831 sites. Eastern Australia accounted for 96% of carp biomass and 92% of the total available wetted habitat area (16,686 km^2) was occupied. To correct these data for variable detection efficiencies, we used existing electrofishing data and undertook additional field experiments to establish relationships between relative and absolute abundances. We then scaled-up site-based estimates to habitat types to generate continental estimates. The number of carp was estimated at 199.2 M (95%Crl: 106 M to 357.6 M) for an 'average' hydrological scenario and 357.5 M (95%Crl: 178.9 M to 685.1 M) for a 'wet' hydrological scenario. In eastern Australia, these numbers correspond with biomasses of 205,774 t (95%Crl: 117,532–356,482 t) (average scenario) and 368,357 t (95%Crl: 184,234–705,630 t) (wet scenario). At a continental scale the total biomass was estimated at 215,456 t for an 'average' hydrological scenario. Perennial lowland rivers had the highest CPUE and greatest biomass density (up to 826 kg/ha) and the modelled biomass exceeded a density-impact threshold of 80–100 kg/ha in 54% of wetlands and 97% of stream area in large lowland rivers. The continental-scale biomass estimates provide a baseline for focusing national conservation strategies to reduce carp populations below thresholds needed to restore aquatic ecosystems at a range of spatial scales.

1. Introduction

Common carp (*Cyprinus carpio*) (hereafter 'carp') is an important freshwater fish species that is widely cultivated in many Asian and some European countries (Rahman, 2015; Biermann and Geist, 2019). Carp are also one of the world's most destructive vertebrate pests (Lowe et al., 2004) having established self-sustaining populations across a diverse array of climatic and habitat conditions in 91 of 120 countries in which they have been introduced (Casal, 2006). In North America, Canada, South America, Australia, India, South Africa, parts of western Europe

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https://doi.org/10.1016/j.biocon.2020.108942
Received 2 November 2020; Received in revised form 17 December 2020; Accepted 19 December 2020
Available online 18 January 2021

and New Zealand, carp have caused serious ecological, economic and social amenity issues and are responsible for ongoing ecosystem degradation and serious declines in the geographic range, biodiversity and abundance of native flora and fauna (Parkos et al., 2003; Vilizzi et al., 2015; Crichigno et al., 2016; Macklin et al., 2016; Maceda-Veiga et al., 2017; Bajer et al., 2009, 2018; Dalu et al., 2020).

In Australia, carp are a major environmental threat. Since the late 1960s, the 'Boolarra strain' has invaded the south-east of the continent and parts of Tasmania and Western Australia (Koehn, 2004). Carp occupy most aquatic habitats ranging from estuarine lakes to upland streams (up to 700 m above sea level, ASL; Driver et al., 2005) and densities (i.e. carp density no/ha or biomass density kg/ha) are highly variable among and within habitats (Koehn et al., 2000). In wetlands and lakes, ecological threats occur when carp exceed a 'density-impact' threshold of 80–100 kg/ha (Bajer et al., 2009, 2016; Brown and Gilligan, 2014; Vilizzi et al., 2014). Carp densities in Australia are commonly 200–400 kg/ha and can exceed 1800 kg/ha in some shallow lakes, far surpassing this density-impact threshold (Bajer and Sorensen, 2010; Farrier et al., 2018) and placing further stress on freshwater ecosystems (Koehn, 2004). As such, a major goal to conserve biodiversity is to reduce carp densities to below the 80–100 kg/ha threshold.

At a global or continental scale, few data are available concerning total population size of non-native animals, with notable exceptions for feral pigs and cats in Australia (Hone, 1990; Legge et al., 2017). For carp, population estimates are limited to specific case-study lakes or river reaches and these have not been 'scaled-up' to examine the national situation (Brown and Walker, 2004; Forsyth et al., 2013; Koehn et al., 2018). As a consequence, restoration actions typically occur at local scales, using integrated pest management principles, often involving a combination of conventional carp control techniques (e.g. wetland screens and commercial harvest; Thwaites et al., 2010; Wisniewski et al., 2015; Stuart and Conallin, 2018). As for other countries where carp are non-native, landscape-scale population reduction has been challenging in large connected rivers, wetlands and floodplains and biodiversity declines continue (Vilizzi et al., 2012; Weber et al., 2016; Pearson et al., 2019).

The Australian Federal Government is considering release of cyprinid herpesvirus-3 (CyHV-3) (hereafter 'carp virus'), as a potential landscape-scale biological control agent to reduce carp below density-impact thresholds and assist ecosystem recovery (FRDC, 2018; McColl et al., 2018; McColl and Sunarto, 2020). There are considerable environmental, economic, social and policy concerns associated with the proposed release of this virus, including concerns related to the virus itself, the clean-up of dead fish, conservation of threatened species, impacts on food webs, and on commercial and recreational fishing (Becker et al., 2018; Marshall et al., 2018; Kopf et al., 2019; McGinness et al., 2020). At a continental-scale, a description of the distribution of carp and their biomass density is essential to address these concerns and to support strategic planning. In particular, estimates of carp density (no/ha), biomass density (kg/ha) and geographic distribution are important factors in informing viral epidemiology; predicting expected water quality, environmental and economic impacts; focusing objectives and targets; resourcing viral release and clean-up strategies; and providing a benchmark from which to determine biocontrol effectiveness and biodiversity recovery, over both short and longer-terms.

The challenge in estimating biomass at such a broad-scale is that both aquatic habitat area and carp numbers are spatially and temporally variable, with dramatic population increases following flooding and declines during drought (Koehn et al., 2016). While some population estimates exist for specific sites (usually in lakes), where there are reliable local monitoring data (e.g. Donkers et al., 2012; Bajer and Sorensen, 2015), these are generally at very small scales and not informative for continental-scale control programs. Major challenges also exist for extrapolating population estimates from these studies to larger areas because carp occupy a broad range of aquatic habitats and their density varies considerably among habitat types in response to climatic and flow conditions (Crook and Gillanders, 2006; Stuart and Jones, 2006). Additional issues constraining extrapolation include variation in detectability among habitats (Bayley and Austen, 2002), uneven coverage of existing survey data and sampling methods that vary among projects (Davies et al., 2010).

In this study, we pioneer a novel model-based approach to provide the first continental-scale estimate of carp density (no/ha) and biomass density (kg/ha) across Australia. Our objective was to assemble available studies and data, then develop and apply robust methods to estimate carp abundance and the corresponding biomass for the entire continental area occupied by carp. We provide estimates of carp density and biomass density, based on 24-years of data, for 'average' and 'wet' hydrological scenarios and demonstrate that continental density and biomass vary greatly in time (Appendix A). We recommend ways in which this knowledge can assist conservation management, especially by quantifying aquatic threats and focusing biodiversity restoration efforts to areas where carp can be driven below density-impact thresholds to improve recovery of native fish populations and aquatic ecosystem function (Braysher, 1993).

2. Methods

2.1. Overview of modelling approach for estimating carp biomass

We employed three major approaches for estimating biomass density, depending on the data available: (i) conversion of existing CPUE data to biomass density, (ii) where no CPUE data existed (Western Australia and irrigation channels) we made a separate informal estimate of biomass based on the spatial area occupied by carp, and (iii) a nominal addition of biomass for the state of Tasmania where carp are functionally eradicated. Each method is further detailed below.

To summarise, the following sequence of steps was required to resolve the challenge of up-scaling from local catch-per-unit-effort (CPUE; no/h) datasets to achieve a continental-scale estimate of carp density and biomass density. More details on the methodological framework (Supplementary Table A1) and major assumptions (Supplementary Table A2) are given in Supplementary material Appendix A. Estimating the continental density and biomass of carp was a multi-step process.

(1) Compile a GIS spatial framework to estimate the spatial area of eight major, carp-occupied aquatic habitat types (non-perennial rivers, perennial rivers, waterholes, estuaries, lakes, storages [i.e. impoundments and reservoirs], wetlands, and irrigation channels; Table 1, Supplementary Table A3).
(2) Assemble a comprehensive database of historic and contemporary site-based estimates of relative carp abundance (i.e. electrofishing CPUE, *ef*CPUE) and associated environmental covariates (e.g. depth, turbidity, electrical conductivity) while also supplementing existing *ef*CPUE data with contemporary sampling in data-poor habitat types (Supplementary Table B1).
(3) Develop predictive models for environmental attributes (Supplementary Table A4 and Fig. A1) that influence CPUE and the average mass of individual carp at a site and use these predictive models to assign values of CPUE and average fish mass to all rivers and wetlands.
(4) Conduct a series of field experiments to determine the relationship between CPUE and the true density and biomass density of carp (i.e. both no/ha and kg/ha, respectively), using capture-mark-recapture population estimates and/or wetland drawdowns to determine capture probability in representative habitats throughout eastern Australia (Lyon et al., 2014; Supplementary Table A5). We then used the conversion factors derived from these habitat-specific relationships to reliably link CPUE to biomass density (kg/ha).

Table 1
Total area (km^2) for each carp-occupied aquatic habitat type by Australian state.

Class	Habitat	ACT	NSW	QLD	SA	VIC	WA	TAS	Total
River	Non-perennial	0	1000	33	19	132	11	0	1195
	Perennial	4	692	37	96	232	15	0	1076
	Waterhole	0	49	182	0	0	0	0	231
Waterbody	Estuary	0	219	0	241	133	118	0	711
	Lake	8	3099	423	951	1232	270	50	6033
	Storage	3	763	328	18	781	79	0	1972
	Wetland	0	3998	772	155	968	33	0	5926
Irrigation channels		0	60	1	0	57	2	0	120
Total		14	9880	1776	1480	3535	528	50	17,264

(5) Correct carp density and biomass density for habitat use preferences in lakes and storages,
(6) Model and map the biomass density of juvenile carp (<150 mm Fork Length, FL).
(7) Develop models to calculate biomass density estimates for eight specific habitat types based on CPUE, average individual fish mass, and the habitat-specific conversion factor. Calculate carp biomass estimates for each river/waterbody by multiplying the mapped area by biomass density (kg/ha). Upscale these estimates to generate a total biomass for seven of the eight habitat types (irrigation channels remain as a knowledge gap, see below) and then an estimate for total carp biomass at the Australian continental scale for 'average' and 'wet' hydrological scenarios. The area of aquatic habitat estimated to represent an 'average' hydrological scenario was determined by excluding ephemeral wetlands and lakes and small intermittent streams (stream order <7 with summer 3 months flow <100 ML/d), as agreed by jurisdictional experts (see Todd et al., 2019; for drought and flood scenarios and Appendix A).
(8) Validate these modelled estimates to assess areas of uncertainty, low reliability and model sensitivity, in relation to site-based studies of absolute abundance (e.g. where lakes dried out and total numbers and biomass were determined; Fig. 1).

Due to a lack of CPUE data, aquatic habitats in Western Australia and irrigation channels in all states were excluded from the formal biomass modelling: a separate estimate was made for the spatial area occupied by carp in these situations.

2.2. Estimates for irrigation channels and for aquatic habitats in Western Australia and Tasmania

Irrigation channel networks in south-eastern Australia were mapped using GIS data from water authorities. There were few CPUE records in the carp database from irrigation channels and so this habitat type was removed from the formal modelling process. A coarse estimate of carp biomass was calculated for three biomass densities (50, 150 and 300 kg/ha) based on the limited existing data (Brown et al., 2003). For aquatic habitats in Western Australia, a similar process was followed: river width was predicted from the eastern Australian river width model to calculate total aquatic habitat area although with no separation of habitats, and the three coarse levels of biomass density were also applied. There was no quantification of uncertainty for carp biomass estimates in irrigation channels or Western Australia, but we consider these as negligible sources of error as they comprise only small components of the continental-scale biomass estimate. In Tasmania, carp first invaded lakes Crescent and Sorell in 1995 but are now functionally

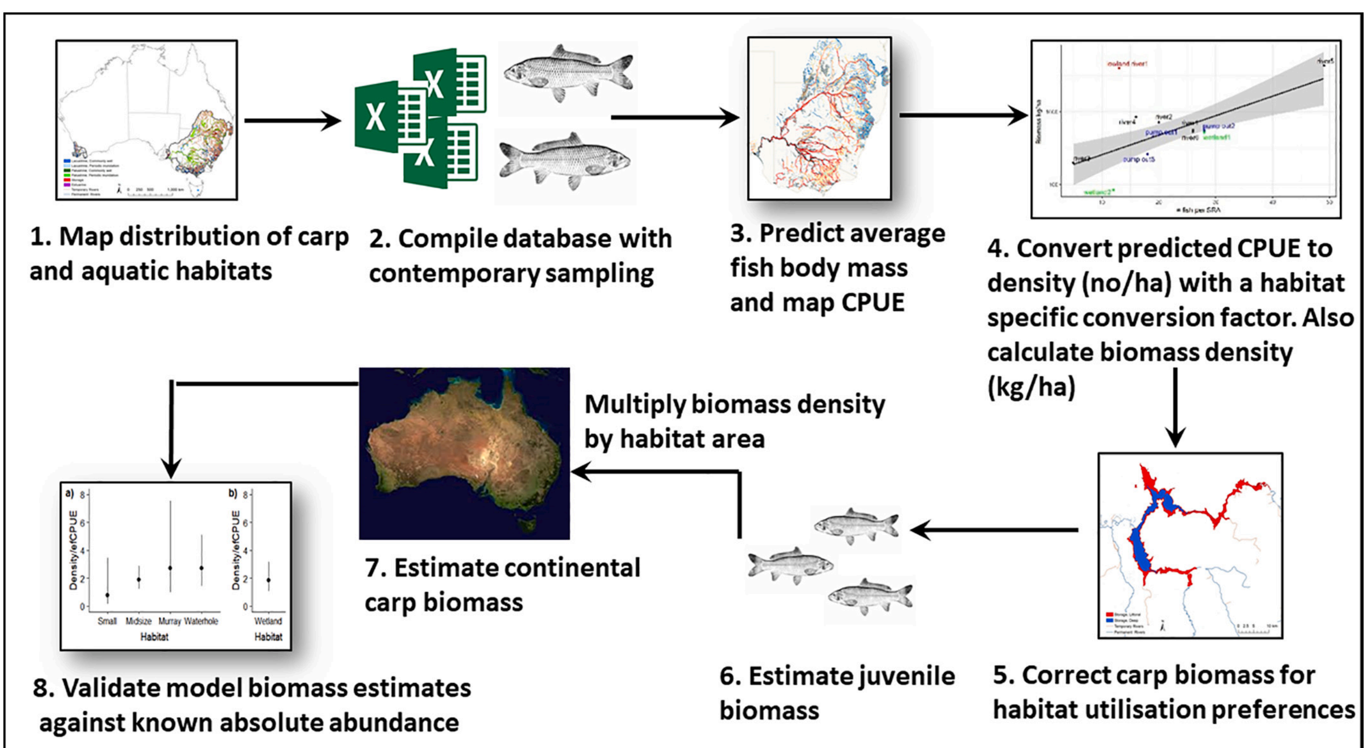

Fig. 1. General framework for estimating the continental biomass of non-native carp.

eradicated and < 20 adult fish are estimated to remain in Lake Sorell. We added an additional 40 kg to the biomass total to represent these fish (Kelly, 2020).

3. Results

3.1. GIS map of carp-occupied habitats

Carp were found in 33 of 191 major river drainages in Australia, spanning 17% of Australia's land mass (1,333,658 km^2) (Fig. 2). From the database, it was apparent that carp have not been recorded in the Northern Territory, sub-tropical/tropical Queensland north of the Brisbane River, and the Lake Eyre Basin. In Western Australia, presence/absence data indicated that carp were largely restricted to urban catchments of Perth. In north-eastern New South Wales (NSW) and eastern Victoria, there were still several major carp-free catchments, such as the Clarence and Snowy rivers, respectively (Supplementary Fig. B7).

Nationally, we estimate that carp occupy 17,264 km^2 of aquatic habitat area primarily in south-eastern Australia. This total includes our modelled estimate of 2502 km^2 of wetted surface area of rivers, 120 km^2 of wetted surface area within irrigation channels, and 14,642 km^2 of standing waterbody and wetland habitat as mapped by state management agencies (Table 1; Supplementary Fig. B1). Standing waterbody habitats (i.e. lakes and wetlands) comprised 85% of the total aquatic habitat area. This area of aquatic habitat was estimated to represent an 'average' hydrological scenario (see Appendix A).

3.2. Carp database and contemporary sampling

Data from 153 research studies were collated, representing an ensemble of 574,145 carp caught at 4831 sites (Fig. 3; Supplementary Table B1). Most data came from the Murray-Darling Basin (MDB) where there was wide spatial coverage across five jurisdictions, from lowland coastal rivers to a maximum altitude of 980 m ASL. Temporally, data were collected between 1994 and 2018, although 72% of studies were after 2010. We carried out additional surveys to augment CPUE information in data-poor habitats identified by jurisdictional experts, including western Victorian rivers, NSW storages, the lower reaches of rivers flowing into the Gippsland lakes, the lower Torrens River and Currency Creek of South Australia, and ephemeral and coastal rivers in Queensland.

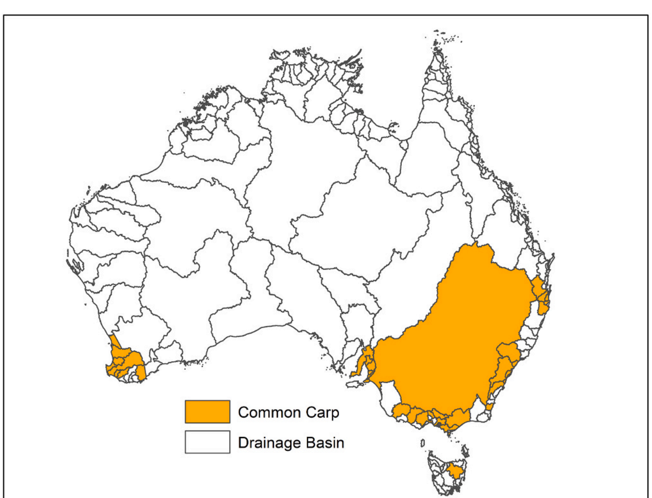

Fig. 2. Geographic range of the non-native common carp, *Cyprinus carpio*, in Australia.

3.3. Map predicted CPUE and the average individual carp mass

Predictive models were used to generate spatial maps of: (a) predicted electrofishing CPUE (*ef*CPUE – no/h) for rivers, and (b) predicted average mass of individual carp (kg) for rivers (Fig. 4). We assessed the model's predictive performance using 10-fold cross validation: the average correlation between predicted and observed data ranged from 0.48–0.65 (S.E. 0.02–0.07) across the models. For *ef*CPUE data, temporal and spatial components were the best predictors (Supplementary Fig. B2). For fish size, the *ef*CPUE was the best predictor as well as annual flow rate. Predicted *ef*CPUE for rivers and waterbodies were highest along the lower Murray, lower Darling and Wimmera rivers. Predicted average mass of individual carp was strongly affected by the presence of recruits, which were more common at lower elevations; hence, the model demonstrated a general increase in individual carp mass at higher altitude river basins and toward the southern extent of their geographic range (Supplementary Fig. B3).

3.4. efCPUE conversion factors

The rates of carp detection using electrofishing (*ef*CPUE) compared with estimated abundance from capture-mark-recapture studies and known abundance from wetland draw-downs, varied from 1% in large perennial rivers to 29% in small wetland habitats. A conversion factor, representing the relationship between carp density (no/ha) and *ef*CPUE (no/h), was determined from the 29 riverine and wetland sites where known abundance data were available. Conversion factors varied among habitats. The lowest was for perennial rivers <50 m width (density/*ef*CPUE ratio = 1.8; 95%Crl: 1.2, 2.7), followed by wetlands (2.7; 95% Crl: 1.6, 4.1), perennial rivers >50 m width (3.3; 95%Crl: 1.3, 8.2), and non-perennial rivers (i.e. waterholes) (4.5; 95%Crl: 2.5, 9.0); but conversion factor estimates had largely overlapping distributions (Supplementary Table B2; Supplementary Fig. B4). Only the conversion factors for non-perennial rivers and small perennial rivers were significantly different (difference log scale = 0.9; 95%Crl: 0.4, 2.1).

3.5. Lake habitat and depth use preferences

For lakes and storages, the CPUE of carp caught from offshore habitats (~200 m from shore) was estimated to decrease by 36.9% (95% credible intervals [95% CI]: 0.5%, 63%) compared to the lake edge habitats (Supplementary Fig. B5). No significant decline was detected for habitats at the intermediate zone (i.e. ~50 m from shore); however, gill net catch rates were very low, contributing to greater uncertainty in these estimates. From these habitat utilisation results and to avoid overestimating carp population abundance within lakes and storages, each lake within the GIS framework was divided into littoral and offshore, using a 200 m boundary at which a ~ 36.9% biomass decrease was applied to the model. There was differential habitat utilisation by carp in deep storages where fish showed a strong preference for relatively shallow water and CPUE declined by 61.9% (95% Credible Intervals [Crl]: −22.5%, 94.2%) between the 2 m and 6 m depth zones. At 12 m depth there was an even greater decline of 81.9% (95%Crl: 30.6%, 98.5%) and nets at 24 m depth collected no carp, resulting in an estimated decline of 99.86% (95%Crl: 99.82%, 100%).

3.6. Juvenile biomass

Juvenile biomass rates (i.e. juvenile biomass per *ef*CPUE) were highest for lowland rivers and were higher in specific time periods, such as 2011 and 2016–2017, usually in April, which coincided with the period immediately following major flood events (Fig. 5). For waterbodies, storages had the lowest juvenile biomass rate (log difference = -1.6 ± 0.5) and waterholes had the highest rates (log difference = 1.2 ± 0.2; Supplementary Fig. B6). For assessing model fit, we performed a 10-fold cross-validation and the correlation was 0.59 ± 0.05, indicating

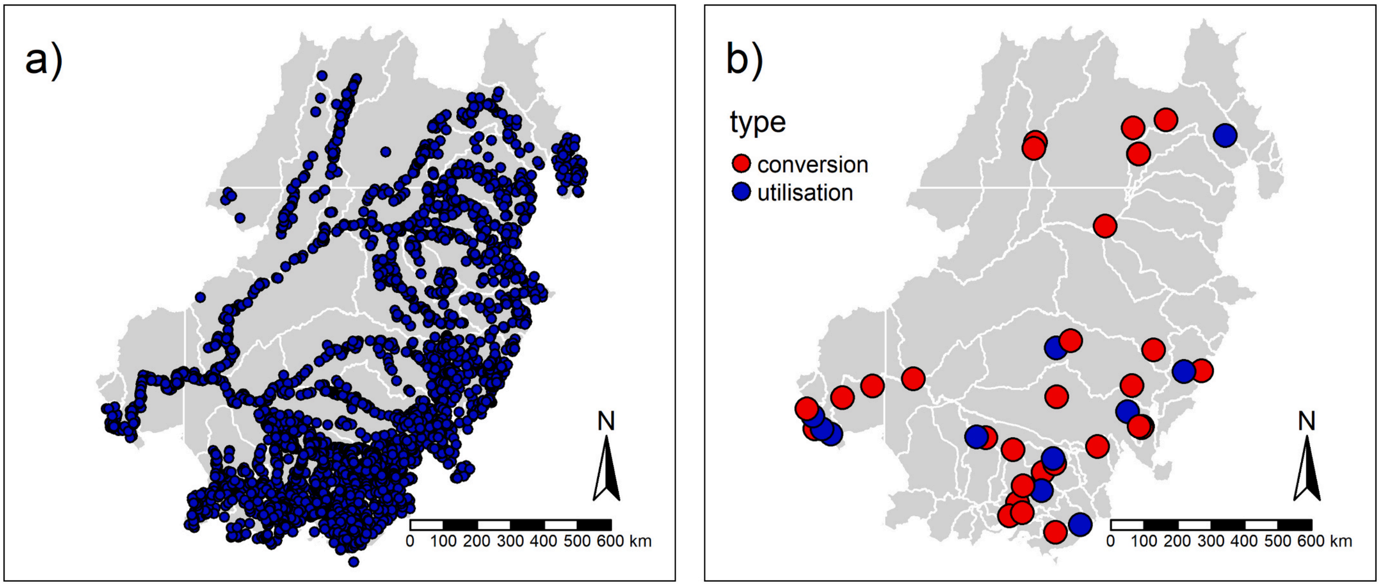

Fig. 3. Eastern Australia showing (a) existing carp CPUE data and (b) sites used for conversion (red dots) and habitat utilisation (blue dots) experiments. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

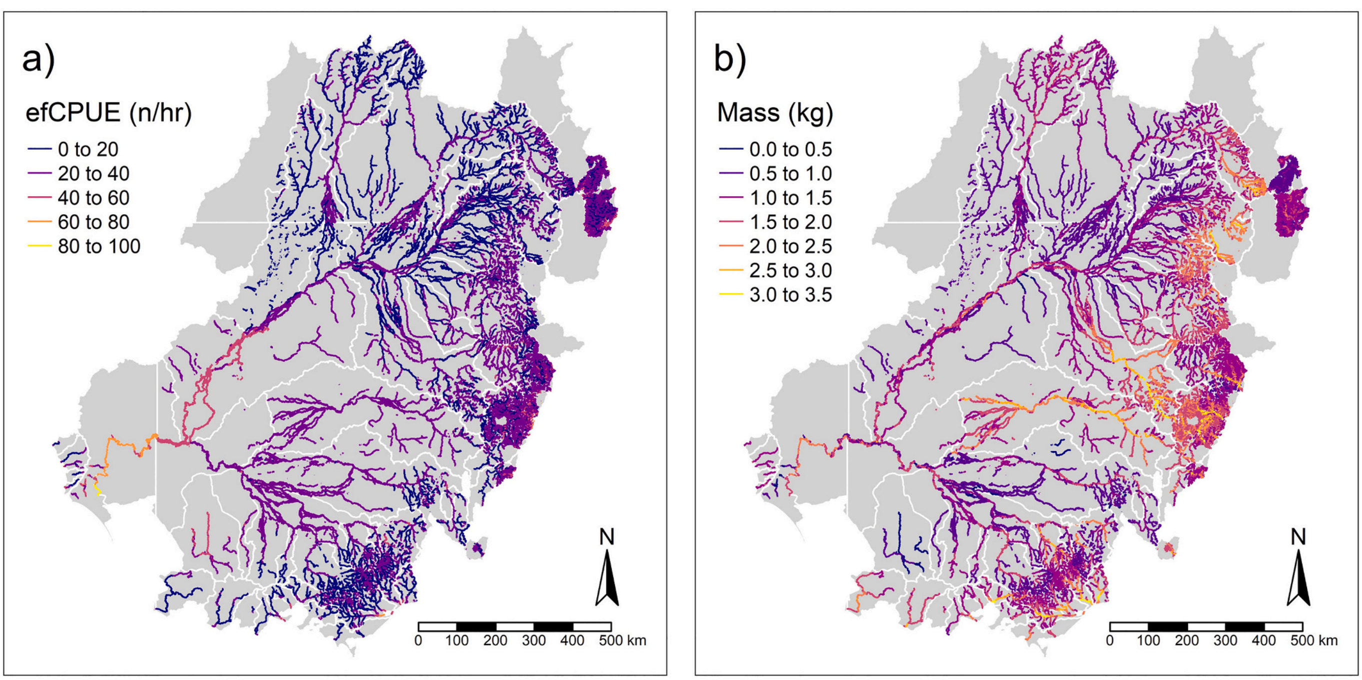

Fig. 4. Maps of (a) predicted electrofishing CPUE (*ef*CPUE) for rivers and (b) predicted average mass (kg) of individual carp for rivers across eastern Australia.

moderate to good fit for the model.

3.7. Continental carp numbers and biomass estimate

Scaling-up for each habitat type, the model estimated carp numbers as fluctuating between 199,200,000 (95%CrI: 106,000,000 to 357,500,000) for an 'average' hydrological scenario and 357,600,000 (95%CrI: 178,900,000 to 685,100,000) for a 'wet' hydrological scenario (i.e. adding an additional area of ephemeral floodplain lakes and wetlands; see Appendix A). Carp biomass was 205,774 t (95%CrI: 117,532–356,482 t) for the average hydrological scenario and 368,357 t (95%CrI: 184,234–705,630 t) for a wet hydrological scenario. During an 'average' hydrological scenario, standing water bodies, dominated by lakes and wetlands, had the highest total biomass of 162,838 t (95%CrI: 79,621–307,561 t) (Table 2). Eastern Australia accounted for ~96% of total biomass density.

Perennial lowland rivers had the highest CPUE, and greatest biomass density estimates (e.g. up to 826 kg/ha; Fig. 6) occurred along the mid and lower reaches of the lower Murray, Darling and Wimmera rivers. By contrast, the upper reaches of perennial rivers, such as the Lachlan River (NSW), generally had lower carp densities (no/ha) but because these were relatively large fish in comparatively smaller aquatic areas, the biomass density (kg/ha) and overall biomass could still be high. In eastern Australia, modelled carp biomass exceeded the density-impact threshold of 80–100 kg/ha in 54% of wetlands, 70% of stream area for all rivers, and 97% of stream area in large lowland rivers (>40 m

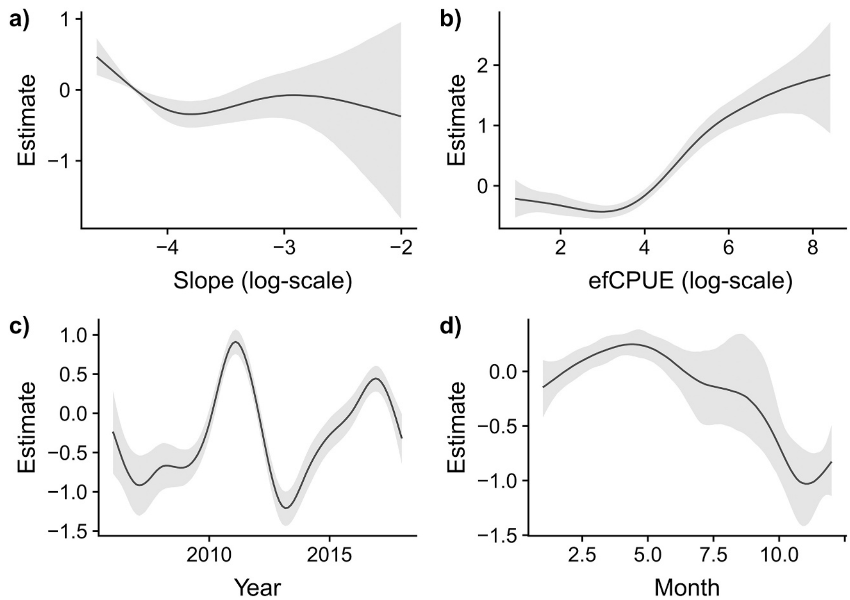

Fig. 5. Effect of stream slope, survey *ef*CPUE, year, and month on juvenile carp biomass rate (i.e. juvenile biomass per *ef*CPUE) demonstrating highest biomass rates associated with lowland rivers, immediately following flooding (i.e. 2011 and 2016–2017), usually in April (Austral autumn). Each panel shows the fitted relationship with 95%Crl and standardised by the mean.

Table 2
Modelled estimates of carp biomass density (kg/ha) by aquatic habitat types in eastern Australia during an 'average' hydrological scenario. Note that total estimates for the eastern Australia model will not be the simple addition of each component as the biomass estimates are means and the distributions are asymmetric (95%Crl in parentheses). Irrigation channels and aquatic habitats in Western Australia are coarse estimates and thus 95%Crl was not included.

Method	Habitat	Habitat class	Biomass (tonnes)
Eastern Australia	River	Non-perennial	13,975 (7383-25,009)
		Perennial	23,251 (10,836-48,403)
		Waterhole	5709 (2382-12,241)
		Total	42,936 (23,055-77,769)
	Waterbody	Estuary	10,267 (3849-24,049)
		Lake	72,232 (36,860-134,134)
		Storage	18,825 (8795-39,155)
		Wetland	61,512 (25,474-125,550)
		Total	162,838 (79,621-307,561)
	River + waterbody		205,774 (117532–356,482)
Irrigation channels	Irrigation channels		1755
Western Australia	Rivers and wetlands		7927
Tasmania	Tasmania (Lake Sorell)		0.04
Total			215,456

wide).

Some coastal rivers, such as the Glenelg River (Victoria), had a relatively low (42 kg/ha) average biomass density. Juvenile biomass was highest for waterholes, perennial and non-perennial lowland rivers and wetlands. Riverine adult and juvenile biomass were higher in the lowlands, especially in autumn after the breeding period. Spikes in biomass followed major flooding in 2010–2011 and 2016–2017. Storages had the lowest juvenile biomass (Supplementary Fig. B6).

3.8. Model validation

To validate the modelled estimates and to identify areas of uncertainty, low reliability and model sensitivity, we compared modelled estimates of absolute biomass to nine site-based studies of absolute abundance obtained from wetland/lake drying events and mark-recapture studies where total biomass was determined (Fig. 7). Overall, 50% of the 95%Crl intervals from modelled estimates contained the absolute biomass. The greatest discrepancies were for a large lake system in the lower Murray (lower lakes, South Australia) and in the Lachlan system of western NSW (Lake Brewster). In both cases the biomass model predicted a higher biomass density: for the lower Murray (350 kg/ha) compared with that extrapolated from a mark-recapture study (20 kg/ha; Koehn et al., 2018); and for Lake Brewster (160 kg/ha) compared with a commercial harvest of 23 t from a remnant wetland pool when extrapolated to the whole lake area (4 kg/ha; Keith Bell, K&C Global Fisheries, pers. com.). These low 'actual' biomass densities are likely severe underestimates because the lower lakes support a commercial fishery (Earl, 2019) and at Lake Brewster many carp from isolated waterholes were not collected. Hence, our higher modelled estimates are likely more realistic for these habitats.

3.9. Irrigation channels, Western Australia and Tasmania

Irrigation channels, and aquatic habitats in Western Australia and Tasmania were not included in the modelled biomass estimates. Instead, for irrigation channels we estimated a total area of 117 km^2 and a carp biomass of 585, 1755 and 3570 t for low (50 kg/ha), medium (150 kg/ha) and high (300 kg/ha) biomass densities, respectively. For Western Australia, the total area occupied by carp was 528 km^2 and the same low, medium and high absolute biomass estimates were 2643, 7927 and

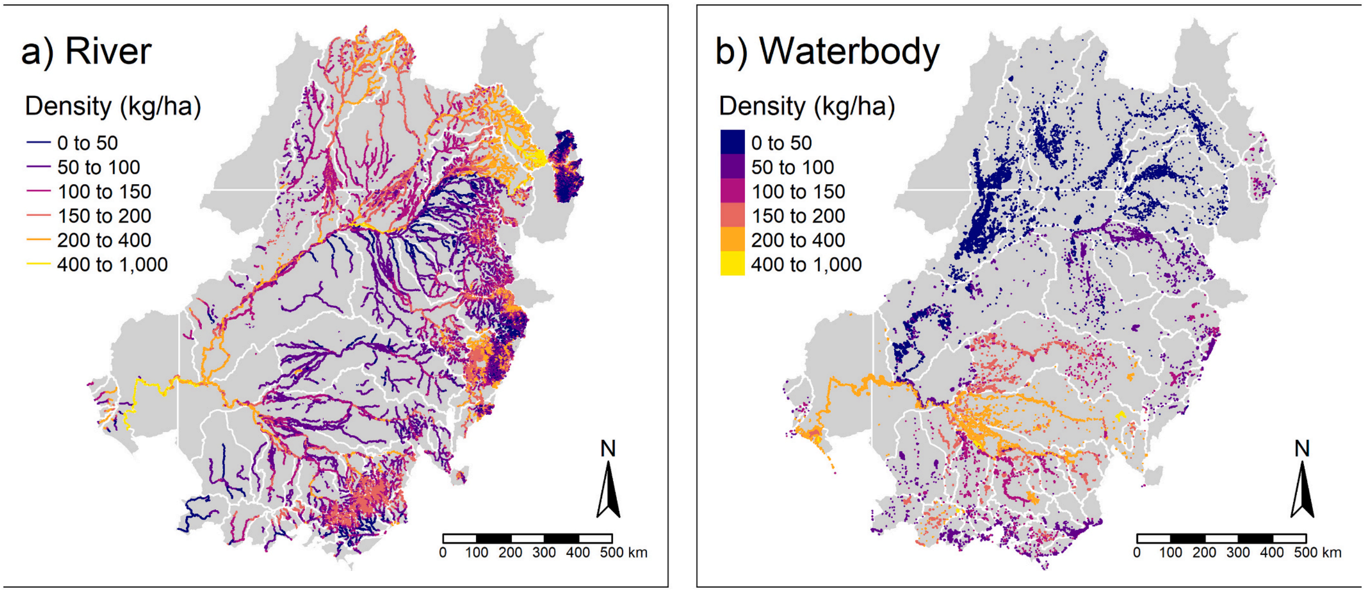

Fig. 6. Maps of modelled estimates of carp biomass density (kg/ha) for eastern Australia for a) river systems, and b) standing waterbodies.

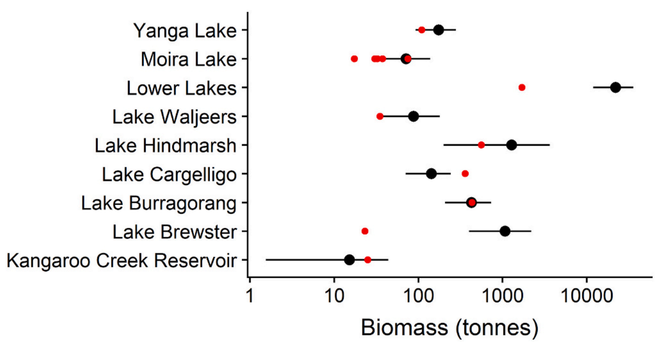

Fig. 7. Comparison of modelled estimates of carp biomass and observed absolute biomass for nine lake/wetland habitats. Black points and lines show the mean and 95%CrI for modelled biomass and red dots are absolute biomass. For Moira Lake, there were multiple years of records. Note that the x-axis is log-scaled so that all examples could be shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

15,855 t, respectively. In terms of the estimate for total continental biomass, we added the middle density (150 kg/ha) scenario for irrigation channels and Western Australia. In Tasmania, there are an estimated <20 adult fish (i.e. <40 kg total weight), which was added to the national biomass estimate.

4. Discussion

4.1. Continental carp biomass

In the 45 years since the 'Boolarra' strain of carp first arrived in Australia (Shearer and Mulley, 1978), they have invaded a broad geographic range and threaten ecosystem function in all major aquatic habitats. The epicentre of their invasion and current biodiversity threat is in south-eastern Australia where they now inhabit approximately 16,686 km^2 of aquatic habitat including 92% of aquatic environments in the Murray-Darling and South-East Coast drainage divisions. We estimated a continental carp abundance of 199.2 M (95%CrI: 106–357.6 M) and biomass of 215,456 t (95%CrI: 117,532–356,482 t) during an 'average' hydrological scenario, with even greater numbers during a 'wet' hydrological scenario when juveniles (<150 mm long) are more abundant. Our estimate of the continental distribution of carp provides an integrated national picture of carp populations, with eastern Australia accounting for ~96% of total biomass (205,774 t). Not surprisingly, the precision of these continental estimates is broad, as reflected in the Bayesian credible intervals. Hence, the upper and lower bounds of these estimates should be included as a critical part of planning for conservation actions, noting that the ends of the 95% credible intervals are the most unstable (Hone and Buckmaster, 2015).

We found major differences in relative carp abundance among habitat types, with a higher predicted biomass in perennial rivers and wetlands compared to water storages, where littoral zones are generally narrower and the water cooler. Spatially, there were carp 'hotspots' (i.e. where biomass density was >500 kg/ha), such as the lowland reaches of large rivers. Regulated, slow-flowing lowland rivers and adjacent permanent and semi-permanent wetlands are habitats for carp spawning and recruitment (Stuart and Jones, 2006) and the relatively high predicted biomass was likely driven by both adult and juvenile carp (Conallin et al., 2012, 2016; Koehn et al., 2016, 2018). Analogous high-density carp populations, with their attendant biodiversity losses, occur in similar slow-flowing weir pools with permanent adjacent lakes and wetlands in North and South America (Penne and Pierce, 2008; Maiztegui et al., 2019), and parts of Europe (Maceda-Veiga et al., 2017).

Once carp exceed a density-impact threshold of 80–100 kg/ha, recognised globally as causing ecological harm in wetlands and lakes, impacts include: increased water turbidity; and declines in aquatic vegetation, invertebrates and native fish (Miller and Crowl, 2006; Badiou and Goldsborough, 2014; Bayer et al., 2009; Vilizzi et al., 2015; Dalu et al., 2020). Our modelled estimates indicate that this density-impact threshold is exceeded in 54% of wetlands, 70% of stream area for all rivers, and 97% of stream area in large rivers (>40 m wide). Hence, carp continue to degrade and threaten ecosystem function across a majority of aquatic habitats in eastern Australia.

Our site-specific estimates of biomass density and associated credible intervals are broadly similar to previous studies in Australia (150–690 kg/ha; Hume et al., 1983; Fletcher et al., 1985), and those reported globally, including from Canada (490–1830 kg/ha; Barton et al., 2000), USA (105–2409 kg/ha; Farrier et al., 2018), and New Zealand (40–325 kg/ha for Koi carp; Hicks et al., 2015). Presentation of relative abundance estimates as 'heat' maps provides a spatial hierarchy of biomass density estimates that managers can use to identify 'hotspots' (e.g.

>500 kg/ha) and also low-density areas (e.g. <100 kg/ha) where carp could be maintained below density-impact thresholds for ecosystem recovery.

Carp are often regarded as having a cosmopolitan distribution but, in reality, many aquatic habitats and vast areas of the Australian continent remain uninvaded. This includes the Northern Territory, tropical/sub-tropical Queensland, the Lake Eyre Basin, and much of Western Australia where they are largely restricted to urban catchments in Perth. In north-eastern NSW and eastern Victoria, there were several major carp-free catchments, such as the Clarence and Snowy rivers, respectively. By contrast, carp have established bridgeheads into some high-altitude rivers and lakes, such as montane areas of the upper Murrumbidgee River (980 m ASL; Miles, 2012) and Lake Sorell in Tasmania (804 m ASL; Wisniewski et al., 2015). Carp have also formed permanent populations in other physiologically challenging habitats, such as the lower reaches of rivers, estuaries (i.e. 1 m ASL) and saline wetlands where maximum salinity can approach half that of seawater (17,500 mg L^{-1}; Whiterod and Walker, 2006). Hence, from a continental perspective, the spatial distribution of carp is still 'patchy' and likely related to factors such as an uneven human-assisted spread and differing biological and environmental interactions in receiving habitats (Petrovskaya et al., 2017). To optimise biodiversity recovery strategies, increased efforts to protect the remaining carp-free systems are required along with expanded mapping of population density and a closer examination of the factors that lead carp to cause biodiversity losses in some habitats but not others (Bajer et al., 2019; Poole and Bajer, 2019).

4.2. Reliability of the continental biomass estimate

There are several inherent assumptions, limitations, and uncertainties when predicting continental carp biomass for which further refinement of methods and data could increase accuracy (Pearson et al., 2019). These refinements include: (i) increasing the quality of the spatial data for carp occurrence and CPUE, especially for estuaries, irrigation channels and non-perennial rivers; (ii) undertaking additional site-based estimates of detectability and total abundance (and thus generating more precise conversion factors) (Lyon et al., 2014), particularly for aquatic habitats with limited data such as storages, large fast-flowing rivers, remote wetlands, irrigation channels, farm dams and estuaries; and (iii) further validation of modelled estimates of carp biomass with data on total abundance and mass from a larger number of wetland/lake draining events. Juvenile (<150 mm FL) biomass was likely under-estimated because there was no information on capture probability and smaller fish have a lower detection probability (Dolan and Miranda, 2003; Feeken et al., 2019).

Understanding the sensitivity of each component of these estimates of carp density and biomass density may provide further insights into the accuracy of the model. We chose not to test model sensitivity for two main reasons. First, there was considerable variation in the estimates at the individual river segment or waterbody polygon scale, as indicated by the large credible intervals. Therefore, the model and its outputs already incorporate substantial uncertainty. Second, the spatial map of aquatic habitats strongly affects the biomass estimate and for tractability we assumed a 'known' spatial scenario. In reality, this spatial layer is highly dynamic and there are large uncertainties with regard to actual water-body area and river widths. This underscores an opportunity to improve model performance by further refining the spatial mapping and CPUE data to reduce uncertainty. Nevertheless, the modelled estimates of carp density and biomass were realistic when compared to the known absolute abundance of carp in several wetlands and lakes. For managers involved in conserving biodiversity, we are confident that the models provide a strong baseline for actions but suggest planning for uncertainty by preparing for biomass at the upper confidence intervals of our estimates.

4.3. Future directions

The continental estimates of carp biomass presented in this study are for two hydrological scenarios, based on 24-years of survey data which were collected when populations fluctuated between maximum and minimum densities following flood and droughts (Koehn et al., 2016). For our biomass estimates, the underlying CPUE and models of individual carp mass had a temporal component but only in the sense that they described an historical trend with no antecedent hydrological conditions or population processes explicitly incorporated into the model. Hence, the continental estimate of biomass will vary greatly between years and so should be used cautiously (Hone and Buckmaster, 2015). We suggest that the development and use of a dynamic population model (Koehn et al., 2018; Todd et al., 2019) would enable modelling for a series of hydrological scenarios, and potentially identify circumstances where carp exert their greatest ecological pressure.

The methods developed here to estimate the continental biomass of carp were for a single taxon but could be applied to other non-native or native species to enhance the evidence base needed to effectively limit further biodiversity losses. Continental-scale biomass models may also be useful for managing non-native carp in North America (Gibson-Reinemer et al., 2017), and Koi carp in New Zealand (Champion, 2018). A similar approach could be used to provide population estimates of native fish of high conservation value, such as riverine populations of endangered Murray cod (*Maccullochella peelii*), especially where there are existing detection efficiencies and conversion factors (Lyon et al., 2014), from which the success of restoration programs could be measured.

5. Conclusions

This study provides a first quantitative understanding of the location and magnitude of carp populations across the Australian continent at a range of scales. Our estimates highlight the spatial extent to which this non-native species represents a profound threat to diverse ecosystems across vast areas of Australia's aquatic environment. Major detrimental impacts have already occurred, with carp biomass densities (kg/ha) exceeding the density-impact threshold in 54% of wetlands and 97% of stream area in large lowland rivers. These estimates of total continental biomass and its spatial variation provide an important baseline that will assist conservation managers to spatially prioritise areas for action, evaluate implications for biocontrol, and develop plans for more effectively reducing carp and their ecosystem impacts. To highlight future global directions for managing ecosystem threats, the continental-scale carp population estimate provides a baseline from which to: (i) focus national conservation strategies to reduce carp populations below thresholds needed to restore aquatic ecosystems at local and regional scales; (ii) help set appropriate national and local conservation targets; and (iii) track ecosystem recovery (Doherty et al., 2019).

Role of the funding sources

The sponsors of this study have had no influence on the interpretation of data; in the writing of the manuscript; or in the decision to submit the paper for publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This project was funded by the Fisheries Research & Development Corporation (Project 2016-153). Our grateful thanks to Matt Barwick, Jennifer Marshall, Toby Piddocke and Jamie Allnutt (FRDC) for their support. For field contributions we thank: Graeme Hackett, Peter Fairbrother, Matt Jones, Andrew Pickworth and Kim Loeun (Arthur Rylah Institute), Michael Rodgers, Patrick Martin, Luke van Lawick and Dylan van der Meulen (NSW DPI), Neil Wellman, George Giatas, Luciana Bucater, David Short and David Schmarr (SARDI), David Nixon, Rod Cheetham, Keith Chilcott (QDAF) and Jonathan Marshall (DES), and Mark Jekabsons, Zohara Lucas and Josh Van Lier (ACT EPSDD). We thank the many state agency researchers and private consulting firms who contributed data, including Clayton Sharpe (CPS Enviro), Dion Iervasi (Austral Research and Consulting) and Joe Pera (WaterNSW). For helpful discussions on the presence/absence of carp in Western Australia and Tasmania, we thank Steve Beatty and John Diggle, respectively. Thanks also to commercial fishers, Keith Bell (K&C Fisheries Global) and Gary Warwick for contributions. We are grateful to Andrew Boulton, Dave Ramsey and Tracey Reagan for valuable comments on a draft of the manuscript. Production of this paper was supported by the Applied Aquatic Ecology writing retreat initiative. This project was completed under Victorian Fisheries Permits RP827, RP1196 and ARI animal ethics permit AEC 17-010; NSW Fisheries and Animal Care and Ethics Permits ACEC 17/05 and P01/0059(A)-4.0Permit F93/158(C)-9.0; South Australian Fisheries Management Act 2007: Section 115, Ministerial Exemption ME9903001; Qld General Fisheries Permit 186281, Qld Animal Ethics Permit CA2017/09/1106, and ACT EPSDD Ethics permit CEAE 13-18.

Appendix A. Supplementary methods and results

Supplementary methods and results to this article can be found online at https://doi.org/10.1016/j.biocon.2020.108942.

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