

A compendium of ecological knowledge for restoration of freshwater fishes in Australia's Murray–Darling Basin

John D. Koehn^{id A,B,T}, Scott M. Raymond^A, Ivor Stuart^A, Charles R. Todd^{id A}, Stephen R. Balcombe^C, Brenton P. Zampatti^{D,R}, Heleena Bamford^{E,S}, Brett A. Ingram^{id F}, Christopher M. Bice^{D,G}, Kate Burndred^H, Gavin Butler^I, Lee Baumgartner^B, Pam Clunie^A, Iain Ellis^J, Jamin P. Forbes^B, Michael Hutchison^K, Wayne M. Koster^{id A}, Mark Lintermans^L, Jarod P. Lyon^A, Martin Mallen-Cooper^M, Matthew McLellan^N, Luke Pearce^O, Jordi Ryall^A, Clayton Sharpe^P, Daniel J. Stoessel^{id A}, Jason D. Thiem^N, Zeb Tonkin^A, Anthony Townsend^Q and Qifeng Ye^D

^AApplied Aquatic Ecology, Arthur Rylah Institute for Environmental Research, Department of Environment, Land, Water and Planning, 123 Brown Street, Heidelberg, Vic. 3084, Australia.

^BInstitute for Land, Water and Society, Charles Sturt University, PO Box 789, Albury, NSW 2640, Australia.

^CAustralian Rivers Institute, Griffith University, 170 Kessels Road, Nathan, Qld 4111, Australia.

^DInland Waters and Catchment Ecology Program, South Australian Research and Development Institute, Aquatic Sciences, PO Box 120, Henley Beach, SA 5022, Australia.

^EEnvironmental Watering Plan Implementation, Murray–Darling Basin Authority, GPO Box 1801, Canberra, ACT 2601, Australia.

^FVictorian Fisheries Authority, Private Bag 20, Alexandra, Vic. 3714, Australia.

^GSchool of Biological Sciences, The University of Adelaide, Adelaide, SA 5005, Australia.

^HLand and Water Science, Department of Natural Resources, Mines and Energy, Level 1, 44 Nelson Street, Mackay, Qld 4740, Australia.

^INSW Department of Primary Industries, Fisheries, Grafton Fisheries Centre, Private Mail Bag 2, Grafton, NSW 2460, Australia.

^JMurray–Darling Unit, NSW Department of Primary Industries, Fisheries, 32 Enterprise Way, Buronga, NSW 2739, Australia.

^KBribie Island Research Centre, Department of Agriculture and Fisheries, PO Box 2066, Woorim, Qld 4507, Australia.

^LCentre for Applied Water Science, Institute for Applied Ecology, University of Canberra, Canberra, ACT 2601, Australia.

^MFishway Consulting Services, 8 Tudor Place, Saint Ives Chase, NSW 2075, Australia.

^NNSW Department of Primary Industries, Fisheries, Narrandera Fisheries Centre, PO Box 182, Narrandera, NSW 2700 Australia.

^OAquatic Ecosystems, NSW Department of Primary Industries, Unit 5, 620 Macauley Street, Albury, NSW 2640, Australia.

^PNSW Water & Wetlands Conservation Branch, National Parks and Wildlife Service, PO Box 363, Buronga, NSW 2730, Australia.

^QMurray–Darling Unit, NSW Department of Primary Industries, Fisheries, 4 Marsden Park Road, Calala, NSW 2340, Australia.

^RPresent address: CSIRO – Land and Water, Locked Bag 2, Glen Osmond, SA 5064, Australia.

^SPresent address: Murray–Darling Unit, NSW Department of Primary Industries, Fisheries, TAFE Building, K Block, New England Institute, 116 Allingham Street, Armidale, NSW 2350, Australia.

^TCorresponding author. Email: john.koehn@delwp.vic.gov.au

Abstract. Many freshwater fishes are imperilled globally, and there is a need for easily accessible, contemporary ecological knowledge to guide management. This compendium contains knowledge collated from over 600 publications and 27 expert workshops to support the restoration of 9 priority native freshwater fish species, representative of the range of life-history strategies and values in south-eastern Australia's Murray–Darling Basin. To help prioritise future research investment and restoration actions, ecological knowledge and threats were assessed for each species and life stage. There is considerable new knowledge (80% of publications used were from the past 20 years), but this varied among species and life stages, with most known about adults, then egg, juvenile and larval stages (in that order). The biggest knowledge gaps concerned early life stage requirements, survival, recruitment, growth rates, condition and movements. Key threats include reduced longitudinal and lateral connectivity, altered flows, loss of refugia, reductions in both flowing (lotic) and slackwater riverine habitats, degradation of wetland habitats, alien species interactions and loss of aquatic vegetation. Examples and case studies illustrating the application of this knowledge to underpin effective restoration management are provided. This extensive ecological evidence base for multiple species is presented in a tabular format to assist a range of readers.

Keywords: Australia, environmental flows, functional traits, knowledge transfer, native freshwater fish, rehabilitation.

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Introduction

Globally, freshwater biota and their ecosystems are under severe threat and in need of conservation and restoration (Dudgeon *et al.* 2006; Flitcroft *et al.* 2019). Although the threats to freshwater fishes and their habitats have been extensively documented (e.g. Cadwallader 1978; Malmqvist and Rundle 2002; Koehn and Lintermans 2012), there is often limited understanding or an unconsolidated knowledge base for the biology and ecology of many species (Cooke *et al.* 2012). Furthermore, natural resource management should be guided by cohesive, contemporary science (Ryder *et al.* 2010), but incorporating ecological knowledge into practical management strategies, and thus investment and action plans, remains a challenge. This can be due to several factors, including scientific knowledge quickly being superseded (Stoffels *et al.* 2018) and managers considering scientific literature time consuming to read and complex to interpret (Pullin *et al.* 2004). In addition, the time between undertaking research and the publication of findings can be considerable, meaning that results are often unavailable to managers within appropriate time frames or are in difficult-to-access reports. Furthermore, assessment of management interventions can require studies that span many years, which can delay the uptake of promising approaches. Much research is also confined to a single species or site, resulting in disparate knowledge sources with findings that may not be transferable system wide, or applicable to multispecies or multisite management efforts. Therefore, there is a need to consolidate the outcomes of research (Cooke *et al.* 2017) and to improve knowledge transfer between researchers and managers (Cvitanovic *et al.* 2015).

Conceptual models can be useful for synthesising and explicitly defining ecological relationships and responses, and are particularly needed for guiding water management (Likens *et al.* 2009; Poff and Zimmerman 2010). Internationally, effective management of riverine ecosystems and the species they support is often compromised by poor coordination of science and management efforts. There are rarely efforts to collate and compile research findings across multiple researchers for the benefit of multiple users (Counihan *et al.* 2018). Summarising

such research outcomes into a single publication can provide a useful resource for decision makers.

Large river ecosystems are heavily affected by the cumulative and potentially synergistic effects of multiple stressors (Tockner *et al.* 2010), but research and monitoring programs are often designed to investigate only single stressors or impacts. Consequently, although such datasets may contribute to the overall body of knowledge, they may not be fit for purpose in terms of being comprehensive, scalable or transferable to other restoration programs. Efforts to combine such datasets and knowledge have been successful in the US (Ward *et al.* 2017; Counihan *et al.* 2018) and Europe (Catalán *et al.* 2019), but there have been no recent similar peer-reviewed publications that consolidate existing data or contemporary knowledge for inland fishes in Australia (but see Pusey *et al.* 2004) to directly assist current management.

Australia's Murray–Darling has been listed among the world's top 10 river systems at environmental risk (Wong *et al.* 2007), with the Murray–Darling Basin (MDB) being one of the most regulated river basins (Nilsson *et al.* 2005). Only 40–50% of the MDB's main stem rivers remain free flowing (Liermann *et al.* 2012; Grill *et al.* 2015, 2019), and many of those have their hydrology altered to some degree by regulation or extraction. The MDB covers $>1 \times 10^6$ km², involves six jurisdictions and is known as 'Australia's food bowl' (Koehn 2015). Its rivers and catchments are now mostly in poor ecological condition (Davies *et al.* 2008, 2010, 2012). Long-held concerns continue regarding the overallocation of water, flow regulation and environmental damage (Walker *et al.* 1995; Kingsford 2000; Lester *et al.* 2011). End-of-system flows are now zero for 40% of the time, compared with 1% of the time under natural flow conditions (CSIRO 2008), and extensive river reaches have been converted from lotic (flowing water) to lentic (still water) environments by weirs and reduced flows (Maheshwari *et al.* 1995; Mallen-Cooper and Zampatti 2018). The effects of these anthropogenic flow alterations were worsened during the Millennium Drought (1997–2010; Murphy and Timbal 2008; van Dijk *et al.* 2013), further affecting environmental assets (Kingsford *et al.* 2011). Of considerable concern

are predictions that indicate climate change will exacerbate such climatic extremes, affecting not only river flows (CSIRO 2008; Fiddes and Timbal 2017), but also fishes and their habitats (Balcombe *et al.* 2011; Morrongiello *et al.* 2011). Indeed, severe drought conditions, large-scale fish kills and bushfires during late 2019 and early 2020 have further heightened these concerns (Vertessy *et al.* 2019; Legge *et al.* 2020).

However, flow alteration is only one of the many threats to MDB fishes. Of additional concern are barriers to movements (4000 major barriers in the MDB; Baumgartner *et al.* 2014b), interactions with alien species, habitat loss and alteration, cold-water pollution, fish kills and commercial (past) and recreational fishing, all of which have heavily affected populations (Koehn and Lintermans 2012). MDB fish populations have suffered substantial declines, with almost half the species now being listed as threatened under state or national legislation (Lintermans 2007; Table 1). Consequently, remediation of these threats has been identified as being necessary for the recovery of MDB fishes (Koehn *et al.* 2014b; Baumgartner *et al.* 2020), and this resulted in the development of a comprehensive restoration program (the Native Fish Strategy; Barrett 2004; Murray–Darling Basin Commission 2004; Koehn and Lintermans 2012; Koehn *et al.* 2019b) which has recently been revised to The Native Fish Recovery Strategy (Murray–Darling Basin Authority 2020). In addition, the Murray–Darling Basin Plan (Murray–Darling Basin Authority 2011) has the objective of improving flows through increased delivery of water for the environment (Hart 2016a, 2016b; Stewardson and Guarino 2018). Both restoration programs recognise the requirement for policy setting and decision making to have a strong scientific foundation and to be guided by contemporary knowledge (Murray–Darling Basin Commission 2004; Swirepik *et al.* 2016).

A key purpose of such restoration programs is to consider the ecological requirements of the fishes affected by human-induced ecosystem alterations (Cooke *et al.* 2012; Baumgartner *et al.* 2020). Water for the environment can be used to re-establish critical components of flow regimes to benefit biota (Bunn and Arthington 2002), but ideally this would be based on detailed knowledge of flow–ecology relationships (Davies *et al.* 2014). Such ecological knowledge is not always readily available or reported in a consistent manner that is useful to management, particularly for all species and their various life stages. This rapidly developing sphere of water management (Arthington 2012) requires a range of data sources and knowledge to guide decision making (King and Louw 1998). Considerable knowledge gaps remain regarding both fundamental and applied ecology that could hinder restoration for many MDB species (Stoffels *et al.* 2018; Koehn *et al.* 2019a), and the need for access to the most up-to-date knowledge to support restorative management for native fishes has driven the creation of this knowledge compendium.

Through this compendium, we aim to at least partially address the overall need for knowledge for nine priority MDB freshwater fish species. The species were chosen in conjunction with national (Murray–Darling Basin Authority) and state fish and water management agencies to meet their priorities and to represent both large- and small-bodied species across a range of habitats, life-history types and public values (biodiversity, conservation, cultural, recreational; Koehn *et al.* 2019a).

We collated information from a wide range of scientific journals, reports and studies, incorporated knowledge provided by experts through workshops and organised the currently available key conceptual and empirical ecological knowledge to provide easy access. Knowledge categories were chosen to support the rebuilding of fish populations through environmental flow and complementary restoration programs. Assessments of the impacts of threats and the status of our current knowledge of the various ecological components were made to guide management priorities and future research directions and investment. This compendium will be of value to a diverse audience, including researchers, students, policy makers and water and other natural resources managers, and it contains case studies to illustrate how the compiled scientific information can be used to better inform management (Fig. 1).

Materials and methods

The MDB

The MDB covers 14% of Australia's land area and is a predominantly semi-arid environment, with the Darling River (2740 km long) system in the north, largely fed by semi-monsoonal summer rainfall, and the Murray River (2530 km long) system in the south, fed by winter and spring rainfall (Fig. 2; see Mackay and Eastburn 1990; Breckwoldt *et al.* 2004). Hence, the MDB is often classified into southern (SMDB) and northern (NMDB) components. There are considerable spatial and temporal differences in the key ecological drivers (seasonal, climatic, geomorphological and hydrological drivers) across the MDB. The most notable differences relate to the temperature gradient from north to south (higher in the north) and the rainfall gradient from east to west (high to low, coinciding with high to low elevation; Balcombe *et al.* 2011). The significant environmental and ecological differences between the SMDB and NMDB are briefly summarised in Table S1, available as Supplementary material to this paper. These strong climatic gradients influence the hydrological variability throughout the systems and determine how water is managed within the MDB.

The SMDB includes the Murray River and tributaries and, for practical management rather than ecological reasons, the lower Darling River up to Menindee Lakes (Fig. 2). The natural hydrology of the Murray River and major tributaries (e.g. Goulburn and Murrumbidgee rivers) was characterised by interannual variability, but had consistent seasonal patterns with permanent lotic habitats (Mallen-Cooper and Zampatti 2018). These rivers are now highly regulated by headwater dams that store and re-regulate flows to support irrigated agriculture, which has two major effects on hydrology: (1) seasonal reversal of flows (high summer flows, low winter flows) immediately downstream of dams; and (2) the loss of flow in all seasons downstream of irrigation areas (Mackay and Eastburn 1990; Thoms *et al.* 2000; Nilsson *et al.* 2005).

The NMDB is considered as the entire catchment of the Barwon–Darling rivers and tributaries downstream to Menindee Lakes (Fig. 2). The hydrology and river ecology of the NMDB has two natural groupings: (1) the westward-flowing tributaries from the elevated tablelands, which are near perennial, have high gradient upland reaches and have some upland-specific species; and (2) arid rivers of the north and north-west that are

Table 1. Conservation or other status of key fish species in the Murray–Darling Basin (MDB)

Conservation statuses are based on the International Union for Conservation of Nature (IUCN) Red List (<https://www.iucnredlist.org/>, accessed 11 July 2020), the *Environment Protection and Biodiversity Conservation Act* (EPBC) Species Profile and Threats database (<http://www.environment.gov.au/cgi-bin/sprat/public/publicthreatenedlist.pl?wanted=fauna>, accessed 11 July 2020) the Advisory List for Victoria (Department of Sustainability and Environment 2013) and the Action Plan for South Australian Freshwater Fishes (Hammer et al. 2009). Reference numbers given in parentheses correspond to the following: 1, National Murray Cod Recovery Team (2010b); 2, ACT Government (2017); 3, Hammer et al. (2009); 4, Trout Cod Recovery Team (2008b); 5, Clunie and Koehn (2001a); 6, Clunie and Koehn (2001b); 7, Hammer (2002); 8, Lintermans and Pearce (2017); 9, Department of Environment, Land, Water and Planning (2017); 10, DELWP action statements (<https://www.environment.vic.gov.au/conserving-threatened-species/action-statements>, accessed 11 July 2020); 11, Whiterod (2019); 12, ACT Government (2018); 13, Department of Agriculture, Water and the Environment (2018); 14, Backhouse et al. (2008). CE, critically endangered; En, endangered; EPop, endangered population; Ex, extinct; LC, least concern; N, national recovery plans (<http://www.environment.gov.au/cgi-bin/sprat/public/publicshowwallrps.pl>, accessed 11 September 2020); NL, not listed; NT, near threatened; O, other recovery plans; Rex, regionally extinct; S, state or territory recovery plans; V, vulnerable; Vpop, vulnerable population

	Murray cod	Trout cod	Golden perch	Silver perch	Macquarie perch	Freshwater catfish	Southern pygmy perch	Murray hardyhead	Olive perchlet
Conservation status									
IUCN	LC	V	LC ^A	NT	En ^B	LC ^C	NT ^C	CE	LC ^C
National (EPBC)	V	En	NL	CE	En ^C	NL	NL	En	NL
Qld	NL	–	NL	NL ^D	–	NL	–	–	NL
NSW	NL	En	NL	V	En ^C	EPop ^F	En	CE	EPop ^F
ACT	NL	En	NL	En	En ^B	–	–	–	–
Vic.	V	CE	NT	V	En ^B	En	VPop ^G	CE	REx
SA	En	Ex	NL	En	Ex	En	En	CE	CE
Recovery plans	N, S, O (1, 2, 3)	N, S (4, 10, 12)	–	O (5, 10, 12)	N, S (13, 12)	O (6, 10)	O (7, 8, 11)	N, O (3, 9, 11, 14)	O (3)
Angling species	Yes	Yes	Yes	Yes	Yes	Yes	No	No	No
Past commercial fishery	Yes	Yes	Yes ^E	Yes	Yes	Yes	No	No	No

^AMDB, Fitzroy River, Bulloo River and Lake Eyre populations combined.

^BMDB taxon only.

^CCoastal and MDB populations combined.

^DNot listed, but a no-take species in the Paroo and Warrego rivers.

^ECommercial fishery still exists in the Lower Lakes of the Murray River in SA.

^FOnly MDB populations of freshwater catfish and olive perchlet are listed in NSW.

^GOnly MDB lineage for species listed in Vic.

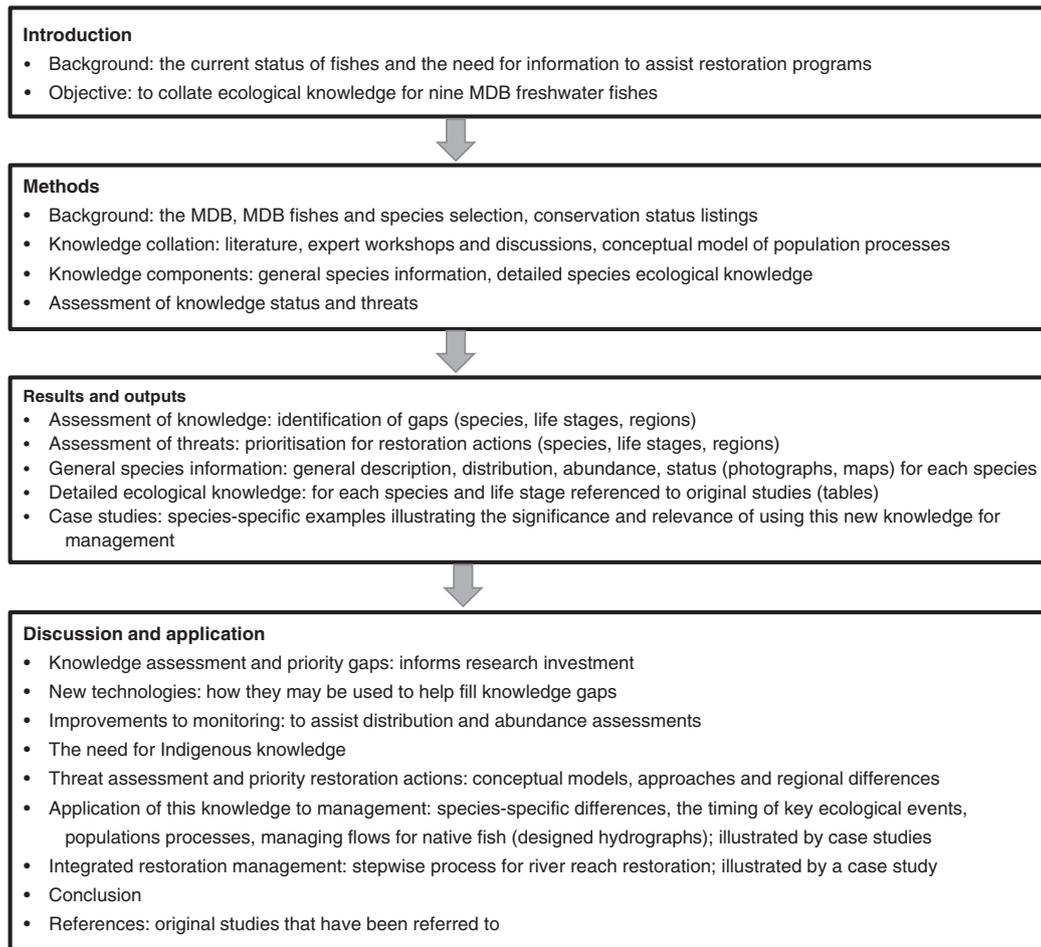


Fig. 1. Conceptual outline of the knowledge collation process and structure of this publication. MDB, Murray–Darling Basin.

intermittent rivers that may not flow half the time, have low gradients and have some specific arid species. Under natural conditions, the Barwon–Darling river system itself was near perennial, receiving flow from all westward-flowing tributaries (Mallen-Cooper and Zampatti, *in press*). The hydrology of the arid rivers exhibits greater intra- and interannual variability than the westward-flowing tributaries, and the NMDB in general exhibits greater variability than the SMDB. Flow is now highly affected by storage dams in the westward-flowing tributaries and by direct water abstraction and off-stream storage in the arid rivers (Breckwoldt *et al.* 2004).

MDB fishes and species selection

Because of the generally semi-arid nature of the MDB, its variable climate and moderate flow volumes, the native fish fauna is reasonably depauperate. Defining an exact number of native fish species for the MDB is surprisingly difficult, given ongoing taxonomic revisions and the inclusion (or not) of diadromous, estuarine and translocated native species. Until recently, only 46 obligate native freshwater species were described (Unmack 2001, 2013; Lintermans 2007). The further description of three new *Galaxias* species (Raadik 2014) increased this number to

49, which is likely to increase further with a number of cryptic species of Galaxiidae, *Hypseleotris* and *Gadopsis* currently being described (T. Raadik, Arthur Rylah Institute for Environmental Research, pers. comm., M. Lintermans and P. Unmack, University of Canberra, unpubl. data). Distributions vary from species that span almost the entire MDB (e.g. golden perch, *Macquaria ambigua*) to those with more restricted ranges that are limited to either the NMDB (e.g. Hyrtl's tandan (catfish), *Neosilurus hyrtlii*) or the SMDB (e.g. southern pygmy perch, *Nannoperca australis*). There have been marked reductions in abundance and contractions in distribution for many species, with numerous localised extinctions. Almost half (47%) the recognised species are now considered threatened taxa (Lintermans 2007; Table 1) by the International Union for Conservation of Nature (IUCN), many having been of concern for considerable time (Ingram *et al.* 2000). Overall, native fish populations have been estimated to be at <10% of pre-European settlement levels (mid-1800s; Murray–Darling Basin Commission 2004, Koehn *et al.* 2014b; Murray–Darling Basin Authority 2020). In addition, there are 12 alien fish species present in the MDB (Lintermans 2007; M. Lintermans, University of Canberra, unpubl. data).

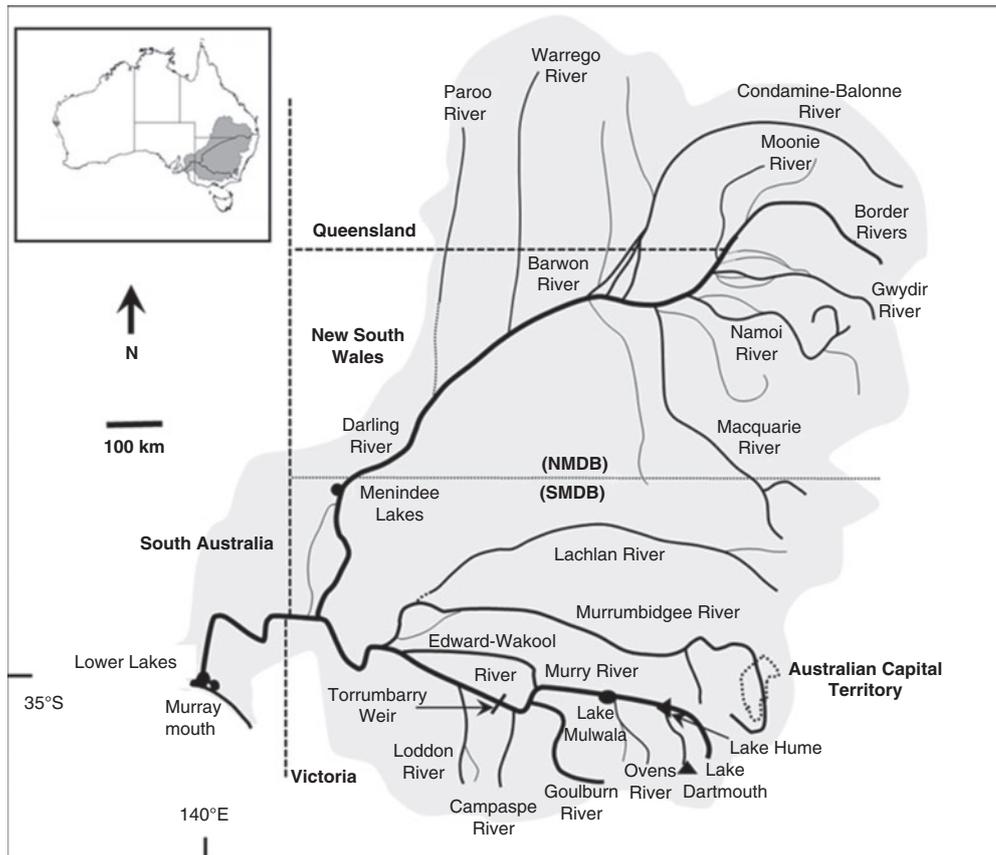


Fig. 2. Map of the Murray–Darling Basin (MDB), indicating major rivers, key features and delineation of the northern (NMDB) and southern (SMDB) regions.

Although ecosystem and multispecies management is considered the ideal, most focus in the MDB pertains to individual species in specific locations, and popular, large-bodied, recreationally fished species in particular (Saddler *et al.* 2013; Ebner *et al.* 2016; Koehn *et al.* 2019a). The ecological knowledge detailed in this compendium relates to nine native freshwater fishes recognised as high-priority species within the MDB (Koehn *et al.* 2019a), namely Murray cod (*Maccullochella peelii*), trout cod (*Maccullochella macquariensis*), golden perch, silver perch (*Bidyanus bidyanus*), Macquarie perch (*Macquaria australasica*), freshwater catfish (*Tandanus tandanus*), southern pygmy perch, Murray hardyhead (*Craterocephalus fluviatilis*) and olive perchlet (*Ambassis agassizii*) (Fig. 3). These species represent a range of life-history strategies (e.g. Winemiller and Rose 1992; Humphries *et al.* 1999; Growns 2004; Baumgartner *et al.* 2014a; Mallen-Cooper and Zampatti 2015), sizes (adult lengths ranging from 60 mm to >1 m), habitat preferences (rivers and wetlands), values (cultural, recreational, conservation) and management status (e.g. threatened species, those sought by recreational anglers). However, all nine species have some form of conservation listing at either the national or state level, with many listings being accompanied by local or national recovery plans (Table 1). All have been identified as likely to benefit from water for the environment (Koehn *et al.* 2014a) and other restoration efforts (Koehn and Lintermans 2012).

We recognise that this selection of species does not fully represent the MDB fish community in its entirety. Four of the species considered occur only in the SMDB, whereas only one occurs solely in the NMDB; the remaining four species occur in both the SMDB and NMDB. However, this selection does approximate the regional distribution of non-diadromous MDB species, with 34% occurring only in the SMDB, 20% occurring only in the NMDB and 46% occurring basin wide (M. Lintermans, University of Canberra, unpubl. data). Some key omissions that should be addressed in future reviews include the specious families of Eleotridae and Galaxiidae, including many of the most threatened small-bodied species (Lintermans *et al.* 2020), important highly abundant species, such as bony herring (*Nematalosa erebi*), and diadromous and estuarine species (Zampatti *et al.* 2010).

Conservation status listings

Among conservation listings there is considerable variation in composition, listing status and current relevance. The national *Environment Protection and Biodiversity Conservation Act* 1999 and state jurisdictional listings (Table 1) are driven by public nominations and are therefore not necessarily comprehensive or contemporary: there are species not listed that may be at higher risk of extinction than some of those listed. The list of the Australian Society for Fish Biology (<https://www.asfb.org.au/committees/#ThreatenedFishesCommittee>, accessed

19 August 2020), the national professional society for fish and fisheries, has been collated using a more comprehensive and intentional assessment process, and has informed the most recent IUCN assessment (2019; M. Lintermans, University of Canberra, unpubl. data), where almost all of Australia's freshwater fish were assessed. However, this IUCN assessment only assesses the status of species within the national or international setting, without considering the status in particular regions, or of populations or subspecies. There are several species for which MDB populations are under significant threat (e.g. freshwater catfish, southern pygmy perch), despite these species being relatively secure in coastal catchments outside the MDB (Gilligan and Clunie 2019; Pearce *et al.* 2019). It is important to note that the effects of fish kills from blackwater, drought and the recent fires have not yet been considered in any assessments (e.g. Vertessy *et al.* 2019; Legge *et al.* 2020) and that most recovery plans have not been funded or implemented and are generally in need of revision. This highlights the need for dedicated expert processes to ensure that the conservation status of all species (not just popular ones) is regularly assessed to ensure listings remain contemporary.

Knowledge collation

Ecological and biological knowledge was initially collated with the aim of supporting the development of population models to inform environmental flow and conservation planning in the MDB for the nine selected species (e.g. see Todd and Lintermans 2015; Todd *et al.* 2017). However, the potential for this knowledge to support restoration efforts more widely was soon recognised by the managers and researchers involved in that process, resulting in this publication. Managers clearly identified their need for easy access to such information, preferably from one authoritative source, to help them make informed decisions. In this study, knowledge was summarised from more than 600 publications (both peer-reviewed publications and reports, >80% of which had been published in the past 20 years, i.e. from the year 2000 onwards) and from 27 species-specific expert workshops involving more than 63 individual fish ecologists and fisheries and water managers from across the MDB. Publications were identified from known existing publications (e.g. Humphries and Walker 2013), systematic database searches (Google Scholar, Web of Science) and the knowledge and publication collections held by the authors and their associates. This approach was deemed to be the most appropriate to produce a comprehensive compendium of the available literature (especially reports). On rare occasions, where studies were not available within the MDB, information was inferred from closely related taxa or areas outside the MDB. This information was clearly identified as from such sources. Although efforts were made to include all available studies during the systematic collations process, it is recognised that occasional publications or details may have been missed, or are not referred to for brevity or to avoid duplication.

Understanding ecological concepts and principles is essential to managing freshwater fishes (Lapointe *et al.* 2014) and our inclusive, structured, facilitated workshops were organised with the aim of developing an up-to-date conceptual understanding of the ecology of each species. Each workshop provided a forum where conclusions could be arrived at by consensus around

components needed to support the requirements of both population models and management (see King and Louw 1998). The particular aim of workshop discussions and knowledge inputs on the ecological requirements was the construction of knowledge of the life stages (eggs, larvae, juveniles and adults) and population drivers (determining survival, recruitment and movements), conceptually outlined in Fig. 4, especially the factors affecting successful recruitment (King *et al.* 2009b).

Unfortunately, in studies relating to the breeding of fishes, a range of definitions is often used to describe recruitment (e.g. 'to the postlarval life stages', 'to age 0+', 'into a fishery'). To avoid confusion, the stage to which recruitment is being referred should be clearly stated in studies because, although the presence of single life-history stages (eggs, larvae) may be useful interim outcomes measures, it is the combined survival of all life stages that determines population recovery. This paper generally considers recruitment as progression into the adult population, with the combination of the species fecundity and the number of adults contributing to the outputs from spawning (number of eggs; Fig. 4).

The use of experts within the collaborative workshop framework encouraged wide-ranging discussions regarding the ecology of species, research results and concepts, and the inclusion of information from across the large spatial scales of the MDB. This allowed the refinement of an updated conceptual ecological understanding for each species. Recent or unpublished knowledge and data, revised data relationships (e.g. age–fecundity relationships) and expert opinion (used minimally and denoted as such in Tables 4–12) has been included if it could be verified in the workshops. Although some caution should always be used regarding expert opinion or reports not supported by peer-reviewed literature (Morgan 2014), the inclusion of such information following workshop vetting met the urgent need to access recent (and in some cases unpublished) science by managers (Koehn *et al.* 2019a). Other information relating to non-ecological aspects of the species in this paper (e.g. phylogeny (see Humphries and Walker 2013 and chapters therein) and aquaculture production) was only included if it related to the population processes outlined above (Fig. 4).

Knowledge components of this paper

General species information

For each fish species, we provide brief description and details of distribution and abundance. Fig. 3 contains a photograph, general distribution map and summary of biological information (life span, length, weight; for an additional summary and location details, see also Lintermans 2007; <https://fishesofaustralia.net.au>, accessed 19 August 2020). Conservation status and other values (recreation, hatchery production etc.) are provided in Table 1. However, distribution and conservation status are dependent on the availability of data from contemporary surveys. In some cases, these data are limited by a lack of attention to some regions or habitats (especially wetlands), inadequate effort (Lintermans and Robinson 2018; Scheele *et al.* 2019) or consideration of sampling method detection rates (e.g. Lyon *et al.* 2014a). Further illustrations, identification keys, biogeography and taxonomic relationships are available elsewhere (e.g. Cadwallader and Backhouse 1983;

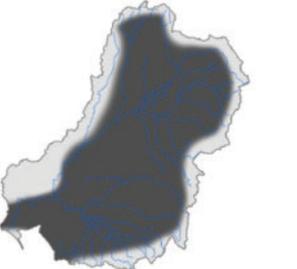
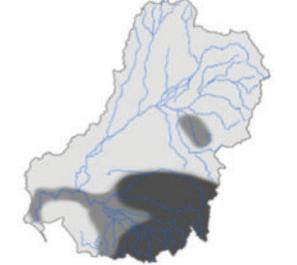
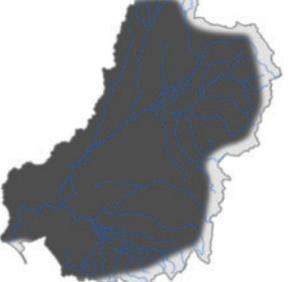
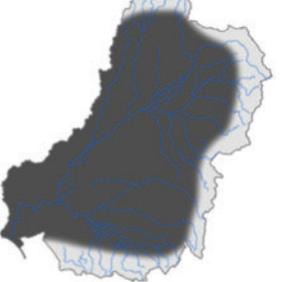
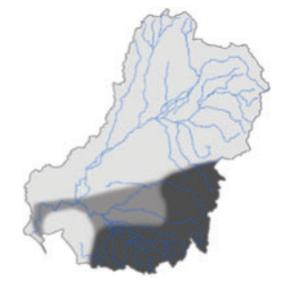
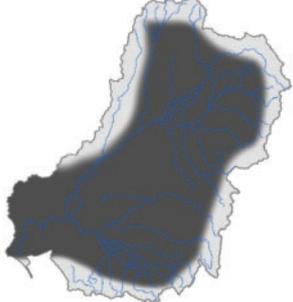
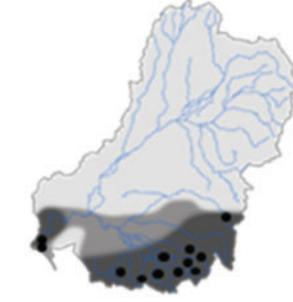
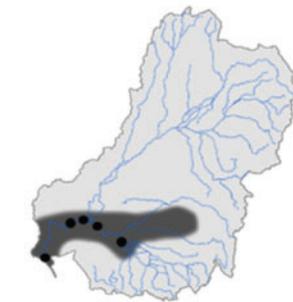
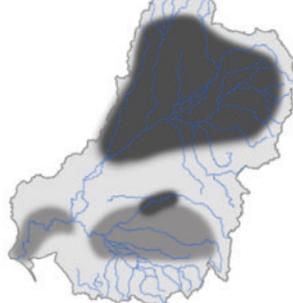
Species and illustration	Distribution	Summary information	
<p>Murray cod <i>Maccullochella peelii</i></p> 		<p>Life span: 48 years</p>	<p>Weight: 113 kg (30 kg)</p>
<p>Trout cod <i>Maccullochella macquariensis</i></p> 		<p>Life span: 21 years</p>	<p>Weight: 16 kg (5 kg)</p>
<p>Golden perch <i>Macquaria ambigua</i></p> 		<p>Life span: 26 years (river)</p>	<p>Weight: 23 kg (4 kg)</p>
<p>Silver perch <i>Bidyanus bidyanus</i></p> 		<p>Life span: 27 years (17 years in rivers)</p>	<p>Weight: 8 kg (1.5 kg)</p>
<p>Macquarie perch <i>Macquaria australisica</i></p> 		<p>Life span: ~30 years</p>	<p>Weight: 3.6 kg (1.2 kg)</p>
<p>Length: 1.8 m (1.2 m)</p>	<p>Status: C, RF, Aq, S</p>	<p>Length: 910 mm</p>	<p>Status: C, RF, Aq, S</p>
<p>Length: 760 mm (400 mm)</p>	<p>Status: C, RF, Aq, S</p>	<p>Length: 500 m (450 mm)</p>	<p>Status: C, RF, Aq, S</p>
<p>Length: 500 mm</p>	<p>Status: C, RF, Aq, S</p>	<p>Length: 500 mm</p>	<p>Status: C, RF, Aq, S</p>

Fig. 3. Photographs of the different species, along with indicative distribution throughout the Murray–Darling Basin (light shading, historical distribution; dark shading, current potential distribution; black dots, confirmed surviving but isolated populations), longevity (maximum recorded, with common age, length and weight in parentheses) and status (C, conservation listing; RF, recreational fishing; Aq, aquaculture production; S, stocked into the wild) for each species. Note that freshwater catfish have been bred but have limited commercial production (Clunie and Koehn 2001b). (Photographs courtesy of Gunther Schmida and Michael Hammer.)

<p>Freshwater catfish <i>Tandanus tandanus</i></p> 		<p>Life span: 8 years</p>	<p>Weight: 6.8 kg (1.8 kg)</p>
<p>Southern pygmy perch <i>Nannoperca australis</i></p> 		<p>Life span: 5+ years (1–5 years)</p>	<p>Weight: <8 g</p>
<p>Murray hardyhead <i>Craterocephalus fluviatilis</i></p> 		<p>Life span: 1–1.5 years</p>	<p>Weight: <5 g</p>
<p>Olive perchlet <i>Ambassis agassizii</i></p> 		<p>Life span: 3–4 years in wild 8 years in captivity</p>	<p>Weight: <8 g</p>
		<p>Length: 900 mm (500 mm)</p>	<p>Status: C, RF</p>
		<p>Length: 85 mm</p>	<p>Status: C</p>
		<p>Length: 90 mm (60 mm)</p>	<p>Status: C</p>
		<p>Length: 76 mm (50 mm)</p>	<p>Status: C</p>

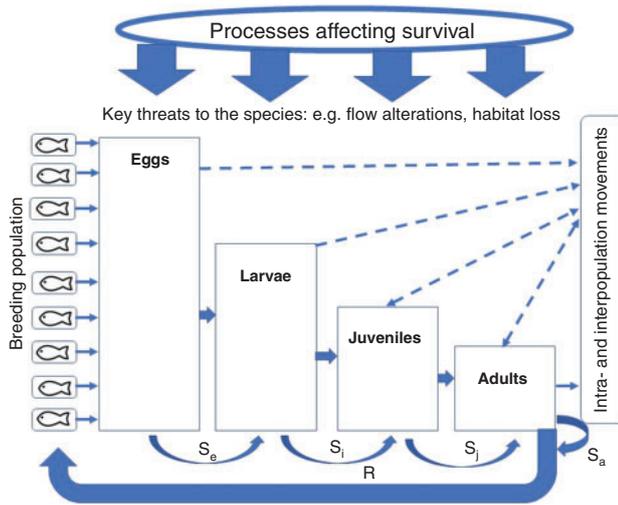


Fig. 4. Conceptual model of the life cycle for fish (egg, larvae, juveniles, adults) indicating threats and population processes affecting survival rates for each life stage (S_e , eggs; S_l , larvae; S_j , juveniles; S_a , adults) and subsequent recruitment (R) into the adult (breeding) population. Potential movements within or among populations are shown by dashed arrows.

Merrick and Schmida 1984; McDowall 1996; Allen *et al.* 2002; Pusey *et al.* 2004; Lintermans 2007; Unmack 2013).

Species detailed ecological knowledge

For each species, detailed ecological knowledge is included with regard to prespawning (maturity, fecundity and eggs), spawning (description, season, conditions, location), post-spawning (hatching, larvae), recruitment (survival), growth, habitats, movements (eggs and larvae, juveniles, adults) and behaviour.

Assessments of knowledge status and threats

For each species and life stage (eggs, larvae, juveniles and adults), knowledge status for each category was independently assessed by the 29 authors. Assessments were only undertaken by those authors confident of their ability to do so in each case. This resulted in a difference in the mean number of assessments of SMDB ($n = 18$) and NMDB ($n = 9$) species. The available knowledge was scored as a proportion of the knowledge that the authors considered is required to adequately manage the species' recovery from 1 to 5 as follows: 1, 0–19% of knowledge required; 2, 20–39% of knowledge required; 3, 40–59% of knowledge required; 4, 60–79% of knowledge required; 5, 80–100% of knowledge required. For each knowledge category for each species and life stage, median values were calculated from all assessment scores. Based on the findings of the workshops, assessment of the potential effects of a range of threats (flow related and non-flow related) on each species was also independently undertaken by the authors for both the SMDB and NMDB. Some threats only occur in some areas, or at particular times, and brief descriptors have been provided to indicate the scope of each threat, in addition to its likely impact (Table S2). Each threat was scored on a scale of 1–5 for each species (1, low level of impact; 5, high level of impact) with median values calculated from all assessment scores.

Results

Assessment of knowledge

Assessment scores for each knowledge category for each species and life stage, indicating the available level of knowledge and highlighting key gaps, are presented as a heat grid in Table 2. Only 7% of life stage knowledge cells had a score indicating a 'high' level of knowledge available ($\geq 80\%$ of required knowledge available; score ≥ 4). A high level of life stage knowledge was mostly associated with the adults of larger key recreational or threatened species (i.e. Murray cod, trout cod and golden perch). At the other end of the scale, 7% of life stage knowledge cells had median scores of ≤ 1.5 , indicating generally poor knowledge ($< 20\%$ of required knowledge available). Approximately 55% of cells had median scores of ≤ 2.5 , indicating limited knowledge was available, whereas the remaining cells ($\sim 31\%$) scored 2.5–4, indicating moderate knowledge was available (Table 2). The knowledge available varied between species, with most known about the large-bodied Murray cod and the least known about the small-bodied olive perchlet. Across all species, most was known about adults, followed by egg, juvenile and larval stages (in that order; Fig. S1a). The gaps in knowledge about survival and recruitment, growth and fish condition, movements and flow requirements, especially for larvae and juveniles, require the most attention (Fig. S1b).

There was surprisingly little difference in the knowledge assessment scores for species between the NMDB and the SMDB (Fig. S2). However, we recognise the potential bias here relating to the greater number of SMDB-focused species and knowledge sources. Assessment of the literature used to collate technical knowledge of species for this paper indicated that 70% of research studies had been conducted in or addressed only SMDB species. Only 14% of studies had been solely conducted in or addressed NMDB species, with a further 16% of studies including both SMDB and NMDB species.

Assessment of threats

Assessment scores for the threats to each species are presented in a heat grid in Table 3 to indicate the threats of greatest potential impact, and there is further ranking of scores in Fig. 5. Golden perch and silver perch had the greatest number of individual potential threats, mostly related to water management, such as altered flows, the loss of lotic habitats, movement cues and pathways and barriers to longitudinal and lateral connectivity. Across all species, flow-related threats resulted in reduced movement pathways, altered flow seasonality and loss of refugia (Fig. 5). Additional flow-related impacts included loss of riverine backwater and slackwater habitats (see Humphries *et al.* 2006; Vietz *et al.* 2013) resulting from high irrigation flows and, conversely, loss of riverine lotic habitats by the creation of weir pools. Other lentic habitats, such as wetlands, are also reduced by river regulation and reductions in high flows. Key non-flow-related threats included the effects of alien species, barriers to longitudinal and lateral connectivity, decreased water quality and loss of wetlands aquatic vegetation (Fig. 5).

The loss of wetlands and aquatic vegetation most affected freshwater catfish, southern pygmy perch, Murray hardyhead and olive perchlet. These species were also considered to be at most risk from the effects of alien carp (*Cyprinus carpio*)

Table 2. Assessment of the knowledge available for each life stage for each species

Available knowledge was scored as follows: 1, 0–19% of knowledge needed is available; 2, 20–39% of knowledge needed is available; 3, 40–59% of knowledge needed is available; 4, 60–79% of knowledge needed is available; 5, >80% of knowledge needed is available. Numbers in cells indicate median scores, and colours reflect these scores (green, high degree of knowledge; red, greatest knowledge gaps). Blank cells are not applicable to the particular life stage. A, adults; E, eggs; J, juveniles; L, larvae

Knowledge category	Murray cod			Trout cod			Golden perch			Silver perch			Macquarie perch			Freshwater catfish			Southern pygmy perch			Murray hardyhead			Olive perchlet					
	E	L	A	E	L	A	E	L	A	E	L	A	E	L	A	E	L	A	E	L	A	E	L	A	E	L	A			
Spawning	4.0			3.0	3.0		3.0	3.0		3.0	3.0		3.0	3.0		3.0	3.0		3.0	2.5		3.0	2.5		3.0	2.0		3.0	2.0	
Spawning conditions																														
Survival (recruitment)	2.5			2.0	3.0		2.0	2.0		2.0	2.0		2.0	2.0		2.0	2.0		2.0	2.0		2.0	2.0		2.0	2.0		2.0	2.0	
Growth and condition																														
Movements																														
Physical habitat requirements																														
Water quality tolerances																														
Flow requirements																														

(Table 3). Altered flow seasonality and loss of aquatic vegetation were the greatest threats in the SMDB (Fig. 5). The loss of refugia, the loss of early life stages to irrigation diversions and pumps and the loss of movement pathways and longitudinal connectivity were more evident in the NMDB (Fig. 5). The species subject to recreational fishing (Murray cod and golden perch) were considered vulnerable to overfishing, especially in isolated waterholes. Overall, the greatest variation in assessment scores related to the effects of loss of spawning and movement cues and the loss of lotic habitats, with generally greater variation observed in the scores for the NMDB (Fig. S3). This likely reflects the lesser certainty of knowledge and the lower number of assessment scores applicable to the NMDB. It must be noted that these assessments only apply to the species in this study and although the ranking of scores may alter slightly if all MDB species were included, post-assessment expert discussions considered them to be generally representative of threats to fishes in MDB river systems.

General species information

General information for each species (a general description and information on its distribution and abundance) is provided in the text below, and this is complemented by the detailed species ecological knowledge (referenced) presented in Tables 4–12. This general information supplements Fig. 3 and provides a summary for those readers less familiar with these species. Distributional data were summarised from existing texts (e.g. Gehrke and Harris 2000, 2001; Lintermans 2007) and recent surveys.

Murray cod Maccullochella peelii (Mitchell, 1838) (Fig. 3a)

General description. The Murray cod is long-lived, large-bodied, demersal (Koehn 2009a), apex predator (Ebner 2006; Baumgartner 2007) that is considered a river channel specialist with a high affinity for in-stream woody habitat (Koehn 2009b). It lays demersal adhesive eggs on hard substrates, with the male providing parental care to eggs and larvae (Rowland 1983a, 1998b). Larvae can undergo drift after hatch (Koehn and Harrington 2006). This iconic species has high conservation, biodiversity, cultural and recreational values (Ebner et al. 2016). It is currently conservation listed nationally, but is also extremely popular with recreational fishers (Koehn and Todd 2012), which has prompted substantial investment in stock enhancement. All jurisdictions have fishery regulations that attempt to manage harvesting and to protect breeding stocks (Rowland 1985, 2005). Detailed knowledge on the ecological attributes of the Murray cod is given in Table 4.

Distribution and abundance. The Murray cod remains widely distributed throughout most of its natural range (most of the MDB), but there have been some localised extinctions, such as has been suggested for the Paroo River (Sarac et al. 2011), and considerable declines in abundance (Cadwallader and Gooley 1984; Ye et al. 2000, 2008; Rowland 2005; Mallen-Cooper and Brand 2007; Zampatti et al. 2014). Murray cod once supported a considerable commercial fishery across its southern range (Reid et al. 1997; Rowland 2005; Humphries and Winemiller 2009), but concerns about overfishing and declining catches have been reported since the early 1900s

Table 3. Assessment of flow-related and non-flow-related threats to each species

Threats were scored from 1 (lowest level of threat) to 5 (highest level of threat). Numbers in cells indicate median scores, and colours reflect these scores (dark green, lowest level of threat; red, highest level of threat). Blank cells are not applicable to the particular region. Descriptors of the threats and some guidance regarding categories are provided in Table S2. N, northern Murray–Darling Basin; S, southern Murray–Darling Basin

Threats	Murray cod		Trout cod		Golden perch		Silver perch		Macquarie perch		Freshwater catfish		Southern pygmy perch		Murray hardyhead		Olive perchlet		
	S	N	S	N	S	N	S	N	S	N	S	N	S	N	S	N	S	N	
Flow related																			
Decreased overbank flooding	3.0	3.0	3.0	3.0	4.0	4.0	3.5	3.0	1.0	3.0	2.0	2.0	3.0	3.0	4.0	2.0	3.0	2.0	3.0
Decreased in-channel flows	3.0	3.0	3.0	3.0	4.0	4.0	4.0	3.0	3.0	4.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
Altered flow seasonality	3.0	3.0	4.0	4.0	3.0	3.0	3.0	3.0	4.0	4.0	3.0	3.0	3.0	3.0	3.0	3.0	3.0	3.0	3.0
Reduced spawning cues	2.0	2.0	2.0	2.0	4.0	4.0	4.0	4.0	4.0	4.0	1.0	1.0	1.0	1.0	2.0	2.0	1.0	1.0	1.0
Reduced movement cues	2.0	2.0	2.0	2.0	4.0	4.0	4.0	4.0	4.0	4.0	2.0	2.0	1.0	1.0	2.0	2.0	1.0	1.0	2.0
Reduced movement pathways	3.0	3.0	2.0	2.0	4.0	4.0	4.0	4.0	4.0	4.0	3.0	3.0	3.0	3.0	3.0	3.0	2.0	2.0	3.0
Loss of lentic habitats	1.0	1.0	1.0	1.0	3.0	3.0	3.0	3.0	2.0	2.0	4.0	4.0	4.0	4.0	4.0	4.0	4.0	4.0	4.0
Loss of riverine lotic habitats	4.0	3.5	4.0	4.0	4.0	4.0	4.0	4.0	4.0	4.0	2.0	2.0	1.0	1.0	1.0	2.0	2.0	2.0	2.0
Loss of refugia	2.0	4.0	2.0	2.0	2.0	4.0	2.0	2.0	3.0	3.0	4.0	4.0	4.0	4.0	4.0	4.0	2.0	4.0	4.0
Non-flow related																			
Loss to pumps	2.0	3.0	1.0	1.0	2.0	3.0	2.5	3.0	1.0	1.0	3.0	3.0	1.0	1.0	1.0	1.0	2.0	2.0	2.0
Loss into irrigation channels	3.0	2.0	2.5	2.5	3.0	3.0	3.0	3.0	1.0	1.0	2.0	2.0	1.0	1.0	1.0	1.0	2.0	2.0	2.0
Cold water pollution	3.0	3.5	3.5	3.5	3.0	3.0	3.0	3.0	3.0	3.0	3.0	3.0	2.0	2.0	1.0	1.0	2.0	2.0	2.0
Decreased in-stream structure	4.0	4.0	4.0	4.0	3.0	3.0	2.5	2.0	2.0	2.0	2.0	2.0	2.0	2.0	1.0	1.0	2.0	2.0	2.0
Decreased aquatic vegetation	2.0	2.0	2.0	2.0	2.0	2.0	3.0	3.0	3.0	3.0	4.0	4.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0
Decreased wetlands	1.0	1.0	1.0	1.0	3.0	3.0	2.5	3.0	1.0	1.0	4.0	4.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0
Barriers to longitudinal connectivity	3.0	3.0	3.0	3.0	5.0	5.0	5.0	5.0	4.0	4.0	3.0	3.0	2.0	2.0	2.0	2.0	3.0	3.0	3.0
Barriers to lateral connectivity	2.0	2.0	2.5	2.5	4.0	4.0	3.0	4.0	3.0	3.0	4.0	4.0	4.0	4.0	3.5	3.5	4.0	4.0	4.0
Sedimentation	3.0	3.0	3.0	3.0	2.0	2.0	2.0	2.0	4.0	4.0	4.0	4.0	3.0	3.0	2.0	2.0	4.0	4.0	4.0
Decreased water quality	4.0	4.0	3.5	3.5	3.0	3.0	3.0	3.0	3.0	3.0	4.0	4.0	3.0	3.0	3.0	3.0	4.0	4.0	4.0
Alien species impacts	3.0	2.5	3.0	3.0	3.0	3.0	3.0	3.0	4.0	4.0	5.0	5.0	5.0	5.0	4.0	4.0	4.0	4.0	4.0
Recreational fishing	3.0	3.5	4.0	4.0	3.0	3.0	2.0	2.0	3.0	3.0	3.0	3.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0

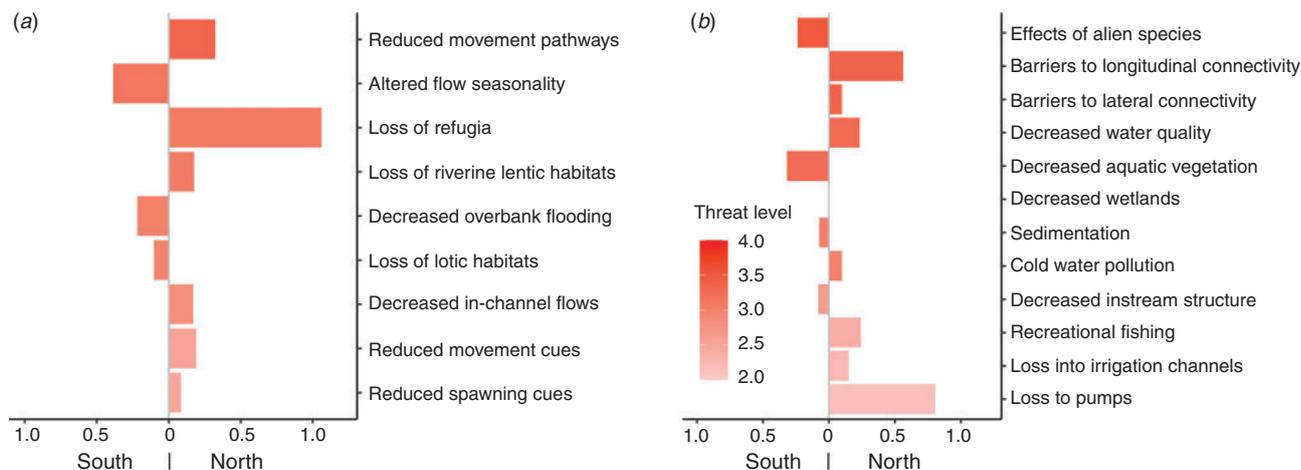


Fig. 5. (a) Flow-related and (b) non-flow-related threats to Murray–Darling Basin (MDB) fishes listed from top to bottom by their average assessment score (across all species and sub-basins), with the shading indicating the average threat level (e.g. darker red = higher threat). Horizontal bars indicate differences in threat levels between the northern and southern MDB (where ‘0’ indicates the same level of threat); that is, bars to the right of centre indicate a higher threat in the northern MDB (NMDB) and bars to the left indicate a higher threat in the southern MDB (SMDB).

(Dannevig 1903; Dakin and Kesteven 1938; Rowland 1989, 2005). Declines in catches eventually saw all commercial fisheries closed by the early 2000s (Rowland 2005). Widely produced in hatcheries and stocked for recreational fishing (Rowland 2005; Ingram *et al.* 2011; Forbes *et al.* 2015a, 2015b; Hunt and Jones 2018), Murray cod have been translocated and stocked outside the MDB (Cadwallader and Gooley 1984), as well as farmed for human consumption (Haldane 2014). There has been a partial recovery of populations in some areas, and the species was not considered threatened in the 2019 IUCN Red List assessment (Gilligan *et al.* 2019), but there have been numerous large-scale fish kills in the past two decades (Koehn 2005b; King *et al.* 2012; Thiem *et al.* 2017; Vertessy *et al.* 2019). Although there has been no MDB-wide dedicated long-term Murray cod-specific monitoring, it is a key species considered under broad-scale monitoring, such as in the Sustainable Rivers Audit from 2004 to 2013 (Davies *et al.* 2008, 2010, 2012; Murray–Darling Basin Authority, unpubl. data), the unpublished Murray–Darling Basin Fish Survey from 2015 to 2020 (see Gwinn *et al.* 2019, 2020) and state monitoring programs. However, the stock status across the MDB has been described as ‘poorly understood and undefined’ (Ye *et al.* 2018). It is worth noting that all four members of the genus *Maccullochella* are considered threatened, with Murray cod and trout cod being present in the MDB (Lintermans *et al.* 2004).

Trout cod *Maccullochella macquariensis* (Cuvier, 1829) (Fig. 3b)

General description. The trout cod is a moderate- to large-bodied, long-lived apex predator, mainly found in the SMDB (but also the Macquarie River) that is a river channel specialist with a high affinity for in-stream woody habitat (Nicol *et al.* 2007; Baumgartner *et al.* 2014a; Koehn and Nicol 2014). Like other cod species, trout cod lay demersal adhesive eggs on hard substrates, with the male presumably providing parental care (see Table 3). Larvae can undergo drift after hatch (Koehn and Harrington

2006). Closely related to Murray cod, and only being formally described in 1972 (Berra and Weatherley 1972), trout cod has long been considered threatened (Berra 1974) and is listed as a threatened species (Table 1). Renowned for its aggression and fighting qualities as a sport fish (Berra 1974; Cadwallader 1977), the trout cod is readily captured by recreational fishers, although now largely protected from harvest. Detailed knowledge on the ecological attributes of the trout cod is given in Table 5.

Distribution and abundance. Historically, trout cod were widespread in the mid-upper reaches of the Murray, Murrumbidgee and Macquarie river systems (Douglas *et al.* 1994), but they are now reduced to a single truly natural population in the Murray River downstream of Lake Mulwala (Douglas *et al.* 1994). Over the past few decades this population has expanded downstream for several hundred kilometres (Douglas *et al.* 2012; Koehn *et al.* 2013). There was early taxonomic confusion and misidentification of cod, so some details about their past distribution remain uncertain, but an extensive decline in the range and abundance of trout cod occurred from the 1950s to the 1970s (Cadwallader and Gooley 1984; Faragher *et al.* 1993; Douglas *et al.* 1994; Trueman 2012a). Sites of significant population losses in the past 60 years include the Murray River (Cadwallader 1977), Lachlan River (late 1960s; Trueman 2012a), Lake Sambell (apparently 1970; Cadwallader and Gooley 1984), the upper Murrumbidgee River (1970s; Lintermans *et al.* 1988) and the lower Mitta Mitta River downstream of Lake Dartmouth (following its construction, completed in 1979; Koehn *et al.* 1995). Conservation stocking and translocation programs (mainly 0+ fish) have recently resulted in populations being re-established in the mid- and upper Murrumbidgee (including tributaries), upper Murray, lower Goulburn and lower Ovens rivers (Koehn *et al.* 2013), Seven Creeks (Goulburn catchment, Vic.), Cataract Dam (Nepean catchment, NSW; Douglas *et al.* 1994; Lintermans *et al.* 2015) and Lake Sambell (Ovens catchment, Vic.). The successful re-establishment of the Ovens River population (Bearlin *et al.* 2002; Lyon *et al.* 2012) has led to expansion into

the Murray River upstream of Lake Mulwala. Stocking of on-grown hatchery-reared fish (age 2+) has had limited success (Ebner *et al.* 2007; Ebner and Thiem 2009).

Golden perch *Macquaria ambigua* (Richardson, 1845)
(Fig. 3c)

General description. The golden perch is a medium- to large-bodied, long-lived top-level predator and river channel and floodplain specialist that can move large distances (Reynolds 1983; Ebner 2006; Koehn and Nicol 2016) and typically prefers in-stream structure (mostly wood) as daytime habitat (Crook *et al.* 2001; Koehn and Nicol 2014; Koster *et al.* 2020). The golden perch has pelagic eggs and larvae that undergo passive drift in flowing waters. It is keenly sought by anglers and is widely produced by hatcheries and stocked into rivers and impoundments (Rowland *et al.* 1983; Rowland 2013; Forbes *et al.* 2015b; Crook *et al.* 2016; Hunt and Jones 2018). Spawning, recruitment and movement responses are typically linked to elevated flows in the SMDB (Reynolds 1983; O'Connor *et al.* 2005; Zampatti and Leigh 2013b; Baumgartner *et al.* 2014b; Koster *et al.* 2014, 2017; Llewellyn 2014; Zampatti *et al.* 2018; Thiem *et al.* 2020), but in the NMDB reproduction can occur in the absence of connecting flows in isolated waterholes (Balcombe *et al.* 2006); this has also been observed in some impoundments in the SMDB (Battaglione 1991; M. Lintermans, University of Canberra, unpubl. data). Detailed knowledge on the ecological attributes of golden perch is given in Table 6.

Distribution and abundance. The golden perch remains widespread throughout most of the MDB (Lintermans 2007; Trueman 2012a), although it is likely absent above some barriers (Brumley 1987). It once supported an extensive commercial fishery in the SMDB (Cadwallader 1977) in the lower Murray River channel in South Australia (SA), but this was closed in 2002 (Ferguson and Ye 2012), and the commercial fishery is now restricted to lakes Alexandrina and Albert (the lower lakes), with annual catches of ~50–150 tonnes (Mg) in 2002–13, peaking at 150 Mg in 2005–06 (Earl 2019).

Silver perch *Bidyanus bidyanus* (Mitchell, 1838) (Fig. 3d)

General description. The silver perch is a long-lived, medium- to large-bodied, omnivorous, schooling river channel specialist with spawning and movements linked to rising flows (Tonkin *et al.* 2017a). It is a highly mobile species, with pelagic eggs and larvae that undergo passive drift in flowing waters (Rowland 2009). Nationally listed as threatened, the silver perch is cultured in hatcheries for the restaurant trade (Rowland *et al.* 1995; Rowland 2004, 2009) and is widely stocked (mainly in impoundments) throughout the MDB and outside its natural range for conservation and recreational purposes (Clunie and Koehn 2001c, 2001d). Detailed knowledge on the ecological attributes of the silver perch is given in Table 7.

Distribution and abundance. Once widespread in most MDB lowland river reaches, the silver perch has suffered substantial declines in abundance and range (Lintermans 2007; Trueman 2012a), especially in the mid-Darling River and NMDB, where it is now rare (Clunie and Koehn 2001d), and there is concern for its future. The mid-reaches of the Murray River support the highest relative abundances (Tonkin *et al.*

2017a), although even this population has declined substantially from historical levels (94% reduction at the Euston fishway over the past 50 years; Mallen-Cooper and Brand 2007). Variable numbers of fish occupy the NMDB (Warrego–Condamine, Macquarie, Namoi and Border rivers), Edward–Wakool, lower Darling, Murrumbidgee, Loddon, Campaspe and Goulburn rivers and the lower Murray River reaches (all SMDB; Tonkin *et al.* 2019a).

Macquarie perch *Macquaria australasica* Cuvier, 1830
(Fig. 3e)

General description. The Macquarie perch is a long-lived, moderate-bodied, schooling (when juvenile) or solitary (when adult) riverine species (Lintermans 2007) that has also flourished in several reservoirs where there is access to riverine habitats for spawning (e.g. Wharton 1973; Cadwallader 1981; Appleford *et al.* 1998; Tonkin *et al.* 2010; Ebner *et al.* 2011; Lintermans 2012). A macro- and microinvertebrate carnivore, the Macquarie perch has large demersal eggs and exhibits no parental care (Cadwallader and Rogan 1977; Lintermans 2007). It has long been recognised as a threatened species (Burbidge and Jenkins 1984), but is still subject to limited recreational fishing in Victoria and is stocked for conservation purposes (Lintermans *et al.* 2015). Detailed knowledge on the ecological attributes of the Macquarie perch is given in Table 8.

Distribution and abundance. The Macquarie perch is mostly endemic to the SMDB (also the Lachlan and Macquarie rivers), where it was historically widespread and abundant and supported a popular recreational fishery (Cadwallader and Rogan 1977). Since the 1950s, the Macquarie perch has undergone major declines in range (including a reduction of hundreds of kilometres in the Murray River) and abundance, and its distribution has been fragmented into small, discrete, reproductively isolated populations (Cadwallader 1981; Ingram *et al.* 1990, 2000; Pavlova *et al.* 2017). The Macquarie perch survives well in some impoundments (e.g. Lake Dartmouth, Vic.; Cotter Reservoir, ACT), but these populations fluctuate (Tonkin *et al.* 2014). Smaller populations around the ACT have been subject to extirpations (e.g. Ebner *et al.* 2011; Lintermans 2012, 2013b). The Macquarie perch has been translocated within and outside its natural range (e.g. to the Yarra River, Vic.; Cadwallader 1981; Lintermans 2007, 2008, 2013b; Lintermans *et al.* 2015). Reintroduction through translocation and stocking of hatchery-produced juveniles in an attempt to re-establish populations occurs in the Ovens (Vic.), Cotter, Molonglo (ACT) and Retreat (NSW) rivers (Lintermans 2013a; Todd and Lintermans 2015; Pearce 2013).

Freshwater catfish *Tandanus tandanus* Mitchell 1838
(Fig. 3f)

General description. The freshwater catfish is a medium-sized, largely benthic species that occurs in rivers, wetlands and impoundments (Lintermans 2007). A macrocarnivore, the freshwater catfish deposits large demersal, non-adhesive eggs in a nest depression constructed from pebbles and gravel, and exhibits extended parental care (Davis 1977a, 1977b; Clunie and Koehn 2001b; Lintermans 2007). The freshwater catfish can be quite territorial and aggressive, especially when guarding a nest. The MDB population of the freshwater catfish is considered as threatened in NSW, Vic. and SA, but it is a popular recreational

fishing species, although fishing is now mostly limited to impoundments. Juveniles may form loose schools, but adults tend to be solitary when they are not breeding (Cadwallader and Backhouse 1983). Detailed knowledge on the ecological attributes of the freshwater catfish is given in Table 9.

Distribution and abundance. The freshwater catfish is native to the MDB and eastern coastal drainages from central NSW to northern Queensland (Clunie and Koehn 2001a; Gilligan and Clunie 2019). Previously abundant (Roberts and Sainty 1996; Copeland *et al.* 2003; Trueman 2012a), the freshwater catfish once supported occasional commercial fisheries (e.g. on Lake Brewster in NSW and the lower Murray River; Roberts and Sainty 1996; Ye *et al.* 2015) but has experienced significant declines throughout most of its MDB range over the past 60 years (Lake 1971; Reynolds 1976; Pollard *et al.* 1996), especially in regulated rivers. It has been suggested as being extinct in the Paroo River (Sarac *et al.* 2011). The remaining riverine populations that have relatively high abundances largely now occur above impoundments in the NMDB (Clunie and Koehn 2001b). The freshwater catfish is rarely abundant in unimpounded main river channels in the SMDB; most populations are found in weir pools or wetland habitats (Clunie and Koehn 2001b). Conservation concerns have resulted in a national recovery plan being produced, despite the freshwater catfish having no national conservation listing (Clunie and Koehn 2001b).

Southern pygmy perch *Nannoperca australis* Gunther 1861 (Fig. 3g)

General description. The southern pygmy perch is a short-lived, small-bodied, microcarnivorous wetland specialist (Kuiter and Allen 1986; Baumgartner *et al.* 2014a; Whiterod 2019) that also occurs in slow-flowing creeks and is commonly associated with aquatic vegetation (Humphries 1995; Koster 1997). Flooding is not required for spawning, but it may support recruitment and dispersal (Tonkin *et al.* 2008). Demersal non-adhesive eggs are scattered on the substrate with no parental care (Llewellyn 1974; Lintermans 2007). Detailed knowledge on the ecological attributes of the southern pygmy perch is given in Table 10.

Distribution and abundance. The southern pygmy perch is endemic to south-eastern Australia (Llewellyn 1974; Humphries 1995; Hammer 2002) and was once widely distributed in south eastern Australia (not the NMDB), but its range in the SMDB has contracted greatly (Bray and Thompson 2019), where it has been reduced to a series of fragmented and regionally threatened populations (Pearce 2014; Hammer *et al.* 2009; Pearce *et al.* 2019). The southern pygmy perch remains reasonably common in Victorian coastal areas (Lintermans 2007). Translocations to establish new populations are being considered (Whiterod 2019; S. Raymond, Arthur Rylah Institute for Environmental Research, pers. comm).

Murray hardyhead *Craterocephalus fluviatilis* McCulloch, 1913 (Fig. 3h)

General description. The Murray hardyhead is a small-bodied, short-lived, highly mobile, schooling 'wetland specialist' (Ebner *et al.* 2003; Hammer and Wedderburn 2008) found most frequently in freshwater to brackish, still or slow-flowing waters of off-channel habitats, including floodplain billabongs, wetlands

and lakes (Ebner *et al.* 2003; Ellis 2005; Hammer and Wedderburn 2008). The Murray hardyhead is listed as threatened in NSW, Vic. and SA. It is a batch spawner, with eggs deposited on aquatic vegetation during a prolonged breeding season from September to March (Ellis 2005). Its diet consists predominantly of microcrustaceans, with larger individuals also consuming items such as dipteran larvae (Ellis 2006; Wedderburn *et al.* 2013). Detailed knowledge on the ecological attributes of the Murray hardyhead is given in Table 11.

Distribution and abundance. The Murray hardyhead is endemic to the lowland floodplains of the Murray and Murrumbidgee river systems (SMDB), and it has been recorded from Yarrowonga downstream to Lake Alexandrina. Once widespread and abundant, the Murray hardyhead has suffered serious reductions in both distribution and abundance in the past two decades, particularly during the Millennium Drought (Ivantsoff and Crowley 1996; Ebner *et al.* 2003; Wedderburn and Hammer 2003; Lyon and Ryan 2005). Its current distribution is limited to a small number of saline wetlands on the Murray River floodplain downstream of Kerang, where its populations are highly fragmented (Lloyd and Walker 1986; Ebner *et al.* 2003; Wedderburn 2009; Ellis *et al.* 2013). The Murray hardyhead is now locally extinct from at least 17 historically documented sites (Ellis *et al.* 2013) and is presumed extinct in NSW (Gilligan 2005), although reintroductions are now occurring (Stoessel *et al.* 2019; Ellis *et al.* 2020). The remaining populations of Murray hardyhead are fragmented and now largely confined to discrete off-channel habitats upstream of the SA border to the mid-Murray River. These populations are predominantly disconnected from the main river channel, except during flood (Ellis *et al.* 2013). In the lower lakes of the Murray River, the species is patchily distributed across a broad area of connected off-channel and lake edge sites in Lake Alexandrina (Wedderburn and Hammer 2003; Wedderburn *et al.* 2007; Wedderburn 2009), and it is being considered for translocations (Whiterod 2019).

Olive perchlet *Ambassis agassizii* Steindachner 1866 (Fig. 3i)

General description. The olive perchlet is a small-bodied schooling species that inhabits freshwater pools and slow-flowing reaches in rivers, streams and wetlands (Leggett 1984; Allen and Burgess 1990; Allen 1996). The MDB of olive perchlet population is listed as threatened in NSW, SA and Vic. (considered extinct). The olive perchlet occupies littoral vegetation (Hutchison *et al.* 2020), often mid-water (Milton and Arthington 1985), and is most active at night (Allen *et al.* 2002; D. Moffatt (Department of Environment and Science, Qld), pers. comm.). The olive perchlet is a microcarnivore that lays small, adhesive eggs on aquatic plants and rocks on the streambed (Lintermans 2007; Llewellyn 2008). Detailed knowledge on the ecological attributes of the olive perchlet is given in Table 12.

Distribution and abundance. Historically widespread throughout the MDB north of the Murray River, the range of the olive perchlet has contracted to small, patchy populations (Lintermans 2007; Llewellyn 2008). The Border Rivers catchments (NMDB; especially the mid-upper Condamine catchment) remain strongholds, where the olive perchlet are more abundant in tributary streams and floodplain wetlands than in the main river

channel (Hutchison *et al.* 2008; Norris *et al.* 2015). The olive perchlet also occurs in coastal drainages from northern NSW to north Queensland (Lintermans 2007; McNeil *et al.* 2008).

Detailed species ecological knowledge

Significant new ecological knowledge has become available over the past two decades, with >80% of references cited in this paper being published since 2000. This compendium provides a ready information source for individual species, but reference to the original publications is recommended when more detailed knowledge is required. Tables 4–12 include new summary equations on growth and fecundity relationships for seven of the species, derived using methodology similar to Todd and Lintermans (2015). In some cases, we found data and information from studies on the same species to vary, particularly across different regions. Such differing information was included, but it is strongly recommended that the original publications are accessed for more complete interpretation for a particular region or species. Tables 4–12 also include key knowledge gaps and potential threats. Because drought and climate change impacts may exacerbate many other threats (especially those that are water related), susceptibility assessments for most species have also been included (from Crook *et al.* 2010 and Chessman 2013). Key messages for restoration for each species are provided in the ‘Key knowledge gaps and messages for restoration for each species’ section in the Supplementary material and Koehn *et al.* (2020).

Case studies illustrating the relevance of new knowledge to management

To illustrate the significance and relevance of using this contemporary information, case study examples of applications of this new knowledge to future management are provided below.

Case study 1: age of silver perch

Despite being long-lived in some impoundments (up to 27 years), in the 1990s silver perch within the Murray River, although estimated to live up to 17 years, rarely exceeded 11 years (Mallen-Cooper and Stuart 2003, fig. 3). Contemporary sampling indicates that silver perch now rarely exceed 7 years (Tonkin *et al.* 2019a). If this is a true reflection of the age structure of the population, this finding highlights a need for flow sequencing to promote more regular spawning and recruitment than previously thought for silver perch. These spatially and temporally differing age estimates highlight the need for appropriate and contemporary data to be used in modelling and population estimates, and for management.

Case study 2: spawning and salinity tolerances of Murray hardyhead

Increased knowledge of the spawning biology and salinity tolerances of the early life stages (i.e. eggs, larvae and juveniles) of Murray hardyhead (Fig. 6) provides opportunities to improve management at saline sites where the species is present or reintroduced (Ellis *et al.* 2020). Water delivery can (and is) now be targeted towards attaining suitable salinities at critical times for the benefit of spawning, egg development and larval and juvenile survival, and to the detriment of alien competitors and predators.

Case study 3: growth differences

Regional differences in growth rates of golden perch, although originally indicated for three MDB rivers (Mallen-Cooper and Stuart 2003), have now been demonstrated across the species’ geographic range (Fig. 7; Wright *et al.* 2020) and do not follow a north–south (latitudinal) divide, but differences are likely a result of variable habitats and associated productivity within regions. Variability in growth rates also occurs across temporal scales and for other widespread species, such as Murray cod (Rowland 1989; G. Butler (NSW Department of Primary Industries, Fisheries), unpubl. data). Because these biological parameters (and perhaps other variables, such as fecundity) control important population processes (Fig. 4), we advocate using river-specific data where possible (e.g. to develop population models; Todd *et al.* 2017).

Case study 4: recruitment variability

Recruitment rates of golden perch are highly variable spatially and temporally. Recruitment in the less unregulated productive rivers and floodplain lakes of the NMDB appears more frequent than in many rivers of the highly regulated SMDB (Sharpe 2011; Zampatti *et al.* 2019; Stuart and Sharpe 2020). In addition, within both regions, the natal origin of recruits in given localities may be temporally variable. Individuals spawned in certain rivers can substantially augment populations in other rivers, and the contribution of different recruitment sources varies as a function of hydrology, nursery habitats and connectivity (Zampatti *et al.* 2018; Stuart and Sharpe 2020). For golden perch populations, this knowledge reinforces the need for management over broad spatial scales and consideration of inter-regional movements.

Case study 5: movements of golden perch

Imperfect knowledge on the spatial ecology of freshwater fishes often hinders their management (Cooke *et al.* 2016). The recent increase in knowledge about the complex movements of golden perch has been brought together in this paper (Table 6) to provide an updated conceptual movement model (from Koehn and Crook 2013; Koster and Crook 2017) for adults and juveniles (Fig. 8a), as well as eggs and larvae (Fig. 8b), with application of the larger-scale movements to golden perch metapopulations across the MDB (Fig. 8c). The flow-related ecology and population dynamics of golden perch operate over greater spatial scales than previously thought (Zampatti *et al.* 2018, 2019; Stuart and Sharpe 2020), and understanding these dynamics, including the variety of movement types exhibited by different life stages, is essential to improving fish passage science (White *et al.* 2011; O’Connor *et al.* 2015), managing river connectivity issues and maintaining population structure for this wide-ranging species (Silva *et al.* 2018). This knowledge is increasingly important as water management planning progresses from site to connected catchment, and to basin scales (Stewardson and Guarino 2018). Importantly, these movements indicate that there are significant population interactions between the Darling River and the heavily regulated Murray River, including inputs of recruitment pulses (Zampatti *et al.* 2018, 2019; Stuart and Sharpe 2020).

Table 4. Life-history attributes for the Murray cod

ACT, Australian Capital Territory; ARI, Arthur Rylah Institute for Environmental Research; DO, dissolved oxygen; DPI, Department of Primary Industries; EO, expert opinion; F, female(s); M, male(s); MDB, Murray–Darling Basin; NMDB, northern MDB; NSW, New South Wales; NTU, nephelometric turbidity units; SMDB, southern MDB; SWH, structural woody habitat; TL, total length; VFA, Victorian Fisheries Authority; YOY, young-of-the-year

Attribute	Description
Before spawning	
Sexual maturity	4–6 years; 2 kg and 600 mm (F), 0.7 kg and 400 mm (M; Cadwallader and Gooley 1985; Gooley <i>et al.</i> 1995; Rowland 1998b) Size, age and sexual maturity vary throughout the range, with age-at-maturity generally lower in impoundments than in rivers (Forbes <i>et al.</i> 2015a) Size at sexual maturity in the Border rivers (NMDB) is, on average 4 years old and 440 mm for F and M combined (G. Butler, NSW DPI, pers. comm.)
Fecundity and eggs	Fecundity generally related to F size: 6000–10 000 eggs for 2- to 3-kg F; 40 000 eggs for 5-kg F; 90 000 eggs for 23-kg F; 110 000 eggs for 33-kg, 1.15-m F (Stuart and Koehn 2007); and suggested up to 200 000 eggs in very large fish (Lake 1967b; Rowland 1998b) Fecundity in captive broodstock: up to 4900 eggs kg ⁻¹ (Ingram <i>et al.</i> 2012a) Eggs large, 3–3.5 mm in diameter, adhesive (Cadwallader 1979; Cadwallader and Gooley 1984; Rowland 1998a; Gooley <i>et al.</i> 1995); water-hardened eggs: 2.4–3.9 mm in diameter (Ingram <i>et al.</i> 2012a) Condition and fecundity linked to antecedent environmental conditions (EO) Revised fecundity function (C. Todd, ARI, unpubl. data): $Fecundity_{Age} = -386 + \exp(8.57) \times Length_{Age}^{3.36} - (\exp(2.11) \times Length_{Age}^{3.36})^2$
Spawning	
Description	Spawning in river populations appears to occur most years (Rowland 1998b; Humphries 2005; Koehn and Harrington 2006). Generally, form pairs and spawn on one occasion; however, in hatchery ponds, multiple spawning events with multiple partners for both M and F (polygamy and polyandry) have been recorded, with ~17% of total spawning events polygamous (Rourke <i>et al.</i> 2009). Where an F spawned twice in a season, the second spawning contained only ~54% of the eggs of the first, and approximately half the hatchery broodfish failed to spawn at all over a 3-year period (Rourke <i>et al.</i> 2009). Evidence of multiyear pair bonding recorded in the wild from genetic sampling of larvae, with one pair of parents mating for 3 consecutive years (Couch 2018) Hybridisation with trout cod (Wajon 1983; Harris and Dixon 1988; Couch <i>et al.</i> 2016), although rare, occurs naturally where both species occur in sympatry, and has been induced in captive fish in both direct and reciprocal crosses (Douglas <i>et al.</i> 1994; Ingram <i>et al.</i> 2007). Hybrids reared in captivity were fertile and could be back-crossed with Murray cod (Ingram <i>et al.</i> 2012b) M establish nest sites up to 1–2 weeks before spawning, then exhibit parental care, guarding and tending the eggs until they hatch (Rowland 1998a), and generally remain until after the larvae disperse (G. Butler, NSW DPI, unpubl. data). Nest sites are thoroughly cleaned by the M to ensure adhesion of eggs. High degree of variety in nest site selection, including undercut banks, root balls, rocky undercuts, hollow logs and open water. Inexperienced M appear to be poor parents and can abandon nests before the eggs have hatched (S. Rowland, pers. comm.). Older M have been observed to have worn pectoral fins from cleaning and nest tending. M have been recorded sequentially tending multiple broods within the one season, and individuals have also been recorded using the same spawning sites across multiple years
Season	Spawning season for pond-held captive fish typically lasts 1–1.5 months; earlier in the north than the south, and in Vic. earlier in the west than the east (B. Ingram, VFA, unpubl. data). In the wild, predictably spring–summer (mid-October until at least early December) in the SMDB (Humphries 2005; Koehn and Harrington 2006); early September to mid-October in the NMDB (G. Butler, NSW DPI, unpubl. data); potentially similar but starting in early September in the north-western rivers (S. Balcombe, Griffith University, pers. com.); 17 October–10 December in the upper Murrumbidgee River, ACT (Couch 2018)
Conditions	Rising water temperatures to >15°C (Humphries 2005; Koehn and Harrington 2006); 16.5–23.5°C with peak spawning at ~19–20°C (Cadwallader and Gooley 1985; Rowland 1985, 1998a; Gooley <i>et al.</i> 1995; King <i>et al.</i> 2016) In captive pond-held fish, the rate of temperature change increased the incidence of spawning events (B. Ingram, VFA, unpubl. data) Day length may also influence spawning (G. Gooley pers. obs. in Koehn and O’Connor 1990) Relative abundance of larvae is positively associated with increasing discharge (King <i>et al.</i> 2016), but declines with increasing number of flood days in preceding 90 days (King <i>et al.</i> 2016) Spawning occurs over a range of flow conditions and appears not to increase in flood years (Koehn and Harrington 2006; King <i>et al.</i> 2009a) River discharge is important in lower-order streams to allow adults to disperse to locate spawning sites and mates (G. Butler, NSW DPI, pers. obs.)
Location	Predation of eggs in nests by <i>Hypseleotris</i> sp. has been observed (G. Butler, NSW DPI, pers. obs.) Eggs laid on hard substrates such as logs, rocks and clay surfaces (Cadwallader 1979; Cadwallader and Gooley 1984; Gooley <i>et al.</i> 1995; Rowland 1998b; Lintermans 2007) Nest sites in the NMDB are in low-velocity areas (<0.1 m s ⁻¹) to avoid disturbance, and excessively increased flow velocities during this period can lead to nest abandonment or premature post-hatch dispersal of larvae (G. Butler, NSW DPI, pers. comm.) Nests and spawning occur in impoundments, ponds and weir pools, but there is no apparent evidence for hatch and larval survival in lentic habitats (EO)

(Continued)

Table 4. (Continued)

Attribute	Description
After spawning	
Hatching	<p>Can begin 6 days after fertilisation and usually continues over 2–4 days, with variability in length-at-hatch and degree of larval development common: larvae that hatch earlier are less developed and shorter than larvae that hatch later (size range at hatch 6.4–10.5 mm; Ingram <i>et al.</i> 2012a; B. Ingram, VFA, unpubl. data)</p> <p>Incubation period and hatch rates depend largely on water temperatures</p> <p>Larvae hatch with large yolk sacs and feed endogenously for 8–12 days (Lake 1967b; Rowland 1989)</p> <p>Excessively increased flow velocities during nest caring may lead to nest abandonment or result in the premature dispersal of larvae from the nest (G. Butler, NSW DPI, pers. comm.)</p> <p>Relative abundance of larvae is positively associated with increasing discharge, but declines with increasing number of flood days in preceding 90 days (King <i>et al.</i> 2016)</p>
Larvae	<p>In larger flowing river systems, larvae leave the nest site after 8–12 days, rise in the water column and undergo non-obligatory downstream dispersal (Humphries <i>et al.</i> 2002; Koehn and Harrington 2005, 2006). Wild, drifting larvae were 9.5–14.8 mm TL and present for up to 10 weeks (5 weeks either side of a peak in November) in the SMDB (Koehn and Harrington 2006). Larval dispersal 6 November–20 December in the upper Murrumbidgee River (Couch 2018); October in the NMDB (G. Butler, NSW DPI Fisheries, pers. comm.)</p> <p>In hatcheries, larvae tend to clump on the benthos for 4–6 days, after which they can undertake short-burst swims of 10–30 mm in distance and disperse just prior to the onset of feeding (B. Ingram, VFA, unpubl. data)</p> <p>Swimming ability improves rapidly after swim bladder inflation; capable swimmers 1–2 days prior to yolk sac exhaustion</p> <p>Free embryos are large (12 mm) and well developed at the onset of feeding (Tonkin <i>et al.</i> 2006) 9–11 days after hatching (Lake 1967b; Rowland 1989), easily capturing small zooplankton (especially crustaceans and chironomid larvae; Rowland 1985)</p> <p>Larval dispersal in low-velocity waterholes and weir pools is suggested to be achieved through active movement rather than drift (Stuart <i>et al.</i> 2019)</p> <p>It appears that temperature affects rates of development and is likely to determine when larvae leave the nest (Humphries 2005), with collections of larvae increasing with a temperature rise in the previous week (King <i>et al.</i> 2016)</p> <p>Larval and YOY survival appears to be directly reliant on prey abundance, and there is a strong positive relationship between discharge and growth rates, probably indicating a link between flow and riverine productivity (Tonkin <i>et al.</i> 2017b). Larvae are capable of exploiting a large range of prey items, with copepods, cladocerans, chironomid larvae and decapod larvae the most important prey items (Ingram and De Silva 2007; Belton 2015). Larval gut fullness increases with declining yolk reserves and consists almost exclusively of benthic prey, regardless of flow conditions. Fewer empty guts occurred during low-flow compared with high-flow years, and inundation of in-channel benches, dry channels and oxbow lakes did not increase exploitation of pelagic, floodplain-derived zooplankton (Kaminskas and Humphries 2009)</p> <p>Critical swimming speeds of larval stages range from 16.3 to 23.1 cm s⁻¹ (Kopf <i>et al.</i> 2014)</p>
Recruitment	<p>Although spawning appears to occur most years in river populations with flowing reaches (Humphries 2005; Koehn and Harrington 2006), intensity and recruitment success appears variable. Murray cod recruit to some extent in both flood and non-flood years, supporting a broad flow-recruitment model (Humphries <i>et al.</i> 1999; King <i>et al.</i> 2009a), with post-larval survival largely influencing recruitment (Koehn and Harrington 2006). This appears to be strongly linked to lotic conditions and river flows, with good year classes in some rivers coinciding with an increase in discharge or flooding at or soon after spawning (Ye <i>et al.</i> 2000; Rowland 2005). Flooding in late autumn–spring appears to provide optimum conditions for survival and recruitment of larvae and juveniles in rivers (Rowland 1985, 1989, 1998a), with little recruitment during low-flow years in the lentic reaches of the lower Murray River, which consists of slow-flowing weir pools (Pierce 1990; Zampatti <i>et al.</i> 2014). King <i>et al.</i> (2007) found increased recruitment in the year of flooding, although distinct correlations between flows and year classes in the mid-Murray River are less certain (EO)</p> <p>Recruitment has declined in some areas, such as the lower Murray River, coinciding with reduced flooding and flow-pulse frequency, habitat loss and reduced hydrodynamic diversity (especially in flowing habitats), but has been more consistent in lotic habitats, including in flowing Chowilla anabranches (Wilson <i>et al.</i> 2012; Zampatti <i>et al.</i> 2014)</p> <p>Commercial catches in the lower Murray River before 2003 indicate that strong recruitment of Murray cod occurred in 1994 associated with large in-stream and overbank discharges of 20 000–60 000 ML day⁻¹, with low levels in 1998 and 2000 (Ye and Zampatti 2007). In Gunbower Creek (mid-Murray River) and the lower Darling River, recruitment was enhanced with environmental flows that had an annual spring rise with no rapid water level drops, and maximised hydraulic diversity, provided there was an annual winter base flow (Sharpe and Stuart 2018; Stuart <i>et al.</i> 2019)</p> <p>Winter is considered a critical period for YOY survival, and recruitment may be greatly reduced where winter base flows are low and permanent lotic conditions have been lost (Sharpe and Stuart 2018)</p> <p>Water temperature affects egg and larval development, with eggs intolerant to temperatures less than ~15°C, indicating that survivorship will be greatly affected by cold water releases (Ryan <i>et al.</i> 2003). The successful recruitment of stocked fish into the adult population in the Mitta Mitta River only occurred when temperatures (and flows) were suitable (Tonkin <i>et al.</i> 2020a). In parts of the SMDB following catastrophic fish kills, recovery appears to have occurred through natural recruitment and possibly immigration rather than from stocking (Thiem <i>et al.</i> 2017). Although spawning occurs in impoundments, little or no recruitment is evident (Forbes <i>et al.</i> 2016)</p>

(Continued)

Table 4. (Continued)

Attribute	Description
Growth	<p>Growth varies between habitats and regions, with greater maximum lengths in impoundments (1400 mm) than in rivers (1250 mm; Anderson <i>et al.</i> 1992; Gooley 1992; Forbes <i>et al.</i> 2015a). M are marginally larger than F at a given age (Anderson <i>et al.</i> 1992), and length and age at maturity can vary within and between populations (Forbes <i>et al.</i> 2015a)</p> <p>Flow is a significant factor influencing growth, with discharge in spring being the most important variable, along with temperature, antecedent summer–autumn discharge variation and summer–autumn discharge (Tonkin <i>et al.</i> 2017b; Stoffels <i>et al.</i> 2019)</p> <p>The growth of juveniles is predicted to decline directly downstream of an impoundment due largely to energetic costs associated with active metabolism outweighing energetic gains through food consumption (Whiterod <i>et al.</i> 2018). Water and lipid content and whole-body energy density relationships (Whiterod 2010) have been used in a bioenergetic model (Whiterod <i>et al.</i> 2013, 2018), with modelled simulations predicting juvenile growth rates to be greatly reduced (even negative) due to changes in water temperatures and velocities downstream of impoundments (Whiterod <i>et al.</i> 2018). Growth rates increased significantly at temperatures >18.5°C but not at temperatures <15.5°C (Ryan <i>et al.</i> 2003)</p> <p>The weight of hatchery fish can vary from 300 to 800 g by 10 months, depending on conditions and feeding regimes (Haldane 2014). One-year-old farmed Murray cod reach 221–353 mm in length (mean 275 mm) and 150–785 g in weight (mean 322 g; Ingram 2004). In ponds, fry growth is rapid: from 11.0–20.7 mm (mean 14.6 mm) to 33.8–56.9 mm (mean 44.1 mm) in 24–68 days (mean 41 days), an average growth rate of 0.76 mm day⁻¹ (Ingram 2009)</p> <p>Revised growth function (C. Todd, ARI, unpubl. data): $Length_{Age} = 1360 \times (1 - \exp(-0.067 \times (Age + 1.54)))$</p>
Habitats	<p>Occupy a broad range of flowing and standing waters, but are considered a benthic (Koehn 2009a) main river channel specialist, preferentially selecting flowing water: the river channel, floodplain channels in high flows, channels within Lake Mulwala (SMDB; Koehn 2009b) and flowing anabranches (Saddlier <i>et al.</i> 2008)</p> <p>Found in a wide variety of habitats, from deep, turbid, slow-flowing lowland rivers through to fast-flowing, clear and rocky highland streams (Trueman 2012a; Koehn and Nicol 2014; Mallen-Cooper and Zampatti 2015)</p> <p>Adults and YOY select similar microhabitats, based on structural variables regardless of site or hydrologic conditions (Koehn 2009b). In lowland rivers, they show a high affinity for SWH (>75% cover), water depth (2.8 m), proximity to the bank, higher surface flows (0.37 m s⁻¹; Koehn and Nicol 2014), substrate variation and higher overhanging vegetation (Koehn 2009b). There is a strong correlation with high densities of SWH at both microhabitat (Koehn 2009b) and river-reach scales (Boys and Thoms 2006). For the latter, there was an estimated fourfold increase in abundance of Murray cod following changes in SWH density (from existing degraded levels to the estimated natural levels) in several rivers across northern Vic.</p> <p>There is a preference for flowing waters, higher water velocities (Saddlier <i>et al.</i> 2008; Koehn and Nicol 2016; Stuart <i>et al.</i> 2019; S. Raymond, ARI, pers. comm.) and hydraulic diversity (Zampatti <i>et al.</i> 2014; Stuart <i>et al.</i> 2019) in the SMDB, but (contrastingly) selected deeper areas and lower water velocities in the Gwydir River (NMDB; Carpenter-Bundhoo <i>et al.</i> 2020a). However, YOY select shallower habitats, closer to the riverbank, with higher SWH loadings than adults (Koehn 2009b). Numbers increase in near-bank areas when hollows are a component of the SWH (Lieschke <i>et al.</i> 2016). Reinstatement of SWHs has been shown to increase the population size when a source of recruits is close (Lyon <i>et al.</i> 2019)</p> <p>Occur in floodplain channels when they are inundated (Koehn 2009b), but the use of the floodplain proper by adults, juveniles and larvae appears limited (Koehn and Harrington 2005; Leigh and Zampatti 2013; Koehn and Nicol 2014). Inundation of floodplain channels can greatly increase the proportion of preferred channel habitat area (Koehn 2009b). Juveniles <1 year appear to settle in the main river channel at a late larval stage and are generally not found in off-channel habitats (Koehn and Harrington 2005; but see Anderson 1915). Juveniles selected structure over open habitats, preferring rocky rubble (NMDB; Hutchison <i>et al.</i> 2020)</p> <p>The widely reported susceptibility to blackwater events (King <i>et al.</i> 2012; Leigh and Zampatti 2013; Thiem <i>et al.</i> 2017) was confirmed in simulations of hypoxic blackwater using dried river red gum (<i>Eucalyptus camaldulensis</i>) leaf litter, with juveniles sensitive to low DO, with 48 h LC₅₀ mortality at 1.58 ± 0.01 mg L⁻¹ DO and predictions that juvenile mortalities would start with DO concentrations of 2.4–3.1 mg L⁻¹ alone (Small <i>et al.</i> 2014). Aerobic capacity is low, but temperature independent, suggesting some adaptability to fluctuating temperatures (Clark <i>et al.</i> 2005; Small <i>et al.</i> 2014)</p> <p>Allen-Ankins <i>et al.</i> (2012) suggest that the sensory physiology of this species is well adapted to turbid conditions</p> <p>Salinities >0.34 g L⁻¹ are likely to significantly affect recruitment. No larvae survived salinities >0.30 g L⁻¹; the LC₅₀ salinity for 1- and 12-day trails was 2.33 and 0.35 g L⁻¹ respectively. Salinity sensitivities were moderated by raising pH between 6.2 and 8.8 and stimulated by increasing temperatures; oxygen consumption increased significantly at salinities >8.0 g L⁻¹ (Chotipuntu 2003)</p>
Movements	<p>Once considered to be sedentary (Reynolds 1983), although rare individual movements of up to 1498 km had been reported (Anon. 1971). Generally, have restricted home ranges and high site fidelity for most of the year, but can undertake large-scale movements (<120 km), with homing behaviour common (Koehn <i>et al.</i> 2009; Leigh and Zampatti 2013; Llewellyn 2014; Koehn and Nicol 2016; Carpenter-Bundhoo <i>et al.</i> 2020a; Koster <i>et al.</i> 2020). Populations are genetically panmictic (Rourke <i>et al.</i> 2010)</p>
Eggs and larvae	<p>Eggs adhesive and attached to a substrate</p> <p>After hatching, free embryos can potentially drift for 5–7 days (Humphries 2005), during which they can theoretically travel up to 740 km, depending on river flows (Murray River; Koehn 2011). Dispersal is active or by drift, depending on water velocity, and in some cases drift distance can be minimal (Stuart <i>et al.</i> 2019), especially in isolated pools in the NMDB (S. Balcombe, Griffith University, pers. obs.)</p>

(Continued)

Table 4. (Continued)

Attribute	Description
	After absorption of yolk sac, will swim up into the water column and commence active feeding (Cadwallader and Gooley 1985)
	Under regulated high flows, during the spawning season, larvae may have a reduced ability to actively disperse into suitable nursery habitat due to an increase in current velocity above critical swimming thresholds (Kopf <i>et al.</i> 2014). The prolonged (60 min) swimming speed for preflexion larvae is 1.1 cm s ⁻¹ , compared with 5.9 cm s ⁻¹ for flexion larvae, 10.7 cm s ⁻¹ for post-flexion larvae and 10.7 cm s ⁻¹ for meta-larvae (Kopf <i>et al.</i> 2014)
Juveniles	Limited movement over the short term (Jones and Stuart 2007), but some fish may move longer distances (juvenile fish (~450 mm) have been observed moving upstream through the Torrumbarry fishway (mid-Murray River); I. Stuart, ARI, unpubl. data)
	Stocked Murray cod fingerlings appear to have a high degree of site fidelity, especially in the first year following release, but are also capable of dispersing some distance after release (e.g. 9 km after 3 weeks; Ingram <i>et al.</i> 2015)
Adults	Exhibit high degrees of site fidelity and homing (Koehn <i>et al.</i> 2009; Koehn and Nicol 2016)
	Movements occur both upstream and downstream in approximately equal proportions (Saddlier <i>et al.</i> 2008; EO). Movement and activity strongly affected by discharge (Thiem <i>et al.</i> 2018, 2020). Adult pre-spawning movements occur from August to December to a second site, usually followed by rapid, return movements (December–January) with approximately two-thirds of fish returning to their original home site, mostly within several weeks of spawning (Koehn <i>et al.</i> 2009)
	Otolith microchemistry confirms residency within broad geographic regions (hundreds of kilometres), and limited movements between regions over their lifespan (Zampatti <i>et al.</i> 2019)
	Timing of movements is not synchronous between individuals, and the degree of movement varies between individuals, sizes, original location and years. Fish >650 mm move further than fish <650 mm, perhaps due to differences in maturity, and fish from Lake Mulwala move into upstream rivers (Koehn 2006; Koehn <i>et al.</i> 2009). Large variation in individual movements, with one fish recaptured 1224 km upstream after 488 days, and another 12 km downstream after 4431 days (Llewellyn 2014), although the rates of movements within this time span are unknown
	Move extensively between anabranches and the main river channel (Saddlier <i>et al.</i> 2008; Koehn <i>et al.</i> 2009; Leigh and Zampatti 2013), and move between the main channel and floodplains during high-discharge periods and hypoxic blackwater events, then return to channel habitats (Jones and Stuart 2007, 2008; Leigh and Zampatti 2013). Use of ephemeral floodplain habitats is limited (Koehn <i>et al.</i> 2009; Leigh and Zampatti 2013; Koehn and Nicol 2016), but have become stranded in channel pools behind floodplain regulators (Jones and Stuart 2008). More movements, over greater distances, are associated with increased discharge (Koehn <i>et al.</i> 2009; Leigh and Zampatti 2013; Thiem <i>et al.</i> 2020)
	Timing of movements can vary between rivers. Upstream migrations in the lower Murray River (Saddlier <i>et al.</i> 2008) were observed March–May, 5 months prior to spawning migrations in the mid-reaches (Murray and Ovens rivers and Lake Mulwala; Koehn <i>et al.</i> 2009). Increases in flow prior to the spawning season have been shown to be beneficial, allowing adults to move over barriers to seek out mates and nesting sites (G. Butler, NSW DPI, pers. comm.)
	Become less active during periods of low DO (Koster <i>et al.</i> 2020)
Behaviour	Territorial and aggressive, and even cannibalistic, from a young age or size (from 20 mm; B. Ingram, VFA, pers. obs.). Adults considered highly territorial and solitary, except prior to and during the breeding season, when large fish may aggregate around woody habitats (Cadwallader 1979; Cadwallader and Backhouse 1983; Cadwallader and Gooley 1985)
	Considered a swimming generalist, with moderate ability across all aspects of swimming (consistent with typical ambush predators); maintaining low metabolic rates and having small energetic demands compared with more active species (Whiterod 2013; Whiterod <i>et al.</i> 2013)
	Exploration of temperature, swimming speeds, heart beat and oxygen consumption suggests evolution of a temperature-independent factorial aerobic scope in response to fluctuating and unpredictable thermal climates (Clark <i>et al.</i> 2005)
	Activity highest during crepuscular and nocturnal periods with higher water temperatures (19–30°C; January–March). Active throughout the full diel cycle at lower (9–21°C) temperatures, but rarely dormant. Activity peaked during low light, water temperatures of ~20°C and discharge of ~400 ML day ⁻¹ in the Wakool River (SMDB; Thiem <i>et al.</i> 2018). Were less active in a weir pool during periods of decreased DO (Koster <i>et al.</i> 2020)
	Prey consumption by juveniles was no different in turbidity levels of 0–150 NTU or in light verses dark, but did increase with habitat complexity (Allen-Ankins <i>et al.</i> 2012)
Key threats	Key threats have been also identified in the national recovery plan (Koehn 2005a; National Murray Cod Recovery Team 2010a, 2010b; ACT Government 2017) and the Murray cod population model (Todd and Koehn 2009; Koehn and Todd 2012). Key threats include: <ul style="list-style-type: none"> • Loss of instream structure (Nicol <i>et al.</i> 2004; Lyon <i>et al.</i> 2019) • Thermal pollution that limits spawning and egg and larval survival (Todd <i>et al.</i> 2005; Sherman <i>et al.</i> 2007) and affects juvenile growth rates (Whiterod <i>et al.</i> 2018), adult movement behaviour and survival of juvenile fish (Tonkin <i>et al.</i> 2020a) in reaches downstream of major impoundments (Lugg and Copeland 2014) • Fish kills; blackwater and poor water quality (Koehn 2005b; King <i>et al.</i> 2012; Thiem <i>et al.</i> 2017) • Recreational harvesting, which can affect population structure (Nicol <i>et al.</i> 2005; Rogers <i>et al.</i> 2010). The estimated annual national recreational harvest is 128 692 fish (Henry and Lyle 2003); estimated annual catch (±s.d.) in the Murrumbidgee River is 27 276 ± 512 fish, although the release rate is high (Forbes <i>et al.</i> 2015b). Catch rate for boat-based fishers is 0.228 fish angler⁻¹ h⁻¹, which is significantly greater than for shore-based fishers (0.092 fish angler⁻¹ h⁻¹; Forbes <i>et al.</i> 2015b). Overfishing of drought refugia in ephemeral rivers during drought years (EO)

(Continued)

Table 4. (Continued)

Attribute	Description
	<ul style="list-style-type: none"> • Post-capture handling methods, which affect catch–release survival, with fish restrained with bare hands having significantly higher mortality than those restrained using other methods. The estimated highest release mortality is 15% in fishing tournaments (Hall <i>et al.</i> 2012), although this was estimated to be only ~2% under normal fishing conditions in the SMDB (Douglas <i>et al.</i> 2010) • Weir type, with the mortality of larval passage through undershot weirs being 52%, compared with 11% through overshot weirs (Baumgartner <i>et al.</i> 2006). Adults have been observed trapped on power station trash racks when subjected to high water velocities exiting a fishway (Stuart <i>et al.</i> 2010) • Loss of larvae, juveniles and adults into irrigation channels (Gilligan and Schiller 2003; Koehn and Harrington 2005; King and O’Connor 2007; Koehn 2011). • Flow regime changes and loss of lotic riverine habitats. Sudden reductions in water levels during spawning periods, reduced hydraulic complexity (Gibbs <i>et al.</i> 2020) and low winter flows (Stuart <i>et al.</i> 2019) that increase risks to fish (especially YOY) through predation, competition, habitat loss, drying, low productivity and poor water quality (EO). Changes to the natural hydrologic regime can disrupt cues that initiate maturation and spawning, in addition to altering the conditions suitable for recruitment, and may have had more of an effect on post-spawning recruitment than on the prevention of spawning (Humphries and Lake 2000) • Loss of hydraulic complexity due to weir pools in the lower Murray River (Zampatti <i>et al.</i> 2014; Bice <i>et al.</i> 2017; Mallen-Cooper and Zampatti 2018) and effects of floodplain regulators (Mallen-Cooper <i>et al.</i> 2008, 2011) • Barriers restricting juvenile and adult movement (Baumgartner <i>et al.</i> 2014b). <p>Genetic studies have suggested that flow regulation per se may not have been the most critical threat to the persistence of Murray cod over the past century compared with the reduced frequency of large floods, overfishing and chemical pollution (Harrisson <i>et al.</i> 2017; see also Rowland 2005)</p> <p>Considered moderately tolerant to drought (Crook <i>et al.</i> 2010) and climate change effects (Chessman 2013); susceptible to post-wildfire sediment flows (Lyon and O’Connor 2008)</p>

Table 5. Life-history attributes for trout cod

ACT, Australian Capital Territory; ARI, Arthur Rylah Institute for Environmental Research; DPI, Department of Primary Industries; EO, expert opinion; F, female(s); M, male(s); NSW, New South Wales; RBL, relative body lengths; SWH, structural woody habitat; VFA, Victorian Fisheries Authority; YOY, young-of-the-year

Attribute	Description
Before spawning	
Sexual maturity	At 3–5 years, with M generally younger and smaller than F (M >350 mm (570 g) and F >430 mm (1200 g); see Gooley in Koehn and O’Connor 1990; Lyon <i>et al.</i> 2012). Smallest mature F was >245 mm (Cadwallader 1977), but the smallest confirmed to have spawned in the wild was 283 mm, 299 g and 5 years old (Lyon <i>et al.</i> 2012). In the Ovens River, 50% of the population was mature at 325 mm (F) and 250 mm (M), with 90% of the population mature at 394 mm (F) and 318 mm (M; Lyon <i>et al.</i> 2012). In a hatchery, the smallest F that produced viable eggs (eggs that hatched) was 360 mm (580 g), and the smallest running ripe M was 310 mm (390 g; B. Ingram, VFA, unpubl. data)
Fecundity and eggs	Number of eggs stripped from hatchery broodfish ranged from 1 188 to 11 338, with fecundity estimated at 591–5846 eggs kg ⁻¹ (mean 3300 eggs kg ⁻¹ ; Ingram and Rimmer 1992) Trout cod broodstock that spawned naturally in earthen ponds produced up to 28 400 eggs (B. Ingram, VFA, unpubl. data) In the wild, fecundity ranges from 2027 eggs (291 mm F) to 14 000 eggs (450 mm F), with a mean fecundity of 9 eggs g ⁻¹ fish weight (range 7–14 eggs g ⁻¹ ; Lyon <i>et al.</i> 2012). Eggs are relatively large, 2.4–3.9 mm in diameter (mean 3.2 mm) for water-hardened eggs (Ingram <i>et al.</i> 2012a); 2.5–3.6 mm in diameter for round and adhesive eggs (Ingram and Rimmer 1992) Revised fecundity function (C. Todd, ARI, unpubl. data): $Fecundity_{Age} = 1.16 + \exp(-11.65) \times Length_{Age}^{3.18}$
Spawning	
Description	Considered typical ‘nesters’ and ‘guarders’, being classified as an equilibrium species (King <i>et al.</i> 2013). Thought to form pairs, provide parental care to eggs and spawn annually with all eggs released at once (Cadwallader 1977) Oocytes can be resorbed at >21°C (Lake 1967a) Abundance of larvae greatest at 20°C (King <i>et al.</i> 2016) Lyon <i>et al.</i> (2012) observed an uneven sex ratio of 2.5 : 1 F : M Unlike other <i>Maccullochella</i> spp., trout cod rarely spawn unassisted in captivity. In hatchery production, during September–October (with water temperatures rising to ~16°C), mature broodstock are usually removed from the ponds and injected with gonadotrophin, after which eggs and spermatozoa are manually stripped (Rimmer 1987; Ingram and Rimmer 1992) Hybridisation with Murray cod occurs naturally (Wajon 1983; Harris and Dixon 1988) where both species occur sympatrically, and has also been induced in captive fish (Douglas <i>et al.</i> 1995; Ingram <i>et al.</i> 2007). Although Murray cod–trout cod hybrids are rare in the Murray River population (Douglas <i>et al.</i> 1995; ARI, unpubl. data), 5–6% of larvae in the Murrumbidgee River were hybrid, being present at half the sites surveyed (Couch <i>et al.</i> 2016). Survival rates of hybrid larvae are not known. Hybrids reared in captivity were fertile and could be back-crossed with Murray cod (Ingram <i>et al.</i> 2012b).

(Continued)

Table 5. (Continued)

Attribute	Description
Season	Spring (October and November; Koehn and Harrington 2006) Had been considered to occur ~3 weeks before Murray cod, with water temperatures a few degrees cooler (Cadwallader 1977 ; Cadwallader and Backhouse 1983), but wild spawning in the mid-Murray River was found to be concurrent with Murray cod but over a much shorter period (Koehn and Harrington 2006)
Cues	Water temperature and day length (cumulative degree-days) are the most likely cues for spawning (EO)
Conditions	Water temperatures 14–22°C (Ingram and Rimmer 1992), but preferably >15°C (Koehn and Harrington 2006) Flow change does not seem to be a trigger, because spawning occurs over a range of flows in regulated and unregulated rivers (Koehn and Harrington 2006) and impoundments (e.g. Bendora Dam in ACT, Cataract Dam in NSW; M. Lintermans, University of Canberra, unpubl. data)
Location	No observations in nature, although larval capture indicates this probably occurs on hard surfaces, such as boulders, clay and on or in logs, with eggs assumed to be guarded by the M (Cadwallader 1979)
After spawning	
Behaviour	Hatch at 5–9 days, with continued hatching occurring for up to a further 10 days at 15.5–23°C (Ingram and Rimmer 1992), with success rates of 0–98% (mean 50%; B. Ingram, VFA, unpubl. data) Larvae hatch at 6–9 mm (Ingram and Rimmer 1992 ; Ingram and Douglas 1995) Wild-caught drifting larvae were 10.0–18.2 mm, and are present for 2 weeks, with collection peaking in November (Koehn and Harrington 2006) Larval swimming capacity is high, suggesting some measure of active dispersal, not just drift. Larvae had the highest swimming speeds, both critical (maximum absolute 46.4 cm s ⁻¹ and 44.6 RLB s ⁻¹) and prolonged (maximum 15.4 cm s ⁻¹ , 15.6 RLB s ⁻¹) of six native fish species tested (Kopf <i>et al.</i> 2014) In hatcheries, immediately after hatching, healthy larvae formed tight schools that later dispersed once feeding began (Ingram and Rimmer 1992)
Recruitment	Population growth driven primarily by larval and juvenile survival, with a positive relationship with higher growth rates provided by higher summer and autumn flow variability and spring discharge (Tonkin <i>et al.</i> 2017b) Within the 10-year stocking regime developed for the Ovens River (Bearlin <i>et al.</i> 2002), higher survival occurred in only 2 years, with many years contributing little to the population, indicating a long-term stocking strategy is needed for population establishment (Lyon <i>et al.</i> 2012) Recruitment in Bendora Dam (ACT) has also been sporadic, with recruits recorded in 2001, 2011 and 2014 from fish stocked since 1989 (M. Lintermans, University of Canberra, unpubl. data) A stocking program from 1993 to 2001 in the mid-Murrumbidgee River, involving the release of 309 000 fingerlings (Gilligan 2005 ; NSW DPI, unpubl. data), appears to have been successful, with the capture of numerous new recruits (individuals <150 mm) during 2007–15 (NSW DPI, unpubl. data)
Growth	Larvae (6.0–8.8 mm) begin exogenous feeding after 10 days (B. Ingram, VFA, unpubl. data) and in hatchery conditions grow steadily to 36.3–48.6 mm by 60 days, an average growth rate of 0.62 mm day ⁻¹ (Ingram 2009) Wild trout cod larvae at 12.9–15.0 mm ranged in age from 16–20 days (Koehn and Harrington 2006) Growth rates vary with flow conditions, with a positive relationship between summer and autumn flow variability and with spring discharge (Tonkin <i>et al.</i> 2017b) Revised growth function (C. Todd, ARI, unpubl. data): $Length_{Age} = 577.13 \times (1 - \exp(-0.15 \times (Age + 1.29)))$
Habitats	Generally inhabit the mid to upper regions of flowing rivers with suitable cover, in riffles, runs and pools, as well as larger main river channels (Douglas <i>et al.</i> 1994 ; Ingram and Douglas 1995 ; Growth <i>et al.</i> 2004) Adults prefer higher surface flows and suitable in-stream habitat, such as wood, deep water and steep banks (Growth <i>et al.</i> 2004 ; Nicol <i>et al.</i> 2007) In the Murray River, preferred habitats consist of deeper water (2.9 m), faster water velocities (0.49 m s ⁻¹), further from the riverbank, with a high cover (68%) of SWH (Koehn and Nicol 2014). In the Murrumbidgee, adults preferred outer river bends associated with deeper areas and containing more SWH (Ebner and Thiem 2009) Larvae and YOY only appear in the main channel and flowing anabranch channels, not in off-channel river habitats (Koehn and Harrington 2006). They readily use newly reintroduced woody habitats (Nicol <i>et al.</i> 2004 ; Lyon <i>et al.</i> 2019 ; S. Raymond, ARI, pers. comm.), but because movements are limited, it has been suggested that habitat patches be created <1 km apart (Koehn <i>et al.</i> 2008)
Movements	
Eggs and larvae	Eggs adhesive, but larvae are captured in drift nets in flowing water habitats (Koehn and Harrington 2005, 2006). Critical swimming speeds of larval stages range from 23.0 to 40.0 cm s ⁻¹ (Kopf <i>et al.</i> 2014)

(Continued)

Table 5. (Continued)

Attribute	Description
Juveniles	The highest rates of dispersal are likely to be from larval dispersal and juvenile recolonisation, rather than from adult fish (Koehn <i>et al.</i> 2008). Tracking of stocked subadult fish indicates an ability to undertake rapid downstream movements in both upland and lowland habitats, although results were confounded by high mortality, including substantial predation (Ebner <i>et al.</i> 2007; Ebner and Thiem 2009)
Adults	<p>Adults exhibit high site fidelity and homing rates, with generally limited movements but occasional larger-scale excursions (up to 66 km return; Koehn <i>et al.</i> 2008; Ebner and Thiem 2009; Koehn and Nicol 2016)</p> <p>No apparent obligatory migration, with only 10% of fish moving >3 km (Koehn <i>et al.</i> 2008)</p> <p>Most movements <1 km, with 50% of fish showing essentially no movement and 75% of fish moving <25 m (Koehn and Nicol 2016). Core ranges (\pms.d.) variously calculated as 61 ± 41 m (Murray River, linear home range; Koehn <i>et al.</i> 2008), 83 ± 30 m (Murrumbidgee River, diel range; Thiem <i>et al.</i> 2008) and 78 ± 3 m (Murrumbidgee River, home range; Ebner and Thiem 2009). Transitions from small to large (<1 km to >5 km) movements were rare, with little seasonality (Koehn and Nicol 2016). Larger movements of up to 116 km have been recorded with high spring flows (Koehn <i>et al.</i> 2008), and home range shifts of up to 36 km have been observed (Ebner and Thiem 2009), but larger movements in the Murrumbidgee River showed no apparent correlation with flow (Ebner and Thiem 2009). Individual movement rates vary, with the fastest recorded covering 10.9 km in a maximum of 4 h (Ebner and Thiem 2009)</p> <p>Activity peaks in periods of low light, and linear movement range is correlated with fish size (Thiem <i>et al.</i> 2008)</p> <p>Movements into flooded anabranches observed, with limited movements onto the nearby floodplain also reported (Koehn and Nicol 2016). In smaller upland rivers, movements can be restricted due to limited habitat availability and physical barriers, such as waterfalls (Ebner <i>et al.</i> 2009a). Low to moderate numbers of fish move through the fish lock at Lake Mulwala (Stuart <i>et al.</i> 2010; Koehn <i>et al.</i> 2013), with some fish then moving upstream through the lake</p> <p>Limited large movements mean that population expansions or recolonisations occur slowly, as exhibited in the Murray River and stocked populations in the Murrumbidgee, Lower Goulburn and Ovens rivers (Lyon <i>et al.</i> 2012; Koehn <i>et al.</i> 2013; Douglas <i>et al.</i> 2012)</p>
Behaviour	<p>Young fish establish well-defined territories in aquaria (Cadwallader and Gooley 1984)</p> <p>Can be very aggressive</p> <p>Crepuscular in activity (Ebner <i>et al.</i> 2009a; Thiem <i>et al.</i> 2008)</p>
Key threats	<p>Key threats include:</p> <ul style="list-style-type: none"> • Removal of instream woody habitat, especially in the mid-river channel (Nicol <i>et al.</i> 2007; Koehn and Nicol 2014) • Cold water releases that affect spawning and recruitment (Koehn <i>et al.</i> 1995; Todd <i>et al.</i> 2005) • Loss of lotic riverine habitats (EO) • Post-bushfire sediment slugs and blackwater events (Saddler <i>et al.</i> 2002; Lyon and O'Connor 2008; Koster <i>et al.</i> 2009; King <i>et al.</i> 2012); mobile sand bars can also limit deeper habitats and cause barriers, especially in low flows (Lintermans 2004) • In-stream barriers that affect movements (Koehn <i>et al.</i> 2008; Ebner and Thiem 2009) • Loss of larvae into irrigation channels (Koehn and Harrington 2006) and damage passing over weirs (Baumgartner <i>et al.</i> 2006, 2009). Floodplain regulators can also trap fish in floodplain channels after closure (Jones and Stuart 2008) • Predation from introduced species, including redfin (<i>Perca fluviatilis</i>) and brown trout (<i>Salmo trutta</i>; Cadwallader 1996; McDowall 2006) • Susceptibility to disease (Ingram and Rimmer 1992), with several parasites recorded, including many protozoans, such as <i>Chilodonella hexasticha</i>, which has killed hatchery brood fish (Rowland and Ingram 1991; Ingram and Rimmer 1992; Douglas <i>et al.</i> 1994) and has been linked to egg reabsorption. Such susceptibility to infestations from <i>Chilodonella</i> protozoa may threaten wild populations (Ingram and Rimmer 1992; Douglas <i>et al.</i> 1994) <p>Considered an aggressive species and highly susceptible to angling (meaning that despite regulations preventing angler harvest, fishing pressures include illegal catch, misidentification and unintentional harvest; Lyon <i>et al.</i> 2018), potential capture–release stress, injury and mortality (which may be similar to the 2–15% mortality estimated for Murray cod) are considered to be potential threats (Lintermans 2007; Douglas <i>et al.</i> 2010; Hall <i>et al.</i> 2012; Forbes <i>et al.</i> 2020). Population structure appears to be affected by angler harvest (ARI, unpubl. data)</p> <p>Effects of carp are unknown, but may relate to competition, and although there is clear habitat separation in the Murray River (Koehn and Nicol 2014), this may not be so in smaller waters with high carp densities</p> <p>Murray cod may cause competition, predation (EO) and hybridisation (Couch <i>et al.</i> 2016)</p> <p>Considered highly vulnerable to drought (Crook <i>et al.</i> 2010) and climate change impacts (Chessman 2013)</p>

Table 6. Life-history attributes for golden perch

To elucidate the biology of this species in the northern Murray–Darling Basin (NMDB), some aspects of similar subspecies, namely the Fitzroy River golden perch (FRGP; *Cockayne et al. 2013*) and Lake Eyre golden perch (LEGP; *Cockayne et al. 2015*) have been included. ARI, Arthur Rylah Institute for Environmental Research; DSITI, Department of Science, Information Technology and Innovation, Queensland; DO, dissolved oxygen; DPI, Department of Primary Industries; EO, expert opinion; F, female(s); LCF, Length to Caudal Fork; LD₅₀, lethal dose to 50% of test individuals; M, male(s); MDB, Murray–Darling Basin; NSW, New South Wales; SL, standard length; SMDB, southern MDB; TL, total length; VFA, Victorian Fisheries Authority; YOY, young-of-the-year

Attribute	Description
Before spawning	
Sexual maturity	At 3 years for M and 4 years for F (<i>Lake 1967c</i> ; <i>Mallen-Cooper and Stuart 2003</i>), older in rivers than in impoundments (<i>Forbes et al. 2016</i>) At variable sizes, with F larger than M; usually >1.5 kg (<i>Lake 1967c</i>) and >203 mm LCF (<i>Cadwallader 1977</i>) Spawning has been suggested to occur in fish as small as 100 mm in the NMDB (R. Woods, DSITI, and S. Balcombe, Griffith University, unpubl. data)
Fecundity and eggs	High fecundity; up to 750 000 eggs, commonly 350 000; >500 000 eggs for a >2.2-kg F (<i>Lake 1967a</i> ; <i>Cadwallader 1977</i> ; <i>Rowland 1983b</i>) Egg number = 249.16 – (39.02 × fish weight) (<i>Rowland 1983b</i>) In hatchery fish, eggs per F (weight range 780–4080 g; mean 1600 g) ranged from 105 500 to 761 300 (mean 349 900), giving a fecundity relationship of Egg number = 75.213 × weight (g) + 231417 (B. Ingram, VFA, unpubl. data) Two stages of egg development may be present within an ovary (<i>Sharpe 2011</i>), and F can hold eggs in an advanced stage of development for 3–5 months (<i>Cadwallader and Backhouse 1983</i>), with possible resorption of gonads if spawning does not occur (<i>Lake 1967c</i>). Spawned eggs are non-adhesive, semi-pelagic (<i>Cadwallader 1977</i> ; <i>Rowland 1983b</i>), 1–1.5 mm at fertilisation and swell to ~3.3–4.2 mm following water hardening (<i>Lake 1967b</i>), ~2.8–4.2 mm in FRGP (<i>Cockayne et al. 2013</i>) Revised fecundity function (C. Todd, ARI, unpubl. data): $Fecundity_{Age} = \exp(-6.98) \times Length_{Age}^{3.23} - (\exp(-14.43) \times Length_{Age}^{3.23})^2$
Spawning	
Description	Have a flexible spawning strategy (<i>Mallen-Cooper and Stuart 2003</i> ; <i>O'Connor et al. 2005</i> ; <i>Ebner et al. 2009b</i>). Collective spawning suggested to occur in shoals over a brief single period (<i>Mackay 1973</i> ; <i>Cadwallader 1977</i>), noted as at night 3–5 h after sunset (<i>Lake 1967a</i>). Aggregations of adults occasionally observed moving upstream from impounded water to flowing rivers in spring (<i>Battaglene 1991</i> ; <i>Sharpe 2011</i>), with some evidence of spawning in the upper Namoi River (<i>Battaglene 1991</i>) In rivers, appear to seek flowing water (e.g. 0.3 m s ⁻¹ ; EO) in river channel habitats to spawn, and the occurrence of drifting eggs and larvae correspond to rising and falling flows (<i>Zampatti and Leigh 2013b</i>). Although there may be several spawning events, strong recruitment appears to be related to only one or two flow events per season for any site (FRGP; <i>Cockayne et al. 2013</i> ; <i>Koster et al. 2017</i>) No parental care (<i>Mackay 1973</i>) Spawning may also be enhanced by small flow events prior to the spawning period (FRGP; <i>Cockayne et al. 2013</i>) Sex ratios have been recorded as 1 : 1.8–2.2 M : F (<i>Wright et al. 2020</i>)
Season	Mainly spring and early summer in SMDB (October–February; <i>King et al. 2009a</i>); likely to be most of year in NMDB (<i>Balcombe et al. 2006, 2007</i> ; <i>Ebner et al. 2009b</i> ; <i>Sharpe 2011</i>), but mainly October–April (G. Butler, NSW DPI, unpubl. data)
Conditions	In SMDB, are considered to spawn in response to discharge variability, especially increases in flow both within the river channel and overbank flooding. May spawn on both the rising and falling limb of the hydrograph (at water temperatures >17°C; <i>King et al. 2009a</i> ; <i>Zampatti and Leigh 2013a, 2013b</i> ; <i>Zampatti et al. 2015</i> ; <i>Koster et al. 2017</i>) At Menindee Lakes, YOY were back-calculated to have been spawned in late autumn–early winter in association with Darling River water temperatures as low as 14°C, but maximum spawning occurred at >18.5°C (<i>Ebner et al. 2009a</i>). An optimal temperature of >19°C has been suggested for the SMDB (<i>King et al. 2016</i>), with higher temperatures suggested for the NMDB (e.g. >24°C, <i>Lake 1967c</i> ; 23–27°C, <i>Department of Environment and Resource Management 2010</i>), along with increases in flows (<i>Department of Environment and Resource Management 2010</i>), as suggested for FRGP and LEGP (>23°C; <i>Roberts et al. 2008</i> ; <i>Cockayne et al. 2013</i>) LEGP spawned across most of the year, at times when flows increased, but commonly during first flow events and temperatures of >26°C (<i>Cockayne et al. 2015</i>) The rate of reproductive development can increase quickly, depending on the availability of food, allowing the species to conserve energy when food is scarce but to take advantage of increased availability during floods (<i>Collins and Anderson 1999</i>) Spawning can also occur in isolated waterholes with little or no passing flow in the arid NMDB, meaning that the life cycle can be completed without passing flows, or interpool movements (<i>Balcombe et al. 2006</i>)
Location	Although there is no evidence for the direct use of ephemeral floodplains for spawning in the NMDB, LEGP have been reported to spawn in these habitats (<i>Balcombe et al. 2007</i>) and appear to otherwise behave similarly to golden perch in arid NMDB (<i>Balcombe et al. 2006</i>). LEGP spawning also occurred during within-channel flows and was not dependent on floodplain inundation (<i>Cockayne et al. 2015</i>) There is some evidence that adult golden perch tend to congregate at main stem–tributary junctions during the spawning season (<i>O'Connor et al. 2005</i> ; <i>Koster et al. 2014</i>).

(Continued)

Table 6. (Continued)

Attribute	Description
After spawning	
Hatching	In hatcheries, egg hatch and mortality rates are greatly affected by temperature and water movement (providing water aeration; B. Ingram, VFA, pers. obs.). Incubation periods at temperatures of 28, 25, 22, 19 and 16°C were ~12, 36, 48, 72 and 72 h respectively. Complete mortality was observed at <13°C, with 60–70% mortality at 16°C, 22–60% at 19°C, 18% at 22°C, 8% at 25°C and 5% at 28°C. The temperature response occurred between 26°C and 14°C, with a LD ₅₀ of 17.5°C (Ryan <i>et al.</i> 2003) Of 117 F that shed eggs in a hatchery, hatch was observed in 29% of batches, with hatch rates of 2–99% (mean 62%; B. Ingram, VFA, unpubl. data)
Larvae	Larvae not well-developed at hatch (3.1–3.4 mm, Lake 1967b; 5–6 mm, Rowland 1983b; 2.4 mm FRGP, Cockayne <i>et al.</i> 2013), become free swimming (but are poor swimmers), move up into the water column and are positively phototactic (B. Ingram, VFA, unpubl. data), and feed at ~5 days (Lake 1967b; Llewellyn 2014) Larvae stocked into earthen fry ponds grew from 4.5 mm (mean SL) to 31 mm in 46 days; giving growth coefficients of 0.04 mm day ⁻¹ and 0.15 mg ⁻¹ mg day ⁻¹ (Arumugam and Geddes 1987) First micro-increments in larval otoliths were thought to have occurred from 3 to 13 days (mean 6 days; Brown and Wooden 2007), but increment counts of known-age larvae exceed the known-age at hatch by one increment, which incorporates egg development before hatch (Zampatti and Leigh 2013a) Larvae are 5–6 mm at 5–16 days and 21.1–44.4 mm (0.12–1.17 g) at 41–88 days, with survival rates of 0–53.1% (mean 13%) and growth rates of 0.24–0.93 mm day ⁻¹ (Brown and Hall 2003) Survival rates vary from 10 to 60% in hatcheries, averaging ~40% in plankton ponds (Thurstan 1992) At first feed, the type and size of prey is restricted by poor swimming and pursuit abilities and small mouth gape size; larvae and fry >10 mm are able to pursue a wider range of zooplankters, feeding visually, mainly on small crustaceans and insect larvae (Thurstan 1992) Larvae have been collected from floodplain lakes (Neira <i>et al.</i> 1998; Ebner <i>et al.</i> 2009b), and 0+ fish (2–12 months) were consistently sampled at Menindee Lakes (Sharpe 2011; Stuart and Sharpe 2020) and other floodplain sites in the NMDB when inundated, suggesting these provide rearing habitat for these species (Rolls and Wilson 2010). Daily food consumption of larvae and fry increased from 33 to 5600 µg dryweight day ⁻¹ (Arumugam and Geddes 1987); faster fingerling growth rates reported from productive floodplain sites compared with main rivers (Sharpe 2011) Winter may be a critical period for 0+ survival (i.e. the result of spawning in the previous spring), with diverse aquatic habitats being important for providing shelter and a productive food web so these fish can feed in winter (EO)
Recruitment	Generally episodic and can occur in association with spawning promoted by flows that remain within the river channel, especially with within-channel flow pulses. However, recruitment is noticeably higher when associated with overbank flows (Mallen-Cooper and Stuart 2003; Ye <i>et al.</i> 2008; Ebner <i>et al.</i> 2009b; Sternberg <i>et al.</i> 2012; Cockayne <i>et al.</i> 2013 (FRGP); Zampatti and Leigh 2013a, 2013b; King <i>et al.</i> 2016) Larval survival depends on high densities of appropriately sized zooplankton at first feeding (Rowland <i>et al.</i> 1983; Arumugam and Geddes 1987), and spawning may not necessarily translate to recruitment if this is not available (Roberts <i>et al.</i> 2008; Koster <i>et al.</i> 2017) Significant increases in juvenile abundance occur in the lower Murray River in years during overbank flooding compared with low-flow years (Zampatti and Leigh 2013b). However, some of this change in abundance appears to have resulted from spawning and recruitment in the Darling River, with 1+ fish moving downstream and then into the Murray River (Sharpe 2011; Zampatti and Leigh 2013b; Zampatti <i>et al.</i> 2015; Stuart and Sharpe 2020) Inundated floodplain lakes can provide juvenile nursery habitats, which may increase survival and therefore recruitment to main channel populations after reconnection (Sharpe 2011) The collection of YOY on the floodplain in the NMDB suggests this provides rearing habitats (Rolls and Wilson 2010) Nursery habitats such as Menindee Lakes in the NMDB and large, ‘slow travel’ flows that promote high productivity have been suggested to enhance recruitment rates (Stuart and Sharpe 2020). The level of natural recruitment upstream of Torrumbarry Weir in the Murray and lower Goulburn rivers is thought to be low, with little evidence of localised recruitment (records of late-stage larvae, 0+ and 1+ fish are rare; King <i>et al.</i> 2007, 2009a; Koster <i>et al.</i> 2009). There is no evidence for enhanced recruitment from slow-flowing habitats, such as weir pools or artificial floodplain inundations (EO) Year class strength for the LEGP was related to the number of flow events, not the total annual discharge (Cockayne <i>et al.</i> 2015) Spawning in isolated waterholes with little or no passing flow, in the arid NMDB (Balcombe <i>et al.</i> 2006), allows recruitment to ‘tick over’ in periods of extended low or zero flows, but then be driven by episodic high-flow events as per LEGP (Balcombe <i>et al.</i> 2007), which contribute to ‘boom-and-bust’ population responses to flooding and low-flow conditions in dryland rivers (Sternberg <i>et al.</i> 2012) In the mid-Murray and NMDB, terminal wetlands and lakes (e.g. Menindee Lakes, Yanga Lake and perhaps the Warrego Western Floodplain) may provide key nursery habitats that can enhance recruitment (Ebner <i>et al.</i> 2009b; Sharpe 2011; Stuart and Sharpe 2020), with high survival rates for 0+ and 1+ fish. Reconnection of these habitats in subsequent years is required to allow for recolonisation in the main river (Sharpe 2011). Natural recruitment may be masked by the large numbers of hatchery-stocked fish (EO) Little is known regarding the population dynamics of golden perch in the lower lakes of the Murray River (lakes Alexandrina and Albert): age structures at times reflect age structures in the lower River Murray, but they may also include age classes that are absent from the river, suggesting that localised spawning and recruitment may be occurring (Ye 2005; Mayrhofer 2007; Bice 2010; Ferguson and Ye 2012, 2016) Mortality rates were comparable between the NMDB and SMDB, with an overall annual mortality rate of 18% (Wright <i>et al.</i> 2020).

(Continued)

Table 6. (Continued)

Attribute	Description
Growth	<p>Live to 28 years (Mallen-Cooper and Stuart 2003), regularly aged to 20+ in SMDB (e.g. Murray River channel, Goulburn River, Murray lower lakes; Zampatti <i>et al.</i> 2015)</p> <p>Well adapted to cope with extended periods of food deprivation, storing energy as fat when food is readily available (Collins and Anderson 1995), and reproductive development can respond to an increase in available food (Collins and Anderson 1999)</p> <p>Show variable growth, and length-at-age is highly variable (Anderson <i>et al.</i> 1992), especially across different regions (Mallen-Cooper and Stuart 2003; Wright <i>et al.</i> 2020; see Fig. 7). There is also considerable variability in growth and maximum size for FRGP between sexes and river sub-basins (Roberts <i>et al.</i> 2008). Growth variation from otolith analysis showed sensitivity to environmental parameters, with depression during the Millennium Drought and positive responses to higher river flows and flow pulses (Izzo <i>et al.</i> 2016b). Growth chronology rates for 1972–92, but not 1993–2000, were correlated with average annual values of the Southern Oscillation Index (Pritchard 2004)</p> <p>Grow larger in impoundments than rivers (Forbes <i>et al.</i> 2015a; Ingram <i>et al.</i> 2015)</p> <p>Growth has been positively related to lake area and temperature (Morrongiello <i>et al.</i> 2011b), with most interannual variation explained by water level, minimum DO concentration and length of the growing season (proportion of degree days >20°C; Pritchard 2004). The growth rate for juvenile fish (<90 days) in rearing ponds is $TL = 4.43 + 0.68 \text{ day}^{-1}$ (Thurstan 1992). Fully scaled, 40 mm fingerlings were ~45 days old (Sharpe 2011; Stuart and Sharpe 2020)</p> <p>Length of hatchery larvae at 3 was not affected by barium or magnesium isotope immersion (Woodcock <i>et al.</i> 2011)</p> <p>Juvenile growth is affected by water temperature (Ryan <i>et al.</i> 2003)</p> <p>Revised regional growth functions (see Fig. 7; C. Todd, ARI, unpubl. data):</p> <p style="padding-left: 20px;">All data: $Length_{Age} = 518.53 \times (1 - \exp(-0.247 \times (Age + 0.45)))$</p> <p style="padding-left: 20px;">Main rivers data: $Length_{Age} = 480.48 \times (1 - \exp(-0.32 \times (Age + 0.2)))$</p> <p style="padding-left: 20px;">Western Queensland rivers data: $Length_{Age} = 324.36 \times (1 - \exp(-0.60 \times (Age + 0.15)))$</p> <p style="padding-left: 20px;">All rivers data: $Length_{Age} = 404.26 \times (1 - \exp(-0.39 \times (Age + 0.32)))$</p> <p>There is greater variability in age-at-length and higher proportions of smaller golden perch in the NMDB than SMDB according to Wright <i>et al.</i> (2020), who also considered growth rates to be similar between regions, with MDB-wide von Bertalanffy growth model parameters of $L_{\infty} = 447$, $k = 0.32$ and $t_0 = -0.51$, and an MDB-wide length (L)–weight (W) equation of $W = 6.76 \times 10^{-6} L^{3.12}$</p>
Habitats	<p>Main river channels are the primary habitats, but also found in backwaters, lakes and isolated pools, with floodplain channels and inundated floodplain habitats also used when available (Sharpe 2011; Zampatti and Leigh 2013b; Koehn and Nicol 2014). Juveniles and adults use anabranches (Koehn and Nicol 2014), as indicated by the presence of a range of age classes (Douglas <i>et al.</i> 1998). River channels, billabongs and lakes can provide important refuge and overwintering habitats, and isolated waterholes provide vital refuge habitats in NMDB arid rivers (Balcombe <i>et al.</i> 2006). Adults often associated with physical in-stream structure, particularly in-stream wood (Crook <i>et al.</i> 2001; Ryan and O’Mahony 2005; Koehn and Nicol 2014). In main channel habitats of the mid-Murray River, adults prefer mean water depths of 2.6 m and surface water velocities of 0.31 m s^{-1}, accompanied by 80% cover of in-stream wood, with this structure being higher in the water column than for other species (Koehn and Nicol 2014)</p> <p>Habitat use in a weir pool was seasonally variable, with fish more likely to be in areas with greater woody habitat in late summer, and deeper habitats in late winter to early summer (Koster <i>et al.</i> 2020). Juveniles selected structure, including rock piles, over open habitats (Hutchison <i>et al.</i> 2020). More likely to be in deeper areas during the day (Crook <i>et al.</i> 2001; Koster <i>et al.</i> 2020). Generally, have high tolerances for salinity (33 ppt; Merrick and Schmida 1984), turbidity (Cadwallader 1979) and temperature (range 4–37°C; Llewellyn and MacDonald 1980), with a thermal preference of 27°C (Ryan <i>et al.</i> 2003)</p> <p>Can flourish in large impoundments (Forbes <i>et al.</i> 2016), and although there are preferred lake areas (i.e. closer to shore in spring and earlier summer, moving off-shore in mid to late summer), there appears to be no microhabitat preference (Douglas 2009)</p> <p>Hypoxia and polyphenol concentrations may affect larval distributions and limit numbers in some floodplain habitats (Gehrke 1991)</p> <p>Juveniles sensitive to low DO, with 50% mortality at $1.85 \pm 0.01 \text{ mg L}^{-1}$ over 48 h (Small <i>et al.</i> 2014)</p>
Movements	<p>A highly mobile species (Reynolds 1983; Koehn and Nicol 2016), with all life stages having different movement needs, including passive (eggs and early larvae) and potentially active (meta-larvae, juveniles, adults), in both upstream, downstream and lateral directions, presenting a complexity of movement scenarios (Koehn and Crook 2013; Llewellyn 2014; O’Connor <i>et al.</i> 2015; Koster <i>et al.</i> 2017)</p> <p>Commonly found migrating through fishways in large numbers (Mallen-Cooper 1999; Stuart <i>et al.</i> 2008)</p> <p>These movements by the different life stages play an important role in the population dynamics of this species over large spatial scales. Indeed, the populations of the upper river reaches of many rivers may be driven by immigration of adults and juveniles (1+, 2+, 3+), and not so much by localised spawning and recruitment (Koster <i>et al.</i> 2014; Stoffels <i>et al.</i> 2014; Lyon <i>et al.</i> 2019). Accumulations often occur immediately downstream of barriers (Sharpe 2011), a behaviour exploited by Indigenous people for thousands of years at the Brewarrina rock fisheries (Dargin 1976)</p> <p>Migrations appear to be influenced by river discharge (O’Connor <i>et al.</i> 2015), although this is not always the case, with individual movements occurring with steady, rising or falling flows (Zampatti <i>et al.</i> 2019)</p>

(Continued)

Table 6. (Continued)

Attribute	Description
Eggs and larvae	Genetic analyses show that MDB populations have been historically characterised by low levels of genetic variation, with genetic structuring only evident among major drainage basins, indicating surprisingly high rates of dispersal (Faulks <i>et al.</i> 2010b)
	Conceptual movements for all life stages are illustrated in Fig. 8
	In flowing waters, pelagic eggs can drift for 1–2 days and then, after hatch, larvae may drift for a further 10–12 days (EO). This provides a major dispersal mechanism from spawning areas for larvae to then settle in feeding and nursery areas such as terminal lakes (especially in NMDB) or along channel margins (EO)
	Larvae underwent full transition to fully scaled fingerlings during downstream drift or dispersal of >1600 km down the Darling River (Stuart and Sharpe 2020)
	Larvae start to swim and feed at ~5 days (Llewellyn 2014)
	There has been a significant loss of off-stream lakes and wetlands that may provide nursery habitats, with only 11 of a potential 567 sites now still functional in western NSW (Sharpe 2011)
	Swimming performance of the free embryos and larvae is poor, indicating limited ability to swim against currents or influence dispersal in rivers.
Juveniles	Performance increases predominantly during the meta-larval development stage, when all fins are mostly fully developed, with critical swimming speeds of 16.3–23.1 cm s ⁻¹ (Kopf <i>et al.</i> 2014)
	Drift distances depend on flows, and eggs and larvae may require lotic habitats at landscape scales (e.g. 500 km) to promote their survival (Mallen-Cooper and Zampatti 2015)
	Otolith microchemistry shows some movement at 0+, but this age fish seldom appears in fishways; predominantly movements occur at 1+ (Mallen-Cooper and Stuart 2003; Baumgartner <i>et al.</i> 2014b; Zampatti <i>et al.</i> 2018)
	Large numbers of juveniles (immature: 1+, 2+) migrate upstream in autumn in response to increased flows, including relatively small rises (e.g. +0.15 m 24 h ⁻¹ river height; Mallen-Cooper 1999). These juveniles make staged, upstream recolonisation migrations, responding to flow pulses, which stop as flows stabilise (Mallen-Cooper and Stuart 2003). Mature and immature fish may aggregate for days or weeks below weirs, if flows provide sufficient stimulus, but can quickly disperse downstream as flows recede (Mallen-Cooper and Stuart 2003)
	YOY dispersed from Menindee Lakes into the lower Darling River downstream for up to 500 km, which, together with larval drift, potentially equated to a movement of >2100 km by 1 year olds (Stuart and Sharpe 2020)
	Dispersal from stocking sites indicates that some 1+ fish moved nearly 40 km after 1 year (Ingram <i>et al.</i> 2015)
	Otolith ⁸⁷ Sr: ⁸⁶ Sr ratios and water ⁸⁷ Sr: ⁸⁶ Sr isoscapes have been used to retrospectively determine the provenance and migration history of juveniles and adults in the Murray River and its tributaries (e.g. Goulburn and Darling rivers; Zampatti <i>et al.</i> 2015, 2018, 2019). These investigations indicate that the passive downstream movement of eggs and larvae, and subsequent active movement of juveniles and adults, can influence the population demographics in the SMDB over scales of thousands of kilometres. For example, spawning events associated with summer within-channel pulses and bankfull flows in the Darling River may be followed by the dispersal of early life stage (larval) fish into the lower Murray River or retention in the Darling River. When flooding in the Darling and Murray rivers occur in the year after spawning, this may promote the large-scale dispersal of age 1+ fish into the Murray River (Stuart and Sharpe 2020). Subsequently, cohorts of golden perch with a Darling River provenance can occur in year classes in the mid and lower Murray River (and tributaries) over subsequent years (Zampatti <i>et al.</i> 2015, 2018, 2019)
The swimming performance of juveniles is considerably reduced at temperatures <15°C (Lyon <i>et al.</i> 2008)	
Adults	Adults move more regularly and undertake larger, more frequent movements, than Murray cod, trout cod or carp (Koehn and Nicol 2016). Large upstream movements by adults (2300 km: Berri, SA, to Mungindi, Qld), with many examples of 500- to 1000-km movements recorded in association with high flood flows (Reynolds 1983; Koster <i>et al.</i> 2017), including an example of 1000 km in 163 days (Llewellyn 1968). Although larger-scale movements of tens to hundreds of kilometres are common (O'Connor <i>et al.</i> 2005; Leigh and Zampatti 2013; Koster <i>et al.</i> 2014; Marshall <i>et al.</i> 2016; Zampatti <i>et al.</i> 2018), most movements are small for much of the time, with many fish demonstrating limited movements for at least some period of their lives (Crook <i>et al.</i> 2001; Crook 2004; Koehn and Nicol 2016; Thiem <i>et al.</i> 2020). Movements occur in both upstream and downstream directions in approximately equal proportions (Reynolds 1983; McKinnon 1997; O'Connor <i>et al.</i> 2005; Llewellyn 2014; Marshall <i>et al.</i> 2016; Koehn and Nicol 2016). There were considerable individual variations in movement patterns, direction and distances (O'Connor <i>et al.</i> 2005; Llewellyn 2014; Koehn and Nicol 2016; Marshall <i>et al.</i> 2016), although more (also larger) fish moved downstream during high flows (up to 900 km; McKinnon 1997)
	Movements strongly affected by discharge rates (Mallen-Cooper 1999; Thiem <i>et al.</i> 2020). A high percentage of both adults and juvenile fish can move downstream over barriers on high flows, resulting in later aggregations of fish below barriers as they attempt to re-ascend (EO). Although downstream movement over flooded weirs can occur, these weirs can also act as behavioural barriers (O'Connor <i>et al.</i> 2006). During in-channel flows, site fidelity is often displayed (including between years; Koehn and Nicol 2016), but major home range shifts can occur (Crook 2004; Leigh and Zampatti 2013) on a frequent basis (35% chance; Koehn and Nicol 2016)

(Continued)

Table 6. (Continued)

Attribute	Description
	<p>Movement is most likely to occur in spring in the SMDB (Koehn and Nicol 2016), often before spawning (Stuart <i>et al.</i> 2008), and there is strong movement between the Murray River and its tributaries (Koster <i>et al.</i> 2014, 2017; Zampatti <i>et al.</i> 2015). These spatially and temporally complex movement patterns between main stem and tributary locations are influenced by discharge, water temperature and perhaps reproductive behaviour (Koster <i>et al.</i> 2014, 2017). Most movements are limited during winter (<5 km), with strong home range and site fidelity displayed (O'Connor <i>et al.</i> 2005; Koehn and Nicol 2016). Homing behaviour is common, and 53% returned to within 3 km of their release locations when translocated (O'Connor <i>et al.</i> 2005). Koehn and Nicol (2016) reported 17.9% of individuals returning to a previous location, with 14% of fish moving sites 'continuously'. Upstream movements appeared to correspond with periods of sustained warmer temperatures (>20°C) and larger riverine flow pulses (Ryan and O'Mahony 2005), although thresholds for movement cues may differ between the SMDB and NMDB. Large-scale SMDB movements predominantly occur in spring and summer (O'Connor <i>et al.</i> 2005; Marshall <i>et al.</i> 2016), often (but not always) associated with flow (Sharpe 2011), and can be quite rapid (Koehn and Nicol 2016). Long-distance upstream adult movements through Murray River fishways in spring and summer are likely related to spawning (Mallen-Cooper 1999; Stuart <i>et al.</i> 2008; Baumgartner <i>et al.</i> 2014b), coinciding with the occurrence of eggs and larvae and elevated flows (Koster <i>et al.</i> 2017). Greater proportions of the population migrate during major overbank flood events, resulting in population increases due to adult migration from downstream sources (Lyon <i>et al.</i> 2014a), but increases also occur with smaller floods (McKinnon 1997). It appears that flooding in the Murray and Darling rivers promotes the large-scale upstream movement of adult fishes and the consequent restructuring of the demographics of source and sink populations (Koster and Crook 2017; Zampatti <i>et al.</i> 2018). In the lower Murray River, long-distance upstream movements occurred during spring–summer during periods of both stable low flow and small in-channel flow pulses (Zampatti <i>et al.</i> 2018). In the NMDB, most movements occur in response to increased flow events (both upstream and downstream directions), often occurring through many waterholes (Marshall <i>et al.</i> 2016)</p>
Behaviour	<p>Will move into floodplain channels when they become available and occasionally onto the floodplain proper (Koehn and Nicol 2016) Have been shown to become more active during periods of reduced DO levels (Koster <i>et al.</i> 2020) In reservoirs, exhibit home ranges, display homing and are as equally active in winter as in summer (Douglas 2009) Temperatures <12.5°C significantly reduce fast-start swimming performances, with fish at temperatures >15.5°C able to swim at much higher speeds (Ryan <i>et al.</i> 2003; Lyon <i>et al.</i> 2008) Appear susceptible to epizootic ulcerative syndrome (Boys <i>et al.</i> 2012), although effect on populations is unknown In ponds, classified as a macrophagic carnivore feeding mainly on insects and crustaceans (Barlow <i>et al.</i> 1987)</p>
Key threats	<p>Eggs susceptible to shear stresses, with 100% mortality at strain rates >629 s⁻¹; larvae (<25 days) less susceptible, but strain rates of <600 s⁻¹ are suggested (Navarro <i>et al.</i> 2019)</p> <p>Key threats include:</p> <ul style="list-style-type: none"> • Barriers to fish passage that restrict longitudinal and lateral movements (Stuart <i>et al.</i> 2008; Baumgartner <i>et al.</i> 2014a) • Loss of large-scale reaches (e.g. >500 km) flowing water habitats (EO) • Loss and disconnection of off-channel nursery areas such as deflation basins, lakes and wetlands (Sharpe 2011) • Cold water releases from impoundments, which can inhibit spawning, reduce growth rates and affect energy (Ryan <i>et al.</i> 2003; Lugg and Copeland 2014) • Altered flow regimes, especially loss of base flows, within-channel flow pulses, flow peaks, large, overbank floods and broad-scale connected river systems (Stuart and Sharpe 2020) • Water extraction from refuge pools in arid areas (Bond <i>et al.</i> 2015) • Loss of flowing riverine habitats created by weir pools (Walker 2006) and floodplain regulators (Mallen-Cooper <i>et al.</i> 2008, 2011), which may have a substantial effect on the survival of early life stages • Predation and poor water quality, which can affect survival in refuge pools and terminal lakes and wetlands • Low DO from blackwater or algal events (King <i>et al.</i> 2012; Thiem <i>et al.</i> 2017) • Removal of in-stream woody habitat • Dietary overlap with redfin (Wedderburn <i>et al.</i> 2014b) <p>Larval mortality (\pms.d.) is high as they pass through undershot weir gates (95 \pm 1%; Baumgartner <i>et al.</i> 2006); drifting eggs and larvae can also be lost into irrigation off-takes and pumps (King and O'Connor 2007; Boys <i>et al.</i> 2013b), with possible entrainment in hydropower infrastructure (Stuart <i>et al.</i> 2010; Boys <i>et al.</i> 2013a).</p> <p>The effect of carp is unknown, but these species are similar in terms of their habitat use and movements (Koehn and Nicol 2014, 2016)</p> <p>Potential high levels of catch-and-release mortality from recreational fishing using bait (up to 44%; Hall <i>et al.</i> 2015)</p> <p>Considered to have a low vulnerability to drought (Crook <i>et al.</i> 2010) and climate change impacts (Balcombe <i>et al.</i> 2011; Bond <i>et al.</i> 2011; Chessman 2013)</p>

Table 7. Life-history attributes for the silver perch

ARI, Arthur Rylah Institute for Environmental Research; DO, dissolved oxygen; DPI, Department of Primary Industries; EO, expert opinion; F, female(s); M, male(s); L_B , body length; MDB, Murray–Darling Basin; NMDB, northern MDB; NSW, New South Wales; SMDB, southern MDB; VFA, Victorian Fisheries Authority; YOY, young-of-the-year

Attribute	Description
Before spawning	
Sexual maturity	Sexually dimorphic In the wild, M mature at 3 years (250 mm) and F at 4–5 years (300 mm; Mallen-Cooper and Stuart 2003) In hatcheries, M mature at 2 years and F at 3 years (Rowland 2004)
Fecundity and eggs	Fecundity high: up to 500 000 eggs for a 2-kg fish (Lake 1967d) or 139 286 eggs kg ⁻¹ (Rowland 2004) F remain highly fecund for up to 10 years (Rowland 2009) Eggs small (mean diameter 1.2 mm; then 2.5–3.0 mm in diameter for water-hardened eggs; Lake 1967b ; Rowland 1984), non-adhesive, semi pelagic (Merrick and Schmida 1984 ; Merrick 1996 ; Rowland 2009) and sinking in the absence of current (Lake 1967a). Specifically, Lake (1967b) reported that the fine mat-like chorion of eggs readily collects small clay particles, causing the eggs to have increased negative buoyancy and causing settling to the bottom in slow and still water. Tonkin et al. (2007) recorded the greatest concentration of drifting eggs close to shore, near the bottom, suggesting either increased spawning in these microhabitats or, more likely, a gradual settling of eggs in lower water velocities Revised fecundity function (C. Todd, ARI, unpubl. data): $Fecundity_{Age} = \exp(-6.54) \times Length_{Age}^{3.04}$
Spawning	
Description	Communal broadcast spawners that form large schools following an upstream migration Spawning observed to occur on multiple separate trigger events, with some individuals dying following spawning (Lake 1967a) Induced fertilisation rates of 84.5% recorded in hatcheries (Rowland 2004)
Season	Spawn from mid-October to mid-February in the SMDB (King et al. 2007, 2009a ; S. Raymond, ARI, pers. comm.) and from October to April in the NMDB (S. Balcombe, Griffith University, pers. comm.) In the mid-Murray River, spawning occurs in most years (except during a severe blackwater event), including under low, steady, within-channel flows, albeit with a reduced number of eggs (Harris and Gehrke 1994 ; Humphries et al. 2002 ; Gilligan and Schiller 2003 ; King et al. 2016) In the Goulburn River, spawning occurs from November to January, with most eggs being collected during within-channel or bankfull flows In the lower Darling River, spawning occurred in November on a small flow rise (Sharpe and Stuart 2018)
Conditions	Spawning has previously been associated with small changes to discharge and river level (Mallen-Cooper and Stuart 2003 ; King et al. 2009a) in the mid-Murray River, but more recent analysis suggests spawning to be largely water temperature cued, commencing at >18°C (Gilligan and Schiller 2003 ; Koehn and Harrington 2005 ; Tonkin et al. 2007 ; King et al. 2009a), with >20% of predicted maximum spawning occurring at 20–25°C (mean 24°C) (King et al. 2016) Occurrence and abundance of eggs positively associated with discharge and weekly temperature change, with a negative association with an increasing number of flood days in the preceding 3 months (King et al. 2016). Optimised spawning may be best achieved by delivery of flows when temperatures are 22–24°C during a period that is preceded by limited flooding (King et al. 2016) Spawning peaked between 2100 and 0100 hours in the Murray River, with eggs having a propensity to drift in higher densities near shore and at the bottom of the water column (Tonkin et al. 2007)
Location	In river channel habitats with flowing water (e.g. >0.3 m s ⁻¹), which presumably facilitates egg and larval drift and provides adequate oxygenation for eggs (EO) There is no evidence of the direct use of ephemeral floodplains for spawning (King et al. 2007, 2009a) Have been reported to spawn in ponds under cultured conditions; usually associated with a rapid rise in water level when filling ponds (S. Rowland, pers. comm.)
After spawning	
Hatching	Within 30–36 h, and hatch rates of 76.8% recorded in hatcheries (Rowland 2004)
Larvae	Length at hatch 3.6 mm (Lake 1967c), range 3.9–4.6 mm (B. Ingram, VFA, unpubl. data) 2-Week larval stage (NSW Department of Primary Industries 2006), and larvae commence feeding at yolk sac absorption, 5–6 days after hatch (Rowland et al. 1983)
Behaviour	No parental care (Lake 1967b)
Recruitment	In the mid-Murray River, recruitment occurred in most years during a period that encompassed extreme drought and a range of flood events (Mallen-Cooper and Stuart 2003 ; Tonkin et al. 2019a). Over this time, spawning conditions always included water velocity >0.45 m s ⁻¹ and mean daily water temperature 21.5–24°C during November–December (Tonkin et al. 2019a). Conversely, recruitment in the lower Murray is episodic and linked to higher within-channel and overbank flows that create lotic habitats (B. Zampatti, CSIRO, pers. comm.) Although dominant year classes have previously been associated with high flows in spring or summer that inundate floodplains and produce food for larvae (Lake 1967a ; Reynolds 1983 ; Harris and Gehrke 1994), assessment of year class strength in the mid-Murray River shows strongest year classes associated with periods of in-channel flows (as per Mallen-Cooper and Stuart 2003) followed by large overbank flooding (Tonkin et al. 2019a)

(Continued)

Table 7. (Continued)

Attribute	Description
	Increased juvenile growth and survival appears to be related to high flows and productive off-channel habitats (e.g. a large number of juveniles were recently found occupying Lake Boga in northern Vic.; Tonkin <i>et al.</i> 2017c). Recruitment into northern Victorian rivers is likely to rely on connectivity and flow cues in the mid-Murray River and tributaries to facilitate immigration, particularly of juveniles (Mallen-Cooper and Stuart 2003)
	Survival rates from eggs to 40- to 80-mm fish estimated to be ~20% (EO)
	Although widely stocked, there is little evidence of strong survival in rivers, and there appears to be no natural recruitment in most impoundments, Cataract Dam being an exception (EO)
Growth	Length at hatch ~3 mm and grow to ~11 mm by 18 days (Lake 1967c)
	Exhibit variable growth (Mallen-Cooper and Stuart 2003)
	Despite attaining ages of 16+ in the mid-Murray River in the 1990s, <25 years later contemporary populations in the lower and mid-Murray River show few fish >7 years of age (Tonkin <i>et al.</i> 2017c, 2019a; Zampatti <i>et al.</i> 2018). Fish that had migrated from the Murray River to Lake Boga as juveniles were significantly larger and in better condition than the same-aged fish that had remained in the Murray River (Tonkin <i>et al.</i> 2017c). As such, providing juveniles access to floodplains and off-channel habitats is likely to enhance growth and recruitment (EO)
	Revised growth function (C. Todd, ARI, unpubl. data): $Length_{Age} = 460.90 \times (1 - \exp(-0.32 \times (Age + 0.31)))$
Habitat	An obligate, lotic, perennial river channel specialist that occupies a range of habitats from large, faster-flowing river reaches to the slow-flowing, turbid waters of lowland rivers, such as the ephemeral Paroo. Can also survive well in impoundments, but breeding is negligible (Rowland <i>et al.</i> 1995; Clunie and Koehn 2001b). Occasionally found in floodplain lakes (mid-Murray, SMDB; e.g. Moira Lake, Lake Boga) in large numbers after being colonised by juvenile fish (EO; Tonkin <i>et al.</i> 2017c)
	Considered to require perennial flowing water for completion of their whole life cycle, and there is limited evidence for eggs or larvae using off-channel nursery areas (King <i>et al.</i> 2007)
	Suggested to be associated with submerged or emergent aquatic vegetation (Moffatt and Voller 2002), but juveniles found to prefer open water over habitat structure (Hutchison <i>et al.</i> 2020)
	Juveniles sensitive to low DO, with 50% mortality at $1.04 \pm 0.01 \text{ mg L}^{-1}$ over 48 h, with first mortalities under simulated blackwater conditions occurring at 2.8 mg L^{-1} DO, with an LC_{50} of 1.04 mg L^{-1} (Small <i>et al.</i> 2014)
	There is no evidence of direct use of ephemeral floodplains by larvae (King <i>et al.</i> 2007, 2009a)
Movements	Regarded as a highly mobile species with movements for all life stages, often assumed to be similar to golden perch, with passive downstream drift of eggs and larvae and the active movement of juveniles and adults (both up- and downstream), which can influence the population demographics in the MDB over large scales (thousands of kilometres; Zampatti <i>et al.</i> 2018). For example, spawning events associated with spring–summer within-channel pulses and bankfull flows in the Darling and mid-Murray rivers may be followed by the dispersal of early life stages into the lower Murray River. When flooding in the Darling and Murray rivers occurs in the year after spawning, this may promote the large-scale dispersal of 1+ fish into and throughout the Murray River, its tributaries and lakes (Tonkin <i>et al.</i> 2017c, 2019a; Zampatti <i>et al.</i> 2018)
	Good swimming abilities, but there is limited information on movement rates (EO)
	Large numbers of juvenile and adult silver perch move upstream through fishways (Mallen-Cooper 1999)
Eggs and larvae	Drifting of egg (~2 day) and larval phases considered to be 15–18 days (Lake 1967c; NSW Department of Primary Industries 2006)
	Eggs and larvae deposited in weir pools and diversion channels are considered to have high rates of mortality (EO).
	Had the poorest larval swimming speeds among six native fish species, with critical maximum speeds of 0.1 cm s^{-1} or $0.3 \text{ L}_B \text{ s}^{-1}$, prolonged swimming speeds of 1.1 cm s^{-1} or $1.0 \text{ L}_B \text{ s}^{-1}$, and critical swimming speeds between 1.8 and 14 cm s^{-1} (Kopf <i>et al.</i> 2014)
Juveniles	Although very little is known about the ecology of 0+ fish, there is growing evidence highlighting the importance of movement by juveniles (1+ and 2–3+) in driving metapopulation dynamics. YOY are seldom found in fishways, and although otolith micro-chemistry shows some movement in the first year of life, movements predominantly occur at age 1+ (Zampatti <i>et al.</i> 2018), and tens of thousands of 1+ to 2+ fish have been recorded moving upstream through fishways (Mallen-Cooper 1999; Mallen-Cooper and Stuart 2003; Baumgartner <i>et al.</i> 2014b)
	Most movements occur over a broad time frame: October–April
	Large numbers of juveniles recently found occupying Lake Boga appear to have colonised from the mid-Murray River as 1+ fish during a large flood event (Tonkin <i>et al.</i> 2017c)
Adults	Recorded as moving distances up to 1200 km (Tonkin <i>et al.</i> 2017c), often associated with large flow events, including overbank flooding (Reynolds 1983; Tonkin <i>et al.</i> 2017c; Thiem <i>et al.</i> 2020). Movements found to increase substantially during both within-bank river rises and flooding, with the highest rates of detection and multisite detections of fish at Murray River fishways during periods of high magnitude, extended flooding (Tonkin <i>et al.</i> 2017c)
	Most movements occur over a broad time frame: October–April, with spring movements presumed to be associated with spawning (Mallen-Cooper <i>et al.</i> 1995)
	Movements strongly affected by discharge rates and able to be stimulated by small increases in water level (e.g. $+0.15 \text{ m } 24 \text{ h}^{-1}$; Mallen-Cooper and Stuart 2003; J. Thiem, NSW DPI, pers. comm.), declining as flows reduce (Baumgartner <i>et al.</i> 2014b).
	Recolonisation from isolated refuge waterholes is critical in the NMDB; otherwise, there is no evidence to suggest movement patterns would be different to the SMDB (EO)

(Continued)

Table 7. (Continued)

Attribute	Description
Behaviour	Classified as an omnivore, feeding predominantly on zooplankton in ponds (Barlow <i>et al.</i> 1987), insects, crustaceans, molluscs, small fish and aquatic plants (Lintermans 2007) Schooling species (Lintermans 2007) Eggs susceptible to shear stresses, with 100% mortality at strain rates $>148\text{ s}^{-1}$. Larvae (<25 days) less susceptible, but maintaining strain rates of $<600\text{ s}^{-1}$ have been suggested to minimise impacts (Navarro <i>et al.</i> 2019)
Key threats	Key threats include: <ul style="list-style-type: none"> • Loss of long-distance (e.g. >500 km) perennial lotic habitats (EO) • River regulation and reduced flows (EO) • Barriers to movement and fragmentation of connected systems (Mallen-Cooper and Stuart 2003; Baumgartner <i>et al.</i> 2014b; Stuart and Sharpe 2017) • Regulating structures (e.g. weirs in the lower Murray River), which have reduced lotic habitats and compromised the hydrodynamic conditions required for spawning and recruitment, and may have a substantial effect on the survival of early life stages (Bice <i>et al.</i> 2017; Zampatti <i>et al.</i> 2018) • Water diversions, which cause large numbers of pelagic eggs and larvae, as well as juveniles and adults, to be lost into irrigation channels (Gilligan and Schiller 2003; Koehn and Harrington 2005; Boys <i>et al.</i> 2013a, 2013b), and undershot weirs, which cause $>90\%$ mortality for golden perch larvae (Baumgartner <i>et al.</i> 2006) • Low population densities (particularly in the NMDB) and severe fragmentation of populations (especially when exacerbated by water diversions in the NMDB), which can increase conservation risk • Blackwater events, which may negatively affect spawning (S. Raymond, ARI, pers. comm.) • Cold water releases, which limit spawning below weirs and larger impoundments and can depress swimming ability (Parisi <i>et al.</i> 2020) <p>Although unquantified, the effects of carp through competition may be high in areas of high carp density, given their omnivorous dietary overlap Can become stranded behind floodplain regulation structures (Jones and Stuart 2008) They are susceptible to several diseases, including epizootic haematopoietic necrosis virus (Langdon 1989) Considered to have low vulnerability to climate change impacts (Chessman 2013)</p>

Table 8. Life-history attributes for the Macquarie perch

ARI, Arthur Rylah Institute for Environmental Research; DPI, Department of Primary Industries; EC, electrical conductivity units; EO, expert opinion; F, female(s); M, male(s); MDB, Murray–Darling Basin; NMDB, northern MDB; NSW, New South Wales; SMDB, southern MDB; TL, total length; VFA, Victorian Fisheries Authority; YOY, young-of-the-year

Attribute	Description
Before spawning	
Sexual maturity	Generally, at ~ 210 mm and 2 years for M and 300 mm and 3 years for F in rivers (Lake 1967a), and 2–4 years for both sexes in Lake Dartmouth (Gooley and McDonald 1988; Appleford <i>et al.</i> 1998). Most Lake Dartmouth spawning fish (M and F) are >350 mm and >6 years; M can be sexually mature at smaller sizes (<150 mm; Douglas 2002; Lintermans 2007; Tonkin <i>et al.</i> 2009, 2018) Hatchery records indicate running ripe M from 200 mm and 126 g, with F induced to ovulate from 255 mm and 240 g; mature fish from the Yarra River are smaller than those from Lake Dartmouth (B. Ingram, VFA, unpubl. data)
Fecundity and eggs	Fecundity ranges from 30 750 eggs kg^{-1} (Cadwallader and Rogan 1977) and 32 000 eggs kg^{-1} (Wharton 1973) to 100 000 eggs kg^{-1} (Lake 1967a, 1967b). Up to 49 400 eggs kg^{-1} have been hand-stripped from hatchery fish (B. Ingram, VFA, unpubl. data) Eggs are relatively large (1–2 mm in diameter; 2–4 mm in diameter when fertilised and water hardened), oviparous, demersal and slightly adhesive (Cadwallader and Rogan 1977; Ingram <i>et al.</i> 2000) Fecundity function (Todd and Lintermans 2015): $Fecundity_{Age} = \exp(2.295 \times \log(\text{Length}_{Age}) + 2.886)$
Spawning	
Description	Obligate riverine spawner (Cadwallader and Rogan 1977; Ebner <i>et al.</i> 2011) Adults move to spawning locations once day length increases and water temperatures are 13–18°C (Gooley and McDonald 1988; Tonkin <i>et al.</i> 2018), with lake fish often congregating at the river mouth before moving (Cadwallader and Douglas 1986). Movement into the spawning stream from the river mouth has been correlated with a rapid rise in temperature (Douglas 2002). Spawning occurs when temperatures are $>16.5^\circ\text{C}$ from October until late December (Cadwallader 1977; Cadwallader and Rogan 1977; Gooley and McDonald 1988; Ingram <i>et al.</i> 2000; Tonkin <i>et al.</i> 2010, 2016). M appear to move upstream first, then F (Gooley and McDonald 1988) Unlike other <i>Macquaria</i> species (golden perch and Australian bass <i>Macquaria novemaculeata</i>), consistent hatchery production using captive adult stocks has proven difficult (Gooley and McDonald 1988; Ingram <i>et al.</i> 1994; B. Ingram, VFA, pers. comm.). As a result, hatchery-produced fingerlings used for conservation stocking are still largely reliant on annual collections of running-ripe fish from wild populations, although modification of hatchery broodfish holding ponds in recent years to include moving water and habitat enrichment has facilitated enhanced maturation of captive-held broodstock (NSW DPI, unpubl. data)

(Continued)

Table 8. (Continued)

Attribute	Description
	Macquarie perch held in tanks under controlled environment conditions have been induced to spawn over several years, but not reliably (B. Ingram, VFA, unpubl. data)
	The spawning condition of fish from Lake Dartmouth has been positively correlated with lake levels (Gray <i>et al.</i> 2000), and changes in the breeding performance of hatchery broodstock collected from Lake Dartmouth each spawning season have been associated with changes in lake productivity (Ingram and Gooley 1996). The number of eggs stripped per kilogram, fertilisation rate and hatch rate all increase with increasing fish condition (B. Ingram, VFA, unpubl. data). Based on long-term assessments of the Lake Dartmouth population, it is suggested that a healthy spawning stock structure consists of a stable number of large fish and a broad age distribution (Tonkin <i>et al.</i> 2018)
Season	Core period from October to late December (Cadwallader 1977; Cadwallader and Rogan 1977)
Conditions	Temperature had a significant positive effect on the number of eggs detected in two riverine populations, with the greatest abundance of eggs recorded when mean daily water temperatures were >18°C (Tonkin <i>et al.</i> 2017a)
Location	Spawning in both riverine and lacustrine populations appear to occur at only a small number of key lotic sites, where fish form spawning aggregations at the base of pools (e.g. Cadwallader and Rogan 1977; Tonkin <i>et al.</i> 2010; 2016) Several studies have reported that spawning aggregations are non-uniform throughout a river reach, with specific sites holding dense aggregations of fish (e.g. Cadwallader and Rogan 1977; Tonkin <i>et al.</i> 2009, 2010, 2016; Trueman 2012a), despite access to large reaches of apparently similar riverine habitat. If fish cannot reach desired or key spawning sites (i.e. as a response of low flows exacerbating the effects of instream barriers), successful spawning may not occur, with populations in some catchments declining if low flows occur across multiple years (e.g. drought; Lintermans 2013b) or as a result of reduced flows below impoundments (Broadhurst <i>et al.</i> 2017) High-sloping riffles, associated with larger deeper pools containing complex habitat, appear to be the most favoured for spawning (Tonkin <i>et al.</i> 2016). Fertilised eggs lodge in shallow riffle areas in the cobble or pebble substrate immediately downstream of the spawning site to ensure maximum aeration and minimise the risk of smothering by sediments (Cadwallader and Rogan 1977; Ingram <i>et al.</i> 2000). These riffles are generally shallow, mostly <1 m deep with flows of 0.3–0.6 m s ⁻¹ (Cadwallader and Rogan 1977; Gooley in Koehn and O'Connor 1990). Spawning within riffles (i.e. not in pools upstream with subsequent downstream drift) has been recorded in the Cotter River, ACT (Broadhurst <i>et al.</i> 2019)
After spawning	
Hatching	Hatch time is 5–11 days at temperatures of 18–20°C (Ingram <i>et al.</i> 2000), 10–18 days at 18°C (Wharton 1973; Cadwallader and Rogan 1977) Eggs highly susceptible to smothering by sediment (J. Koehn, ARI, unpubl. data)
Larvae	Newly hatched 4.5–6.5 mm in length, pelagic and swept downstream to pools (Gooley in Koehn and O'Connor 1990; Broadhurst <i>et al.</i> 2012) Begin to swim mid-water at 1–2 days (7 mm) and feed on zooplankton at 3–5 days after hatch (Ingram <i>et al.</i> 2000) Fry reared in ponds feed on a range of prey, but the most frequent and abundant prey are cladocerans, copepods and chironomid larvae (Ingram and De Silva 2007)
Behaviour	No parental care (Gooley and McDonald 1988)
Recruitment	After hatching, larvae rapidly transform into juveniles and inhabit low-flow habitats (typically pools), where they are diurnally active (Ebner and Lintermans 2007; Ebner <i>et al.</i> 2009a; Broadhurst <i>et al.</i> 2012) Several studies of both lacustrine (Douglas <i>et al.</i> 2002; Tonkin <i>et al.</i> 2010, 2017a) and riverine (Lintermans 2008, 2013b, 2016; Tonkin <i>et al.</i> 2017a) populations report some recruitment in most years. However, year class strength can be highly variable. In Lake Dartmouth, strong year classes were associated with periods of refilling of the lake, likely attributable to the increases in prey generated by the inundation of littoral areas (Gray <i>et al.</i> 2000; Tonkin <i>et al.</i> 2014). The abundance of YOY recruits showed a strong negative effect of discharge (and, to a lesser degree, discharge variability) during the preceding core egg and larval period (November and December; Tonkin <i>et al.</i> 2017a), suggested to be a result of large flow events disturbing spawning or egg and larval survival. Tonkin <i>et al.</i> (2017a) also reported positive associations between year class strength and the abundance of adult fish and, to a lesser degree, temperature during the spawning period
Growth	Growth increased during the first years of filling and then refilling of Lake Dartmouth, likely attributable to an increase in the availability of prey, generated by the inundation of newly revegetated littoral areas, and strong recruitment followed these years (Cadwallader and Douglas 1986; Tonkin <i>et al.</i> 2014) Fish from Lake Dartmouth have been aged up to 30 years old (Tonkin <i>et al.</i> 2018) Prolonged drawdown of Cotter Reservoir during enlargement works resulted in decreased growth rate of YOY (Lintermans 2013b; M. Lintermans, University of Canberra, unpubl. data) In ponds, growth of fry is rapid, from 7.6–16.6 mm (mean 11.3 mm) to 29.6–49.5 mm (mean 39.5 mm) in 35–54 days (mean 43 days), a mean growth rate of 0.66 mm day ⁻¹ (Ingram 2009) Growth in captivity is slow, with fish in tank grow-out trials reaching 3–22 g (mean 12 g) at 12 months of age and 16–161 g (mean 71 g) at 2 years of age (B. Ingram, VFA, unpubl. data) Growth function (Todd and Lintermans 2015): $Length_{Age} = 43.15 \times \exp(-1.68 \times \exp(-0.3 \times Age))$
Habitat	This riverine species also survives well in impoundments In rivers, occurs in well-defined home sites in areas with cover, such as deep pools, beneath undercut banks and around woody debris and rocky substrates (Broadhurst <i>et al.</i> 2012), preferring slow-moving pools (Bishop and Bell 1978) Are generally dispersed, but may shoal at barriers and during spawning times (Gooley, in Koehn and O'Connor 1990)

(Continued)

Table 8. (Continued)

Attribute	Description
	In lentic waters, inhabit deeper sections, particularly during diurnal hours, likely due to increased avian predation (Thiem <i>et al.</i> 2013) Larvae tend to school and associate in still waters and along steep rock faces near the edge of pools, whereas juveniles are most abundant at the head and foot of pools, where flow is greater (Broadhurst <i>et al.</i> 2012) Constructed rock reefs in the expanded Cotter Reservoir are actively used by adult fish (Lintermans <i>et al.</i> 2010) The LD ₅₀ of fertilised, pre-water-hardened eggs is 2060 EC (O'Brien and Ryan 1997)
Movements	
Eggs and larvae	Some minor movement of eggs as they settle in shallow riffle areas and lodge in the cobble or pebble substrate (EO) Some downstream larval dispersal (either passive or active) from hatching sites to larval and juvenile feeding areas, such as pools (e.g. Broadhurst <i>et al.</i> 2019) or lacustrine (e.g. Douglas 2002) habitats, is also likely
Larvae and juveniles	Dispersal of larvae and juveniles likely to be an important life-history process, considering the localised spawning or non-uniform distribution of early juvenile fish, which have been reported for both riverine and lacustrine populations (King <i>et al.</i> 2013; Tonkin <i>et al.</i> 2016)
Adults	Have relatively small core home ranges in rivers (<4 km), but there have been a few individual home ranges of 20 km recorded (Koster <i>et al.</i> 2013) Mostly active at night In the Cotter Reservoir, with diel movements (\pm s.d.) estimated at 769 \pm 93 m averaged among all seasons, but greater during winter (Thiem <i>et al.</i> 2013), with diel range lengths up to 1972 m (mean 516 \pm 89 m; Ebner <i>et al.</i> 2010) In Lake Dartmouth, 66% of fish were recaptured from the same location; however, 33% were relocated 4–34 km from the original capture point, indicating that some individuals are more mobile (Douglas <i>et al.</i> 2002). Adults moved throughout the lake during all times of the year, with fish moving >24 km in a single day, but they were most likely to migrate then occupy the riverine spawning reach between October and December (Tonkin <i>et al.</i> 2018) In mid to late spring, impounded adults have been noted to move into the inflowing rivers to spawn (Cadwallader and Rogan 1977; Gooley and McDonald 1988; see above), with larger individuals moving earlier and increased movement associated with increased flows (Lintermans <i>et al.</i> 2010) In riverine populations, movements to spawning sites are mostly 8–12 km, occurring on high flows and flow spikes, with most fish moving upstream (90%), but some (10%) moving downstream (P. McGuffie, NSW DPI, unpubl. data)
Behaviour	Shoaling rather than territorial; will use the entire water column; a quiet, docile species (Koehn and O'Connor 1990; Lintermans 2007)
Key threats	Key threats include: <ul style="list-style-type: none"> • Flow regulation in large rivers and loss of lotic habitats • Water extraction in small streams, where refuge pools are vital under drought (Kearns <i>et al.</i> 2012; Tonkin <i>et al.</i> 2018) and low flows can magnify the effects of in-stream barriers (Lintermans 2013a) • Water level management in impoundments, which can have a major effect on populations largely due to the effects of water levels on lake productivity (e.g. Tonkin <i>et al.</i> 2014) and access to riverine spawning habitat (e.g. Broadhurst <i>et al.</i> 2012, 2013) • Cold water releases, which can prevent spawning and recruitment (Koehn <i>et al.</i> 1995) • Increased sediment loads, which can cause loss of spawning habitat and smother eggs, because sediment fills the interstitial substrate spaces (Cadwallader 1977) and larger particles (cobbles) can infill preferred riverine pool habitats (Koehn <i>et al.</i> 1995) • Fire, which causes loss of riparian vegetation, increased water temperatures and potential sediment slugs after intense rainfall that can result in fish kills (Lyon and O'Connor 2008; Kearns <i>et al.</i> 2012) • Unsustainable angler harvest (Hunt <i>et al.</i> 2011) • Drought or prolonged periods of cease-to-flow events, which reduce connectivity between habitats, restrict fish to pools and increase stress and the potential for predation, parasite loading and a decrease in water quality (Kearns <i>et al.</i> 2012) • Removal of in-stream wood, which reduces habitat complexity (Lintermans 2007) • In-stream barriers, which can disconnect populations from habitats and suitable spawning areas (Lintermans 2012, 2013a) • Fishing, particularly overexploitation of spawning aggregations (Cadwallader and Rogan 1977), and illegal fishing, which have likely contributed to population declines in lakes and rivers (Tonkin <i>et al.</i> 2018); post-release mortalities can also affect populations (EO) • Predation by birds such as the great cormorant <i>Phalacrocorax carbo</i> (Ryan <i>et al.</i> 2013), with up to six fish (<275 mm TL) recorded in a single bird stomach (Lintermans <i>et al.</i> 2011) <p>The mid-water behaviour of newly hatched fish appears to render them susceptible to fish predators (Broadhurst <i>et al.</i> 2012). Larval predation by trout and redfin is likely but is unproven (Ebner <i>et al.</i> 2007; M. Lintermans, University of Canberra, unpubl. data), but predation by large adult and brown trout (<i>Salmo trutta</i>) on juveniles has been described for reservoirs (Broadhurst <i>et al.</i> 2018). The effects of carp are unknown, although adult carp have been observed feeding within spawning sites during peak reproductive periods (Tonkin <i>et al.</i> 2009) Redfin may also act as a vector for the epizootic haematopoietic necrosis virus (Lintermans 2012), which causes sudden mortalities (Langdon 1989) Small remnant and now isolated populations exhibit less stable recruitment patterns, and therefore a reduced resilience to environmental extremes (Tonkin <i>et al.</i> 2017a, 2019b), particularly those that are likely to be exacerbated by climate change (as predicted by Balcombe <i>et al.</i> 2011) Considered highly vulnerable to drought (Crook <i>et al.</i> 2010) and moderately vulnerable to climate change impacts (Chessman 2013) Loss of genetic diversity, limiting the ability for populations to adapt to varying environmental drivers (Pavlova <i>et al.</i> 2017)</p>

Table 9. Life-history attributes for freshwater catfish

ARI, Arthur Rylah Institute for Environmental Research; DAF, Department of Agriculture and Fisheries; DNRME, Department of Natural Resources and Mines and Energy; DO, dissolved oxygen; DPI, Department of Primary Industries; EO, expert opinion; F, female(s); M, male(s); MDB, Murray–Darling Basin; NMDB, northern MDB; NSW, New South Wales; SMDB, southern MDB; TL, total length; VFA, Victorian Fisheries Authority

Attribute	Description
Before spawning	
Sexual maturity	Generally, 3–5 years, 1.2 kg (Davis 1977a), although ~50% of fish (M and F) may be mature at 2 years (252 mm for F; B. Zampatti, CSIRO; K. Burndred, DNRME, unpubl. data) The smallest mature F recorded (lower Murray River) was 215 mm TL (Ye <i>et al.</i> 2015)
Fecundity and eggs	Developing eggs are spherical, demersal, non-adhesive, light green to yellow or amber in colour and 2.6–4.0 mm in diameter when water hardened (Lake 1967c; Ingram <i>et al.</i> 2014; Burndred <i>et al.</i> 2017, 2018) Egg size increases with adult body weight and length (Davis 1977b) Fecundity increases with fish size (Pollard <i>et al.</i> 1996): in the NMDB 1.25- to 2-kg fish produced 9000–15 000 eggs (Davis 1977b); hatchery estimates of 18 000–60 000 eggs (Lake 1967b), with 1.4-kg fish producing ~20 000 eggs (Lake 1959). Up to 3371 eggs kg ⁻¹ (mean 2250 eggs kg ⁻¹ for 0.655- to 1.36-kg fish) have been hand-stripped from captive fish (Ingram <i>et al.</i> 2014)
Spawning	
Description	Annual, batch spawner, with nesting and parental care (Lintermans 2007)
Season	November to end of March in the SMDB (Leigh <i>et al.</i> 2008; Cheshire <i>et al.</i> 2012; Ye <i>et al.</i> 2015), and from October to April in the NMDB (Davis 1977b; Pusey <i>et al.</i> 2004; S. Balcombe, Griffith University, unpubl. data) associated with rises in water temperature (Merrick and Midgley 1981)
Conditions	Not linked to flooding (Davis 1977b), although rising water levels may hasten spawning (Lake 1967c) Nest building and spawning do not occur until water temperatures are >24°C (Lake 1967b, Davis 1977b) Running ripe M observed at 18°C in SMDB lakes in mid-November (T. Raadik, ARI, pers. comm.) In NMDB, onset typically coincides with stabilising flow or stream levels and water temperatures increasing to >22°C from July to November (K. Burndred, DNRME, unpubl. data) Larvae commonly collected in the lower Murray River in November (Leigh <i>et al.</i> 2008; Cheshire <i>et al.</i> 2012; Ye <i>et al.</i> 2015) Eggs recorded on nests with <i>in situ</i> water temperatures of 15.1–29.9°C in the NMDB (Burndred <i>et al.</i> 2017) and 21–28.6°C in the SMDB (P. Clunie, ARI, pers. obs.)
Location	M build neat, circular to oval nests, usually 0.6–2.5 m in diameter, of coarse sand, pebbles or gravel, with a central muddy or sandy depression (Pollard <i>et al.</i> 1996; Carpenter-Bundhoo <i>et al.</i> 2020b). Nests are located in both clear areas and close to in-stream habitat, often clustered, with solitary nests rare (Carpenter-Bundhoo <i>et al.</i> 2020b; K. Burndred, DNRME, pers. comm.). Preferred nest sites are on shallower (0.15–2.2 m) outer bends in rivers, where water can be 3–4°C warmer (K. Burndred, DNRME, pers. comm.), and along the shallower margins in lake habitats (P. Clunie, ARI, pers. obs.). Nests are often clustered together in waterholes, or slow-flowing areas, with approximately 80–100 nests observed in a single season within a 2-km reach of stream (Department of Natural Resources and Mines and Energy 2016), and ~70 obvious nests observed in a 3- to 4-ha lake (P. Clunie, ARI, unpubl. data) Nests may be abandoned if there is a sudden increase or decrease in flow that results in rapid water level changes. Upon the return of suitable conditions, fish may return to build or tend to nest at the same site, or in proximity, and successfully resume nesting, but continual water flow fluctuations may lead to complete abandonment (K. Burndred, DNRME, unpubl. data) Where nests have been destroyed by flooding, they have been rebuilt within days (K. Burndred, DNRME, pers. comm.) No cannibalism of eggs has been noted; however, other species have been observed preying on nests in the absence of a guarding M, including spangled perch <i>Leiopotherapon unicolor</i> , banded grunter <i>Amniataba percoides</i> , sooty grunter <i>Hephaestus fuliginosus</i> and redfin (Department of Natural Resources and Mines and Energy 2016; P. Clunie, ARI, pers. obs.) Nests can be readily seen in clear waters, but are likely also present in turbid streams with clay substrates Mortality of eggs increased with water temperatures decreasing to <16°C (Ryan <i>et al.</i> 2003) and rising temperatures to >28°C (K. Burndred, DNRME, unpubl. data)
After spawning	
Behaviour	Parental care is exhibited by the M, which guards the eggs (Lintermans 2007) M stay with the nest and coerce the F to the nest; courtship behaviour of weaving and circling ensues It is possible that several fish use the same nest during the season, and multiple spawning events can occur in a single nest. Although there is typically one M per nest, the nest may be visited by many F; several (up to 12) different aged cohorts of eggs and larvae been found at one nest site, developing simultaneously (P. Clunie, ARI; K. Burndred, DNRME, unpubl. data). F may visit multiple nests, leaving each nest once eggs are deposited (Merrick and Midgley 1981). M remains, exhibiting parental care, swimming around the nest, chasing away other fish and removing unwanted debris (P. Clunie, ARI, pers. obs.) Nest building can commence from 1 to 30 days prior to spawning (K. Burndred, DNRME; P. Clunie, ARI, unpubl. data)
Hatching	Hatch in the wild occurs 4–7 days at 15.7–28.0°C in NMDB (Burndred <i>et al.</i> 2017) In SMDB, hatch occurs at 8–11 days at 15–21°C (Lake 1959, 1967e) or at 7 days at 19–25°C (Lake 1967b), with all larvae gone from nests after 16 days Hatching from 5 days in the hatchery at 21–22°C (Ingram <i>et al.</i> 2014) Wild larvae hatch at 5.1–8.2 mm (at 15.1–29.9°C) and possess a circular yolk and lightly pigmented eyes. Although the larvae lack barbels, pectoral, pelvic and anal fins, they have a well-developed heart and myomeres and are capable of short bursts of wriggling movement (Burndred <i>et al.</i> 2017)

(Continued)

Table 9. (Continued)

Attribute	Description
Larvae	<p>Grow rapidly in the first 24 h, and by 2 days (after hatching) barbel buds appear alongside a functional jaw, and notochord flexion commences. By 5 days, they are 8.9–11.7 mm with caudal fin rays developing</p> <p>The yolk sac is mostly absorbed by 7 days, when the gut and anus are developed, and the first evidence of active feeding and excretion is observed</p> <p>Larvae have distinguishable barbels and are capable of actively swimming in the water column and voraciously consuming prey at ~12 mm (Lake 1967b, 1967e; Burndred <i>et al.</i> 2017)</p> <p>By 16 days, larvae are up to 15.3 mm, possess a full complement of fin rays, the dorsal spine is present, and the skin has become thick, opaque and is fully pigmented (Burndred <i>et al.</i> 2017)</p> <p>After yolk sac absorption, larvae are good swimmers but spend most time sheltering (K. Burndred, DNRME, unpubl. data)</p>
Recruitment	<p>Some recruitment can occur every year, but major peaks have been related to years with overbank floods</p> <p>In the NMDB, recruitment appears to be stronger in years with prolonged suitable nesting or spawning conditions combined with high wet-season flow events (K. Burndred, DNRME, unpubl. data).</p> <p>In the lower Murray River, relative abundance remained low in the main channel and anabranch habitats during the Millennium Drought (Ye <i>et al.</i> 2015), but following extensive flooding and increased in-channel flows (2010–12), there was a significant increase that comprised multiple size and age classes (e.g. 2–12 years in the main channel in 2013–14), with many 0+ and 1+ recruits found in wetlands in 2011–12 (Ye <i>et al.</i> 2015), suggesting that migration from other river habitats as well as recruitment contributed to these changes. Similar pulse recruitments have been observed in southern NSW following flooding in the early 1970s (J. Lieschke, ARI, pers. comm.), in the Euston Lakes, mid-Murray River (Stoffels <i>et al.</i> 2014) and in coastal rivers (M. Rourke, NSW DPI, pers. comm.).</p> <p>Population structure in a Murray River off-channel lake exhibited a significant compositional change following a large natural flood; 0+ and 1+ fish increased in abundance, whereas 2+ and 3+ fish declined, likely caused by recruitment dynamics, as well as age-specific lateral movement (Stoffels <i>et al.</i> 2014)</p>
Growth	<p>Translocated adult fish can successfully establish breeding populations in small, shallow impoundments (P. Clunie, ARI, unpubl. data).</p> <p>Daily otolith increments validated up to 28 days post-hatching for larvae reared in a laboratory (from naturally fertilised wild stock; Burndred <i>et al.</i> 2017)</p> <p>Juveniles grow rapidly, measuring 15–19 mm at 17–21 days, 90 mm in the first winter, 300–340 mm by 16 months, 170–360 mm by 30 months, 250–480 mm by 42 months and 500 mm by 6 years (Lake 1967b; Merrick and Schmida 1984; Pollard <i>et al.</i> 1996)</p> <p>Fish reared in captivity average 4.3 g by 14 weeks of age (B. Ingram, VFA, unpubl. data)</p> <p>Fish 131–195 mm are estimated to be ~1 year, 255–380 mm ~2 years, 330–481 mm ~3 years, 490–505 mm ~4 years, 350–470 mm ~5 years and one fish of 510 mm was estimated to be ~11 years (T. Raadik, ARI, unpubl. data)</p> <p>The growth of juveniles is markedly affected by temperature, with mean weight gains for a 2.98-g fish over 90 days at water temperatures of 12.6, 15.5, 18.5, 21.2 and 24.2°C being 1.0, 1.5, 2.5, 5.3 and 11.0 g respectively (Ryan <i>et al.</i> 2003)</p> <p>In the lower Murray River, there is considerable variation in length-at-age for most age classes: 2-year-old fish 190–290 mm TL; 8-year-old fish 257–482 mm TL; 200-mm-TL fish were 2–6 years. Maximum age 10–12 years (T. Raadik, ARI; K. Burndred, DNRME, unpubl. data; Ye <i>et al.</i> 2015)</p> <p>The von Bertalanffy growth curve for the lower Murray River is $L_t = 407.1577(1 - \exp[-0.3475\{t + 0\}])$, where L_t is TL (mm) and t is age (years; Ye <i>et al.</i> 2015)</p>
Habitats	<p>Considered a habitat generalist found in a range of habitats: rivers, creeks, lakes, waterholes and wetlands (Cadwallader and Backhouse 1983; Wilson <i>et al.</i> 2012; Stoffels <i>et al.</i> 2014; Ye <i>et al.</i> 2015; Carpenter-Bundhoo <i>et al.</i> 2020a)</p> <p>Appear more abundant in shallow waterbodies with steady water levels; lakes and backwaters, large floodplain waterbodies (Lake 1967c); and sluggish rivers with complex physical structure including wood, undercut banks, fringing vegetation and abundant aquatic macrophytes (Davis 1977a, 1977b; Brumley 1987; Llewellyn 1983; Pollard <i>et al.</i> 1996; Hammer <i>et al.</i> 2009; Ye <i>et al.</i> 2015), where they use structural habitat in slower-flowing areas (Pollard <i>et al.</i> 1996; Pusey <i>et al.</i> 2004; Koster <i>et al.</i> 2015)</p> <p>Juveniles found in shallower habitats, whereas adults are more commonly in deeper runs and pools (Clunie and Koehn 2001b; Pusey <i>et al.</i> 2004)</p> <p>In contrast to many of the slow, turbid, vegetated habitats occupied in the SMDB, in the border rivers of the NMDB clear sandy streams are also used (Pusey <i>et al.</i> 2004). In these habitats, adults and juveniles occur primarily over sand, fine gravel, gravel and cobble substrates (15–30% each), and rarely over mud, rocks and bedrock (<5% each; Pusey <i>et al.</i> 2004). Appear to inhabit faster-flowing water in these habitats, and adults are most frequently recorded in undercut banks and are usually associated with overhanging vegetation and in-stream structures (e.g. woody debris, root masses; ~20% each; Department of Natural Resources and Mines and Energy 2016). Juveniles most frequently found among macrophytes, filamentous algae and leaf litter (between 15 and 20% each; Pusey <i>et al.</i> 2004), and often close to riffles (NMDB)</p> <p>Preferred deeper water during the day, although fish moved into the shallows along banks on moonless nights (Grant 1987). Occupy predominantly shallow (<1 m) littoral habitats with high densities of macrophytes and fallen trees during the day (Koster <i>et al.</i> 2015; Department of Natural Resources and Mines and Energy 2016)</p>

(Continued)

Table 9. (Continued)

Attribute	Description
	Have high tolerances to poor water quality, including low DO; temperatures 1–34.8°C (Lake 1967 <i>d</i> ; K. Burndred, DNRME, pers. comm.)
	Tend to be found in larger, more permanent waterholes in the intermittent systems of the NMDB (Balcombe <i>et al.</i> 2006, unpubl. data; Carpenter-Bundhoo <i>et al.</i> 2020 <i>a</i>)
Movements	Juveniles are reasonably tolerant to low DO, with 50% mortality at $0.25 \pm 0.01 \text{ mg L}^{-1}$ over 48 h (Small <i>et al.</i> 2014)
	Generally considered to be largely non-migratory, exhibiting limited movements and tending to remain in the same section of river for most of their lives (Davis 1977 <i>c</i>), with most individuals moving <5 km (Merrick and Schmida 1984; Department of Natural Resources and Mines and Energy 2016). However, during flow events, are often found accumulating below barriers in the NMDB, suggesting upstream movements (S. Balcombe, Griffith University, pers. obs.)
Eggs and larvae	Eggs attached in the nest
	Dispersal of larvae from nests considered to be an active ‘scatter’ as soon as they are physiologically independent and ‘equipped’ to disperse in this way. They remain in reasonably productive, safe habitats (e.g. littoral zones, macrophyte beds, lentic slackwaters etc.) until high flows, when they can disperse and access inundated habitats
	Some larvae are collected drifting in flowing rivers (K. Burndred, DNRME, unpubl. data; Leigh <i>et al.</i> 2008; Ye <i>et al.</i> 2015), and downstream dispersal increased during periods of high flow (Cheshire <i>et al.</i> 2012)
Juveniles	Unknown
Adults	Considered largely sedentary in rivers, with limited movements from a home range (Davis 1977 <i>a</i> , 1977 <i>b</i> ; Reynolds 1983; Koster <i>et al.</i> 2015; Carpenter-Bundhoo <i>et al.</i> 2020 <i>a</i>), resulting in many populations being isolated (Keenan <i>et al.</i> 1996)
	In the Murray River, 60% of recaptured fish had not moved from the area, 37% moved <10 km up- or downstream, and only one fish moved >10 km (Reynolds 1983). In Tahbilk Lagoon (SMDB), typically had limited ranges (median total linear range and 90% linear range of 599 and 173 m respectively), but occasionally moved up to 1.5 km between floodplain and riverine habitats (Koster <i>et al.</i> 2015). In Euston Lakes, catfish moved during overbank flooding (Stoffels <i>et al.</i> 2014, 2016). In the NMDB, 29% of a population exhibited sedentary behaviour (fish remained within their tagging pool), 64% exhibited interpool movements (fish moved between up- and downstream pools, and these movements were mostly undertaken during low-flow conditions), and 7% exhibited larger, reach-scale movements (fish moved up- and downstream throughout numerous pools, within an ~40 km study reach; Burndred <i>et al.</i> 2018)
	Commonly exhibit homing close to original capture point (Davis 1977 <i>b</i>); this behaviour was also reported for translocated fish (Department of Natural Resources and Mines and Energy 2016)
	Movements may have been underestimated, because they are considered good burst swimmers (capable of >1.8 m s ⁻¹), have been found in NMDB fishways and large-scale movements both up- and downstream have been observed (Stuart and Berghuis 2002; Burndred <i>et al.</i> 2018), particularly prior to spawning
	Have been reported dispersing downstream into an estuary on high flows, then using a fishway to return upstream (Stuart and Berghuis 2002)
	Can navigate up- and downstream through short, shallow riffles (e.g. <50 m long, <0.25 m deep, velocity <0.9 m s ⁻¹), culverts and cascades (Burndred <i>et al.</i> 2018)
	Observed moving during all flow events that peaked at >2 m above cease-to-flow levels (Marshall <i>et al.</i> 2016), with 55% of initial event-based movements being upstream (mean distance 25.4 km) and 45% downstream (mean 12.6 km). Individuals passed through an average of three and up to nine waterholes. No difference in length between movement behaviours (Marshall <i>et al.</i> 2016; Burndred <i>et al.</i> 2018). Movement commenced early during flow events, with water temperatures of 15–28°C, but also commenced when water levels were dropping, although small flow events did not appear to initiate movement (Marshall <i>et al.</i> 2016). Although some movements occur under base-flow conditions and elevated flow conditions, probability and frequency of movements between waterholes was greatest following a discharge event (particularly after the first post-winter flow events of the season; Burndred <i>et al.</i> 2018). Movements are typically initiated on the fall of the hydrograph, 4–6 days after peak flow (Burndred <i>et al.</i> 2018)
	Genetic structure within the MDB is not highly differentiated, likely due to high levels of connectivity (Keenan <i>et al.</i> 1996; Rourke and Gilligan 2010, 2015)
Behaviour	Predominantly nocturnal, with activity generally increasing in the late afternoon, continuing throughout the night and then declining soon after sunrise (Davis 1977 <i>a</i> ; Burndred <i>et al.</i> 2018)
	Movement distances are much greater at night and F movement > M movement during the spawning season (Koster <i>et al.</i> 2015)
	Juveniles may form loose schools, whereas adult fish tend to be solitary or grouped in small schools, except when mating (Cadwallader and Backhouse 1983; K. Burndred, DNRME, pers. comm.)
	Fish move from the main channel to shallower habitats, and generally become more active in the weeks prior to nest establishment (K. Burndred, DNRME, unpubl. data)

(Continued)

Table 9. (Continued)

Attribute	Description
Key threats	<p>Key threats include:</p> <ul style="list-style-type: none"> • Wetland loss and disconnection due to drainage, levees and barriers, and river regulation, all of which have significantly reduced the magnitude and frequency of flooding and consequently the size of floodplain areas inundated (Closs <i>et al.</i> 2006). Although weir pools may provide some additional habitats, the overall implications of this habitat change are not clear because the species has also declined in the lower Murray River, which is now essentially a series of large weir pools (Walker 2006) • Rapid changes to flows, with elevated flow events during nesting and spawning periods able to increase the mortality of eggs and larvae by washing them downstream; rapid drawdown can increase egg and larval mortality and cause abandonment of the nest by the guarding M (K. Burndred, DNRME, unpubl. data) • Cold water releases, which can affect spawning and growth and cause localised extinctions downstream of impoundments (EO) • Habitat degradation, particularly loss of preferred structural habitats, such as aquatic plants and undercut banks (EO) • Overfishing of drought refugia in ephemeral rivers during drought years (M. Hutchison, DAF, pers. obs.) • Increased sediment levels, which can potentially smother eggs and may necessitate increased maintenance of nests • Entrainment by irrigation pumps (M. Hutchison, DAF, pers. obs.) <p>Likely to be highly affected by carp. Both species are largely benthic feeders, and there are dietary and habitat overlaps, so there is competition for resources where carp are in high abundance. Carp destroy preferred aquatic vegetated habitats and have been suggested to prey on eggs and disrupt paternal nest care (Hammer <i>et al.</i> 2009; P. Clunie, ARI, pers. obs.). In the NMDB, the most abundant freshwater catfish populations appear to be in carp-free impoundments (M. Hutchison, DAF, pers. obs.). Following a flood and reconnection, an abrupt change to population structure and declines in condition, growth and abundance were attributed to the incursion of carp (Stoffels <i>et al.</i> 2014, 2016).</p> <p>Redfin have been observed investigating nests and likely predate upon eggs, larvae and juveniles (P. Clunie, ARI, pers. obs.)</p> <p>Mozambique tilapia <i>Oreochromis mossambicus</i> and spotted tilapia <i>Tilapia mariae</i> are considered an imminent threat in the NMDB (Arthington <i>et al.</i> 1984).</p> <p>Considered to have high vulnerability to drought (Crook <i>et al.</i> 2010), but reasonably low vulnerability to climate change overall (Chessman 2013)</p> <p>High tolerances to poor water quality may provide some opportunities to survive in refuge waters, then repopulate</p>

Table 10. Life-history attributes for southern pygmy perch

ARI, Arthur Rylah Institute for Environmental Research; DO, dissolved oxygen; DPI, Department of Primary Industries; EO, expert opinion; F, female(s); M, male(s); MDB, Murray–Darling Basin; NMDB, northern MDB; NSW, New South Wales; SMDB, southern MDB; TL, total length

Attribute	Description
Before spawning	
Sexual maturity	At ~1 year and 30–33 mm TL (Humphries 1995; Hammer 2002)
Fecundity and eggs	<p>Fecundity and egg size vary within and between populations, depending on body size, age and environmental conditions (Morrongiello <i>et al.</i> 2012)</p> <p>Fecundity estimated range 40–4000 eggs per F (mean ± s.d. 451.19 ± 359.82 eggs per F; Cadwallader and Backhouse 1983; Kuitert <i>et al.</i> 1996; Morrongiello <i>et al.</i> 2012)</p> <p>Relationship between fecundity (Fe) and length (L):</p> <p>$Fe = 20.096L - 597.220$ (Humphries 1995; combined with data from Morrongiello <i>et al.</i> 2012)</p> <p>$Fe = \exp(0.05068 \times L + 3.2043)$ (Todd <i>et al.</i> 2017)</p> <p>Eggs small (0.91–1.55 mm; Morrongiello <i>et al.</i> 2012), round, transparent, non-adhesive and demersal (Humphries 1995)</p> <p>Fecundity function (Todd <i>et al.</i> 2017):</p> <p>$Fecundity_{Age} = \exp(0.05068 \times \exp(0.1933 \times Age + 3.4597) + 3.2043)$</p>
Spawning	
Description	<p>Egg scatterers, over aquatic vegetation or the benthos within M territories (Mitchell 1976)</p> <p>Bright red fins visible on breeding M (Morrongiello <i>et al.</i> 2010)</p> <p>Courtship displays performed by males</p> <p>Small number of eggs released at each spawning act; spawning appears to occur over 3–4 days, with F spawning several times per season (Mitchell 1976)</p>
Season	Protracted, typically September–December (Llewellyn 1974); September–January (Humphries 1995)
Conditions	Not linked to hydrology but rather to circa-annual cues, particularly water temperature 15–20.5°C (Llewellyn 1974; Humphries 1995; Tonkin <i>et al.</i> 2008)
Location	Typically occurs in slow-flowing habitats with complex physical habitat (Tonkin <i>et al.</i> 2008)
After spawning	
Hatching	2–4 days at 15–18°C (Llewellyn 1974)

(Continued)

Table 10. (Continued)

Attribute	Description
Larvae	Hatch at ~3.5 mm; exogenous feeding commences once the yolk sac has been consumed, at ~5 days after hatching (Llewellyn 1974)
Behaviour	Potential weak paternal protection of eggs and larvae because they are scattered within M territories (Oxleyan pygmy perch, <i>Nannoperca oxleyana</i> ; Knight <i>et al.</i> 2007)
Recruitment	Given the short lifespan, population persistence is largely reliant on annual recruitment Increases in local population abundance are typically observed in November following juvenile recruitment, but recruitment strength may vary between years (Woodward and Malone 2002). Enhanced recruitment has been associated with flooding and elevated water levels in spring in the mid-Murray and lower lakes, presumably due to greater productivity and access to nursery habitats (Bice and Ye 2007; Tonkin <i>et al.</i> 2008). Conversely, in small, highly altered upland streams, large flood events can cause catastrophic population declines because major erosive flooding events can destroy preferred habitats of aquatic vegetation and result in the adults, larvae and eggs being washed downstream, resulting in mortalities, stranding of fish or relocation into unsuitable habitats (Woodward 2005; Pearce 2014) Dry conditions and low water levels during or following the spawning season have been associated with diminished recruitment. Adults may persist within remnant pools, but prolonged dry conditions and associated lack of connectivity, reduced habitat quality (e.g. loss of submerged macrophytes and increased salinity) and limited productivity can cause consecutive years of recruitment failure and ultimately the loss of local populations (Tonkin <i>et al.</i> 2008; Wedderburn <i>et al.</i> 2014a) Flooding may support movement and recruitment and movements in wetland areas (EO) Populations are typically dominated by 0+ and 1+ individuals, suggesting only a small proportion of individuals survive to 2+ (Humphries 1995)
Growth	Otoliths suggest daily and annual increment deposition, but this remains unvalidated; 30 mm TL is attained at ~70 days (Tonkin <i>et al.</i> 2008), 45 mm TL at ~1 year and 52 mm TL at ~1.5 years (Humphries 1995). A 76-mm-TL fish was estimated as 3+ years (Humphries 1995) Age-length relationships: $L_t = 64.12(1 - e^{-0.994(t + 0.309)})$ for F and $L_t = 61.39(1 - e^{-0.989(t + 0.326)})$ for M (Humphries 1995), where L_t is TL (mm) and t is age (years) Growth function (Todd <i>et al.</i> 2017): $Length_{Age} = \exp(0.19 \times Age + 3.46)$
Habitats	Occur in a wide range of both lentic and lotic habitats (Cook <i>et al.</i> 2007), including small creeks, shallow wetlands and lakes nearby to large rivers (Humphries 1995). Most commonly found in off-channel habitats, preferring slow-flowing or still waters associated with macrophytes and woody debris (Llewellyn 1974; Tonkin <i>et al.</i> 2008). Favour shallow littoral habitats, but individuals may be observed at greater depths in areas with macrophytes and not exposed to substantial currents (Humphries 1995) Reliant on the presence of perennial refuge pools during cease-to-flow periods to avoid localised population losses (Dexter <i>et al.</i> 2014) Able to tolerate a broad range of temperatures (3.4–29.5°C; Llewellyn 1974), salinity to 10 ppt (Chessman and Williams 1974) and extremely low DO levels (<1.0 mg L ⁻¹) for short periods of time (McNeil and Closs 2007)
Movements	Considered to be non-migratory, exhibiting limited dispersal ability (Hammer 2002; Dexter <i>et al.</i> 2014) Surveys after high-flow years and floodplain inundation found local colonisation at a greater number of sites (Tonkin <i>et al.</i> 2008). Flooding may provide new habitats, promote productivity and facilitate the movement of the species (Humphries 1995; Tonkin <i>et al.</i> 2008) Genetic analyses indicate a lack of contemporary gene flow between remnant populations in the MDB, which concurs with a largely sedentary life history and limited dispersal (Cole <i>et al.</i> 2016) Slow upstream dispersal of populations exhibited from translocations into a small creek (a total of 528 individuals), with fish detected only 3 km upstream of the stocking site after 9 years (L. Pearce, NSW DPI, pers. comm.)
Eggs and larvae	Movement unlikely, as eggs adhered to vegetation or on the substrate in still waters (Llewellyn 1974; Mitchell 1976; Tonkin <i>et al.</i> 2008)
Juveniles	Unknown
Adults	Considered to be limited (EO)
Behaviour	Seldom found in large numbers (Llewellyn 2014); M territorial during breeding season (Mitchell 1976) Carnivorous (Lintermans 2007)
Key threats	Key threats include: <ul style="list-style-type: none"> • Habitat changes and river regulation resulting in loss of wetland and lentic habitats (Hammer <i>et al.</i> 2009, 2013). Decreased frequency of floodplain inundation has led to a decrease in wetland habitat diversity (many wetlands are now either 'wet' or 'dry'), and this has potentially affected dispersal (NSW Department of Primary Industries 2014). Lowland, shallow, fragmented freshwater habitats where populations persist are particularly susceptible to habitat degradation and unnatural cycles of drying and loss of refuge habitats (Saddler <i>et al.</i> 2013; Dexter <i>et al.</i> 2014) • High-volume flooding in some upland streams causing extensive erosion and habitat (macrophyte) destruction (Pearce 2014, 2015a, 2015b) • Introduced species: predation by redfin and brown trout; competition with and fin nipping by eastern gambusia <i>Gambusia holbrooki</i> (Humphries 1995; Pearce 2014; Wedderburn and Barnes 2016); effects of carp on habitat quality resulting from destruction of aquatic macrophytes and increased turbidity (Jones <i>et al.</i> 2008; do not appear to persist when carp are in high densities, EO) • In-stream barriers inhibiting dispersal (NSW Department of Primary Industries 2014) <p>Considered highly vulnerable to drought (Crook <i>et al.</i> 2010), particularly in small streams in which refuge pools dry up during prolonged drought conditions High vulnerability to climate change impacts (Chessman 2013)</p>

Table 11. Life-history attributes for the Murray hardyhead

ARI, Arthur Rylah Institute for Environmental Research; DO, dissolved oxygen; DPI, Department of Primary Industries; EO, expert opinion; F, female(s); FL, fork length; M, male(s); MDB, Murray–Darling Basin; NMDB, northern MDB; NSW, New South Wales; SMDB, southern MDB; TL, total length

Attribute	Description
Before spawning	
Sexual maturity	M at 27–34 mm and F at 41–43 mm (Lintermans 2007), may be reached within 4–5 months (28–30 mm) for fish spawned early in the breeding season (Ellis 2005), or even 3–4 months (individuals in captivity have reached this size in <2 months; Stoessel <i>et al.</i> 2020)
Fecundity and eggs	Between 30 and 87 ovated eggs (mean \pm s.d. 57 ± 18) and at least five developmental stages were present in a subsample of gravid F in October (Ellis 2005) Fecundity estimated at 200–500 eggs per F, and 50 F spawned ~2500 eggs in captivity over 2 months (D. Stoessel, ARI, unpubl. data) Egg development is likely stimulated by increasing temperature (>20°C) and photoperiod during spring (see Stoessel <i>et al.</i> 2020) Eggs spawned 2 h either side of dawn (at 24°C); water-hardened eggs clear and 1.95 mm in diameter (Stoessel <i>et al.</i> 2020)
Spawning	
Description	Batch spawners, with eggs at various stages of development apparent in the ovaries of mature F (Ellis 2005; Hammer and Wedderburn 2008) Golden hue may be prominent, particularly in M during the spawning period (Ebner <i>et al.</i> 2003; Hammer and Wedderburn 2008)
Season	September–March (Ellis 2005; Hammer and Wedderburn 2008) but, based on larval abundance, peak spawning from late October to early November (Ellis 2005; Ellis <i>et al.</i> 2013; Stoessel <i>et al.</i> 2019). In some years, individuals spawned early in a breeding season may reach maturity in the same season and breed as late as March (Ellis <i>et al.</i> 2013)
Conditions	Water temperatures >24°C are suggested to trigger spawning (Stoessel <i>et al.</i> 2020) Juveniles have been recorded at discrete off-channel sites with salinities 35–50 ppt, but survival is unknown (D. Stoessel, ARI, unpubl. data) No embryos hatched at salinities >40 ppt (Stoessel <i>et al.</i> 2019)
Location	In captivity, egg batches are generally spawned overnight to mid-morning, and in the wild F typically deposit clutches of 4–80 adhesive eggs on submerged vegetation within the top 250 mm of the water column (Hammer and Wedderburn 2008; Ellis <i>et al.</i> 2011; Stoessel <i>et al.</i> 2020)
After spawning	
Hatching	4–10 days at 20–26°C (Hammer and Wedderburn 2008; I. Ellis, NSW DPI, unpubl. data); on average 11 days after spawning at 25°C in captivity (Stoessel <i>et al.</i> 2020) It is likely that most adult fish die after the spawning season (estimated >90% mortality), with few individuals believed to survive into their second year (Ellis <i>et al.</i> 2013) Egg hatch of 30–80% per year estimated from captive breeding trials (I. Ellis, NSW DPI, pers. obs.), but can vary from 0 to 90% depending on salinities (Stoessel <i>et al.</i> 2020)
Larvae	Hatch at 5.19 mm (Stoessel <i>et al.</i> 2020) and develop to juveniles exhibiting adult scale and fin features after 20–30 days (I. Ellis, NSW DPI, unpubl. data) Estimated 30–60% of hatched captive larvae survived to juvenile or immature adult life stages (I. Ellis, NSW DPI, pers. obs.), but this figure can vary from 0 to 80% depending on salinities (D. Stoessel, ARI, unpubl. data) Survival rates of larvae in the wild are unknown Comparatively, the congeneric unspotted hardyhead <i>Craterocephalus fulvus</i> has a mean cumulative larval mortality of 93% from 3–4 days to 24 days (McCasker <i>et al.</i> 2014) Rapid population growth in populations in saline wetlands may be a response to such habitats creating conditions less suited to native and introduced competitive and predatory species, and a reduction in fungal infection in eggs (Stoessel <i>et al.</i> 2020)
Behaviour	No parental care (D. Stoessel, ARI, pers. obs.)
Recruitment	Population size is dictated by annual recruitment, and interannual abundance may vary greatly ('boom and bust') in concurrence with recruitment success and dispersal after flooding Water level variability (which may be enhanced by environmental watering) has been shown to increase the abundance of food (i.e. zooplankton) at discrete sites over the spawning period, and likely results in greater recruitment (Ellis 2006; Wedderburn <i>et al.</i> 2013) Patterns of size class distribution and larval abundance indicate that strongest recruitment events occur in spring and summer; recruitment success appears to decrease for individuals spawned in autumn (in concurrence with decreases in water temperature, productivity and food availability; Ellis 2005). A seasonal shift in modal length is typical of most populations, but the limited number of studies mean there is uncertainty in our understanding of population and recruitment dynamics During the peak of the spawning season in spring, populations are dominated by reproductively mature adult fish (i.e. >40 mm), but by the following autumn there are few fish >40 mm). This pattern suggests a large-scale die-off of adults through summer, and implies the species is largely annual (populations dominated by 0+ individuals) and heavily dependent on annual recruitment. This is supported by preliminary analysis of otolith microstructure from a sample of adult fish (Ellis 2006), with no fish exhibiting multiple 'growth checks' that would indicate survival of over 18 months. This annual pattern of cohort replacement is shown stylistically in Fig. 6 Comparatively, at other sites, populations have been shown to be numerically dominated by larvae in spring. Nevertheless, a portion of mature adult fish (>40 mm) may also be present and may continue to spawn for several months. Furthermore, fish spawned early in the season may grow to maturity and spawn later in the same season, with several cohorts then being present (see Fig. 6b, length v. frequency graphs). Large-scale die-off is suggested to occur towards autumn, when older or less fit individuals succumb to cooler temperatures and a decline in food abundance (D. Stoessel, ARI, unpubl. data). In any case, batch spawning and cohort recruitment is complex and needs to be considered carefully in management

(Continued)

Table 11. (Continued)

Attribute	Description
Growth	<p>Otolith microstructure analysis has been used to estimate length-at-age relationships for juveniles ≤ 120 days old, and periods of slow growth and incremental 'growth checks' are present, potentially indicative of reduced growth during autumn and winter, and render estimates of age unreliable for otoliths with > 120 increments (Ellis 2006)</p> <p>Small individuals of ~ 12 mm FL have been estimated at ~ 50 days (Sharpe <i>et al.</i> 2003), and those of ~ 25–30 mm FL at 60–90 days (Ellis 2006)</p> <p>Larvae at 10 days were 7.7 mm, 32-day-old fish were 12.8 mm, 53-day-old fish were 17.5 mm, 82-day-old fish were 27.9 mm and 120-day-old fish were 35.9 mm (range 28.0–43.0 mm; Stoessel <i>et al.</i> 2020)</p>
Habitats	<p>Mainly present in shallow off-channel freshwater to brackish habitats, including lakes, wetlands, billabongs and still or slow-flowing areas of creeks and drainage channels (Ebner <i>et al.</i> 2003; Ellis 2005; Lyon and Ryan 2005; Hammer and Wedderburn 2008)</p> <p>Mid-Murray region populations occur in saline off-channel lakes or deflation basins, whereas in the Murray lower lakes the species occurs in low numbers, patchily distributed in lake edge habitats and off-channel wetlands (Wedderburn <i>et al.</i> 2007)</p> <p>Typically associated with vegetated microhabitats (particularly the macrophytes <i>Myriophyllum</i> spp., <i>Ceratophyllum demersum</i> and <i>Ruppia</i> spp.; Hammer and Wedderburn 2008) and recently inundated terrestrial plants, grasses and scattered woody debris (Ellis and Kavanagh 2014; L. Suitor, pers. comm.). Also found over open sand banks (Ellis 2005; Ebner <i>et al.</i> 2003). Complex microhabitats provide shelter, a food source and a spawning substrate</p> <p>Often found in schools of distinct size classes (Ellis 2005; Lintermans 2007), likely a consequence of different habitat requirements at different life stages (D. Stoessel, ARI, pers. obs.)</p> <p>Recorded from a wide range of water properties, including pH (6.0–10.4), temperature (8–34°C), DO (3.5–25.0 mg L⁻¹) and salinity (0.4–64 ppt); favour habitats with low turbidities (Wedderburn <i>et al.</i> 2008; Ellis <i>et al.</i> 2013; Stoessel <i>et al.</i> 2019)</p> <p>Juveniles capable of tolerating salinities up to 105 ppt (Stoessel <i>et al.</i> 2020). Most remnant populations are located within saline habitats (> 7 g L⁻¹), possibly due to being more salt tolerant than other competing or predatory species (Ellis 2005; Wedderburn <i>et al.</i> 2008; Hammer <i>et al.</i> 2009; D. Stoessel, ARI, pers. comm.). Salinities of 12–45 ppt are recommended to mediate the competitive interactions with eastern gambusia and other salt-tolerant species (Stoessel <i>et al.</i> 2020)</p> <p>Typically cohabits sites with eastern gambusia and flathead gudgeon <i>Philypnodon grandiceps</i> (Wedderburn <i>et al.</i> 2007, 2012; Hammer and Wedderburn 2008). Competitive exclusion by other fishes (e.g. including carp gudgeon <i>Hypseleotris</i> spp., Australian smelt <i>Retropinna semoni</i> and unspotted hardyhead) may contribute to the absence of Murray hardyhead at otherwise suitable sites with lower salinities (Wedderburn <i>et al.</i> 2012). Eastern gambusia may cause Murray hardyhead to be confined to more saline sites (D. Stoessel, ARI, pers. comm.). By contrast, at less saline sites in the lower lakes, the species may occur in a diverse assemblage (up to 17 species) of freshwater, diadromous and euryhaline estuarine fishes, including carp gudgeon, Australian smelt, bony herring <i>Nematalosa erebi</i>, congolli <i>Pseudaphritis urvillii</i> and blue-spot goby <i>Pseudogobius olorum</i> (Wedderburn <i>et al.</i> 2007; Hammer and Wedderburn 2008; Bice <i>et al.</i> 2011)</p>
Movements	<p>Although the species can complete its life cycle in isolated lakes, genetic investigations suggest that minor movement and gene exchange historically occurred between groups and localities, probably during flooding (Stoessel 2010)</p>
Eggs and larvae	Eggs attached to aquatic vegetation (Stoessel 2007; Hammer and Wedderburn 2008)
Juveniles	Unknown
Adults	Unknown
Behaviour	A schooling (Ebner <i>et al.</i> 2003; Hammer and Wedderburn 2008) omnivore (Lintermans 2007)
Key threats	<p>Persistence in predominantly off-stream wetlands makes them particularly susceptible to river regulation and drought (Ellis <i>et al.</i> 2013)</p> <p>Populations are effectively isolated under regulated flows with decreased flooding frequency and extent compared with a natural flow regime. Therefore, there is a greater risk of demographic events (e.g. failed recruitment, skewed sex ratios), limited dispersive movements for recolonisation after extinction events or genetic mixing between populations (Backhouse <i>et al.</i> 2008)</p> <p>At low salinities, may coexist with carp when they are present at low densities and when vegetation cover is adequate. Where high densities of carp occur, they are likely to disrupt the development and persistence of aquatic vegetation (used as a spawning substrate and shelter from predators by Murray hardyhead) or disturb eggs. Eastern gambusia prefer shallow, slow- or non-flowing, littoral habitat with aquatic vegetation (Lintermans 2007) and have been demonstrated to show aggression towards Murray hardyhead, predate upon larvae (Ellis <i>et al.</i> 2013; I. Ellis, NSW DPI Fisheries, unpubl. data) and exhibit chasing and fin-nipping behaviour towards both juveniles and adults (D. Stoessel, ARI, pers. obs.). Inappropriate watering regimes can create conditions conducive to eastern gambusia (e.g. by lowering salinities at appropriate times; Ellis <i>et al.</i> 2012), a species implicated in the extinction of Murray hardyhead in Woorinen North Lake, north-west Vic. (Stoessel 2010). Some of the threats discussed above are less relevant to the Murray lower lakes, because populations are patchily distributed in lake edge habitats and off-channel wetlands (Wedderburn <i>et al.</i> 2007) that are hydrologically connected</p> <p>High abundances of redfin and carp and in the lower lakes may affect Murray hardyhead (directly by predation and indirectly by reductions in aquatic vegetation respectively)</p> <p>Considered highly vulnerable to climate change impacts (Chessman 2013).</p>

Table 12. Life-history attributes for the olive perchlet

ARI, Arthur Rylah Institute for Environmental Research; DO, dissolved oxygen; DAF, Department of Agriculture and Fisheries; DNR, Department of Natural Resources; DPI, Department of Primary Industries; EO, expert opinion; F, female(s); FL, fork length; M, male(s); MDB, Murray–Darling Basin; NMDB, northern MDB; NSW, New South Wales; Qld, Queensland; SL, standard length; SMDB, southern MDB; TL, total length

Attribute	Description
Before spawning	
Sexual maturity	Both sexes in first year (Milton and Arthington 1985; Llewellyn 2008) Some M survive and breed for 2 years, but most appear to die following second season (Milton and Arthington 1985) F can survive >3 years in the wild (McNeil <i>et al.</i> 2008); have lived for 6 years in captivity (M. Hutchison, DAF, pers. obs.)
Fecundity and eggs	Up to 9966 eggs (58.5 mm TL F), with a relationship of fish $TL = 0.1e^{0.1869x}$ (Llewellyn 2008), where TL is total length and e is number of eggs; 2350 eggs (49 mm F; Lintermans 2007); 230–700 eggs for the Brisbane River (Milton and Arthington 1985) Eggs adhesive and 0.7 mm in diameter (Lintermans 2007), with two size ranges in the ovaries (Llewellyn 2008) Revised fecundity function (C. Todd, ARI, unpubl. data): $Fecundity_{Age} = 2.31 + 0.090 \times Length_{Age}$
Spawning	
Description	Multiple spawner (Llewellyn 2008) Sexual dimorphism exhibited during the breeding season, with mature F distinguished by a broadening of the urinogenital papilla and swelling of the anal region, whereas in mature M the body colour brightens to a silvery white and the papilla remains narrow and pointed (Milton and Arthington 1985)
Season	Spring to autumn, with a peak <i>c.</i> mid-November (Llewellyn 2008) Gonad maturation begins in September; ripe fish appear in October and November in the Brisbane River and spawning only occurs in those months (Milton and Arthington 1985)
Cues	A period of several months of water temperatures rising to >22°C (Milton and Arthington 1985; McNeil <i>et al.</i> 2008)
Conditions	Temperatures >23°C and while they remain 23–27°C, ceasing outside this range (Llewellyn 2008) Spawning recorded in ponds at 19°C in the SMDB; however, a rapid decline from 26 to 22°C associated with high flows resulted in a cessation of spawning (McNeil <i>et al.</i> 2008)
Location	Restricted to river channels in warmer months with very low and predictable, stable water levels (Milton and Arthington 1985) Have been found to migrate into floodplain wetlands in the NMDB on lateral connecting flow events (Hutchison <i>et al.</i> 2008) Minor to medium floods provide access to some NMDB wetlands for breeding and recruitment, with reconnection flow events required for fish to re-enter the river (Hutchison <i>et al.</i> 2008; M. Hutchison, DAF, unpubl. data) Eggs attached to aquatic plants, those least likely to be disturbed by floodwaters or falling water levels (Milton and Arthington 1985), and on rocks on the streambed (Lintermans 2007) In-channel breeding and recruitment during drought conditions have resulted in rapid increases in population numbers in the Border River region of the NMDB. This is likely to be associated with increased growth of macrophytes due to low-flow periods that are then inundated by irrigation releases (G. Butler, NSW DPI Fisheries, pers. comm.)
After spawning	
Behaviour	Hatching occurs at >5–7 days at 22°C, with larvae ~3 mm (Lintermans 2007)
Recruitment	Populations respond strongly to boom–bust cycles associated with floods and droughts and most likely have a highly variable recruitment from year to year, reflecting variability in climate, flow and availability of suitable habitats (McNeil <i>et al.</i> 2008) During years of low flows, all age classes are present in the stream channel, but in years of high flow only a few adults are present (EO)
Growth	Daily otolith growth bands suggest fast development in early life. Fish from the MDB appear to grow larger than those from the Brisbane River and south-east Qld (Milton and Arthington 1985; Pusey <i>et al.</i> 2004; Llewellyn 2008). No significant differences between the sexes (Milton and Arthington 1985). Mean \pm s.d. sizes for 0+, 1+, 2+ and 3+ Brisbane River F fish are 25.5 \pm 0.4, 36.8 \pm 0.4, 47.5 \pm 0.5 and 52.6 \pm 0.3 mm SL respectively; for 0+, 1+ and 2+ years M fish mean \pm s.d. size is 25.8 \pm 0.5, 37.5 \pm 0.4 and 47.1 \pm 0.8 mm SL SL von Bertalanffy growth equation (for both sexes) from the Brisbane River: $L_t = 55.1 \{1 - \exp[-0.006(t + 0.02)]\}$ (Milton and Arthington 1985) In the NMDB, $W = 2.0 \times 10^{-5} L^{3.119}$ (Pusey <i>et al.</i> 2004) In the Lachlan River, fish 18 mm at 52 days and 44 mm at 104 days (McNeil <i>et al.</i> 2008) Pond-reared larvae reached 13 mm TL in 30 days and 25 mm in 80 days (Llewellyn 2008) Revised growth function (C. Todd, ARI, unpubl. data): $Length_{Age} = 62.0 \times (1 - \exp(-0.51 \times (Age + 0.78)))$
Habitats	Vegetated edges of freshwater pools, rivers, creeks, streams, backwaters and swamps, with little or no flow (Allen and Burgess 1990; Lintermans 2007; McNeil <i>et al.</i> 2008), often associated with woody habitat and vegetation (macrophytes and emergent grasses; Lintermans 2007) In the NMDB, 90% of fish came from wetland habitats (Hutchison <i>et al.</i> 2008; Hutchison 2014). Adults selected structure over open habitats and showed a strong affinity for submerged macrophytes (Hutchison <i>et al.</i> 2020). Strongly associated with stable macrophyte areas within isolated main-channel waterholes in the NMDB (S. Balcombe, Griffith University, unpubl. data)
Movements	
Juveniles	Surface schooling behaviour of juveniles, and rising water levels in summer (December–February) are thought to enable downstream dispersal (Milton and Arthington 1985)

(Continued)

Table 12. (Continued)

Attribute	Description
Adults	Generally thought to exhibit little movement, but are dispersed widely by high flows, especially from the river to wetlands (Hutchison <i>et al.</i> 2008). Known to school and migrate upstream in response to river flows (Allen 1996; Lintermans 2007; McNeil <i>et al.</i> 2008). Most adults captured in fyke nets were moving upstream with increased flows (Hutchison <i>et al.</i> 2008). Low abundances in the MDB mean there is little or no information on movement, but in coastal catchments small to moderate numbers have been captured moving upstream through fishways (Stuart and Mallen-Cooper 1999; Stuart and Berghuis 2002; Renfree and Marsden 2006; Moore and Marsden 2013; Marsden <i>et al.</i> 2015; Stuart and Marsden 2019). On several occasions, hundreds (sometimes >2000) of fish (10–70 mm FL) were captured moving up through a fishway connecting a river to a wetland (Ferguson <i>et al.</i> 2008), and hundreds have been recorded moving downstream on a major flow event (D. Roberts, Seqwater, pers. comm.)
Behaviour	Swim mid-water (Milton and Arthington 1985), appearing to be most active at night (Allen <i>et al.</i> 2002; D. Moffatt, DNR Qld, pers. comm.)
Key threats	Juveniles' surface schooling behaviour thought to reduce vulnerability to predators (Milton and Arthington 1985) Key threats include: <ul style="list-style-type: none"> • Drying of refuge habitats, loss of macrophyte habitats and sustained poor water quality (i.e. high turbidity, low DO, high temperatures and high conductivity; McNeil <i>et al.</i> 2008) • Loss of macrophytes due to prolonged high flows (including irrigation releases) and carp (EO) • Flow regulation: loss of the summer low flows in the SMDB that provide stable conditions for spawning (McNeil <i>et al.</i> 2008) and loss of the spring low flows and regulation of summer wet season flows in the NMDB that reduce the frequency and duration of lateral connection events to wetlands (Thoms <i>et al.</i> 2005; Hutchison <i>et al.</i> 2008) • Likely predation from redfin (McNeil <i>et al.</i> 2008) and fin-nipping, as well as predation of eggs and larvae by eastern gambusia (EO) • Barriers restricting movement and connectivity of populations (McNeil <i>et al.</i> 2008) • Loss through pumps (EO) <p>Considered moderately vulnerable to climate change impacts (Chessman 2013)</p>

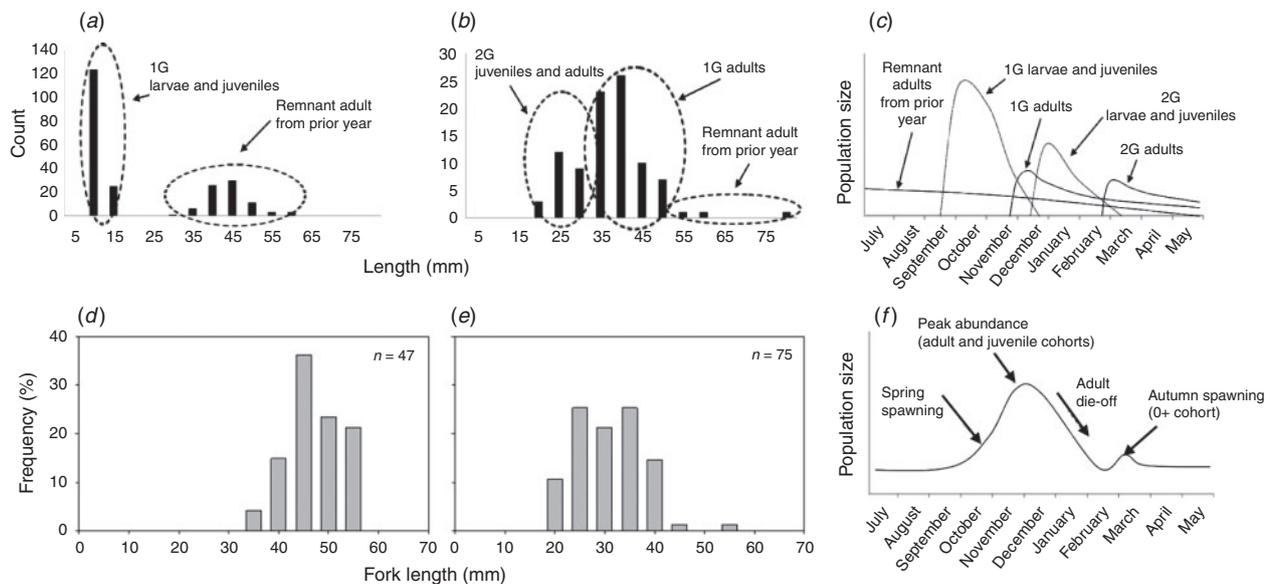


Fig. 6. (a, b) Length–frequency distributions of Murray hardyhead sampled in Round Lake in spring 2007 (a) and autumn 2008 (b). (c) Stylised annual pattern of recruitment for Round Lake (D. Stoessel, Arthur Rylah Institute for Environmental Research). (d, e) Length–frequency distributions of Murray hardyhead sampled at the Finnis River junction in the Lower Lakes in spring 2013 (d) and autumn 2014 (e). (f) Stylised pattern of annual recruitment for the Finnis River (Bice *et al.* 2014). 1G, first generation; 2G, second generation.

Case study 6: different movement strategies

Although the golden perch example above highlights the progress made in our understanding of the movements for this species over time, similar details are not available for all species (Tables 4–12). There are also other aspects of movement that

need to be considered: seasonal and diel patterns of different life stages; intraspecific differences for lakes *v.* river populations; intra- *v.* intergenerational movements; lateral movements to and from river floodplains and side channel habitats; and the variation in movement among individuals within populations

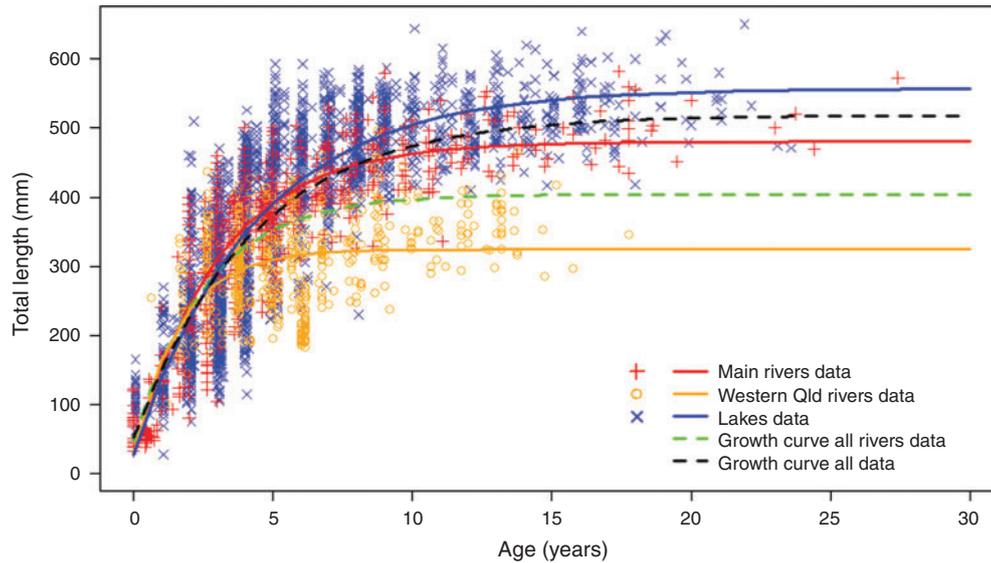


Fig. 7. Variable growth rates for golden perch in the Murray–Darling Basin (data from D. Moffatt, Department of Environment and Science, Qld, and C. Todd, Arthur Rylah Institute for Environmental Research, unpubl. data; Mallen-Cooper and Stuart 2003; Forbes *et al.* 2015a). Equations for these growth curves are included in Table 6.

(e.g. scale, extremes and averages, proportions of the population moving). We provide some examples of these types of movements below.

Macquarie perch in reservoirs have unique requirements compared with riverine populations. Fish in impoundments must leave the reservoir to spawn in inflowing streams (Cadwallader and Rogan 1977; Douglas 2002; Tonkin *et al.* 2010; Lintermans 2012), and such movements are restricted to the spawning season (October–December). Movements within impoundments can be wide ranging and occur throughout the year (Thiem *et al.* 2013). Riverine populations may or may not demonstrate spawning migrations (Koster *et al.* 2014, 2017; Kearns *et al.* 2015), perhaps depending on whether their requirements can be met near their home location. Movements to spawning habitats can be limited by instream barriers unless fish passage or inundation of such barriers occurs (Tonkin *et al.* 2010; Broadhurst *et al.* 2013; Lintermans 2012, 2013b).

Freshwater catfish exhibit variable movement patterns across their range. Although recorded moving widely from rivers onto floodplain wetlands, and between refugial waterholes, most individuals are predominantly sedentary and nocturnal (Koster *et al.* 2015; Burndred *et al.* 2018; Carpenter-Bundhoo *et al.* 2020a, 2020b). Most larger-scale movements are associated with flow events, particularly the first post-winter flows (e.g. Marshall *et al.* 2016; Burndred *et al.* 2018), which do not appear to be consistently related to spawning.

Murray cod move both upstream and downstream, with greatest movements prior to spawning and at night (Koehn *et al.* 2009). Downstream larval drift is an efficient form of dispersal and is affected by rates of flow (Koehn and Harrington 2006; Koehn 2011), and larvae can be damaged passing instream (especially undershot) weirs or entrained by pumps or diversions (Baumgartner *et al.* 2006, 2009).

There is a paucity of movement data for most smaller species (<150-mm total length; e.g. olive perchlet, southern pygmy

perch and Murray hardyhead), not just due to size-related limitations of tagging methods (but see Allan *et al.* 2018), but also because they generally receive less attention than larger-bodied species (Saddler *et al.* 2013; Lintermans *et al.* 2020). However, when studies have occurred, large numbers of individuals of many small species have been found to move (Stuart and Berghuis 2002; Lyon *et al.* 2008). It is often assumed that movements for these species are limited to a local scale, but intergenerational movements caused by high-flow events may be critical for dispersal to, and recolonisation of, isolated habitats. Although these movements may be small compared with that of larger fishes, they should be considered relative to body size, and movements between habitats may be critical (e.g. main river channel to vegetated wetlands).

The diversity of these movement types and the prevailing threats to them (e.g. barriers and loss of connectivity, loss of flow components and alien fish species limiting the ranges of small-bodied fish) indicate that they cannot be remediated by the provision of fish passage alone. Flow cues are required and, in some cases, this may necessitate overbank flows to connect floodplain wetlands, with the appropriate timing, duration and frequency for these connections. Further, the exclusivity of some movements and their cues to individual species or life stages means that management must ensure that all critical movements can be achieved. These case studies highlight the importance of refining key movement and ecological concepts as new knowledge becomes available and using this to maximise restoration outcomes.

Discussion

This compendium of contemporary ecological knowledge integrates scientific outputs, 80% of which were published since 2000, into one peer-reviewed paper. It synthesises our conceptual ecological understanding of nine Australian freshwater fish

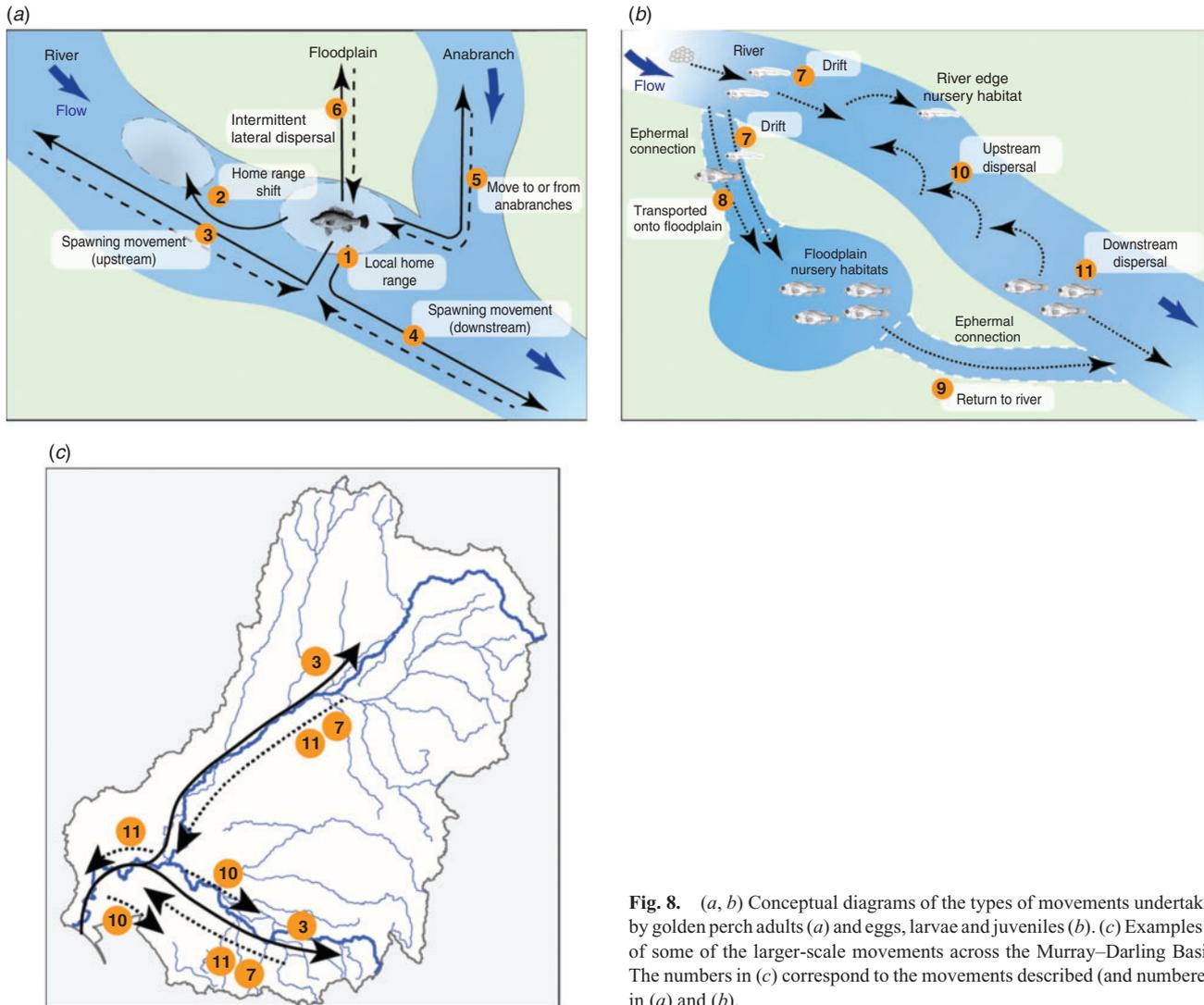


Fig. 8. (a, b) Conceptual diagrams of the types of movements undertaken by golden perch adults (a) and eggs, larvae and juveniles (b). (c) Examples of some of the larger-scale movements across the Murray–Darling Basin. The numbers in (c) correspond to the movements described (and numbered) in (a) and (b).

species to inform improved natural resource management capability and decision making. This specific ecological knowledge can be readily used in conjunction with broader ecological concepts, such as habitat use, movements, reproduction and population dynamics (see Humphries and Walker 2013; Humphries *et al.* 2020).

Knowledge assessment and priority gaps

Overall, our assessment indicates there is wide-ranging, although incomplete, ecological knowledge across all life stages of the nine native fish species. This highlights the need for further targeted research. Not surprisingly, the knowledge gaps identified in this study correspond generally with gaps previously identified by MDB fisheries and water managers (Koehn *et al.* 2019a). Specifically, we found that the survival rates of life stages and recruitment to adults (population dynamics), movement (especially movement of larvae and juveniles) and factors affecting fish growth and condition require the most research

attention. Further knowledge of the relationships linking these components to flow is vital to improving the outcomes of management of water for the environment, including fish population recovery (Poff and Zimmerman 2010; Davies *et al.* 2014; Stewart-Koster *et al.* 2014). We have explicitly identified these key knowledge limitations, which will help set the agenda for future research investment. Filling these gaps could be achieved by an adequately funded, coordinated research plan with clear reference to management needs (Likens *et al.* 2009).

Among the species studied, the greatest knowledge is available for the larger fishes that are popular for recreational fishing, despite the generally recognised need for greater consideration and research attention to smaller species (i.e. adult length <150 mm; Saddler *et al.* 2013; Lintermans *et al.* 2020). The three small species we studied (southern pygmy perch, Murray hardyhead and olive perchlet) consistently scored poorly in our assessment of current ecological knowledge relative to the larger species. Small fishes comprise over half the MDB species

and are among the most threatened, yet their perceived insignificance and the difficulty in applying many research approaches (e.g. electronic tagging; but see [Allan et al. 2018](#)) mean that they have received limited research attention. This must be redressed.

For the larger species, considerable knowledge of spawning, egg and larval survival and water quality requirements comes largely from hatcheries, with less known from the wild. This knowledge is especially needed to understand important issues such as egg and larval dispersal, including drift distances (passive or active drift), and survival in weir pools. The knowledge obtained from hatchery studies, although valuable, must be cautiously applied when managing wild fish populations. Even for well-studied and widespread species, there is a need to revisit fundamental research and generate important data for understudied aspects of their biology or regions within their range. For example, most Murray cod growth and fecundity data were sourced from hatcheries rather than from a broad geographic sample of wild fish, and the data are now fairly dated ([Rowland 1998b](#)). Such information may not reflect changes in population structures (e.g. fewer and larger individuals) or river conditions (e.g. lower river productivity from reduced flows and flooding) over time. Our understanding of Murray cod ecology in upland habitats is also limited, which raises concern regarding the transferability of our knowledge to these areas. Although there is now considerable information available about longitudinal movements for some larger species, movements of smaller species, especially between river and off-channel habitats, remain a neglected area of research ([Lyon et al. 2010](#)).

There was surprisingly little difference in our assessment of the current knowledge between the SMDB and NMDB, despite the disparity in the number of studies in each region. However, it was generally agreed that additional NMDB studies are required, with a consensus that knowledge cannot always simply be transferred across such broad regions. There are important regional ecological differences between the SMDB and NMDB (e.g. the greater importance of refuge pools in the NMDB, Table S1; and differences in growth rates, [Fig. 8](#)). These differences are more likely to occur along a gradient than according to a simplistic north–south delineation (see [Wright et al. 2020](#)). Conversely, the workshop discussions concluded that although there were occasional, regional species-specific differences in ecology (e.g. fecundity, growth), there were also many general similarities in the population drivers across the MDB. Although considerable knowledge gaps were recognised, it was agreed that there was substantial knowledge already available to inform restoration decisions, but that more refined information would reduce the uncertainty of those decisions and maximise beneficial outcomes.

New technologies

Opportunities to address some knowledge gaps will come from new and emerging technologies. Although genetics and genomics were not extensively covered in this paper, this rapidly expanding field has many potential applications ([Moore et al. 2010](#); [Grummer et al. 2019](#)). These approaches continue to reveal new and often cryptic species, increasing the known fish diversity (including the description of new species in the MDB), setting new conservation priorities ([Adams et al. 2011, 2014](#); [Raadik 2014](#)) and informing stocking programs ([Bearlin and](#)

[Tikel 2003](#); [Welsh et al. 2020](#)). A revised understanding of the phylogenetics ([Nock and Baverstock 2008](#); [Nock et al. 2010](#)) and genetic connectivity can provide insights into species' resilience to disturbance and their capacity for adaptation to climate change effects ([Beheregaray et al. 2017](#); [Harrisson et al. 2017](#); [Attard et al. 2018](#)). Genetic rescue ([Pavlova et al. 2017](#)) and mapping of whole genomes ([Austin et al. 2016, 2017](#)) are additional techniques, and such tools may be used to determine connectivity rates, effective population sizes (the proportion of fish reproductively contributing to the population; [Faulks et al. 2010a, 2010b, 2011](#); [Farrington et al. 2014](#)), population structure ([Hill et al. 2015](#)), survival rates and the effects of stocking and translocations ([Rourke et al. 2010, 2011](#); [Weeks et al. 2011](#)). This can be used together with otolith microchemistry to determine natal origin and life-history movement patterns ([Zampatti et al. 2018, 2019](#)). Further use of passive integrated transponders ([Allan et al. 2018](#)), acoustic and radio tags ([Adams et al. 2012](#); [McKenzie et al. 2012](#)), with accompanying remote data collection, can enhance our understanding of connectivity as a key population process over multiple spatial and temporal scales. Otoliths can also be used to determine a range of life-history traits (see [Starrs et al. 2016](#)) and responses to environmental change (e.g. flows, temperature; [Izzo et al. 2016a, 2016b](#)). The development of environmental DNA (eDNA) techniques may enable cost-effective biodiversity assessments ([Bylemans et al. 2018](#)), the detection of threatened or alien species ([MacDonald et al. 2014](#); [Janosik and Johnston 2015](#) [Shaw et al. 2017](#); [Hinlo et al. 2018](#)) and measurement of breeding status ([Bylemans et al. 2017](#)) or biodiversity ([Civade et al. 2016](#)).

Remote monitoring using drones ([Tyler et al. 2018](#)) and underwater video can help our understanding of aspects such as spawning behaviour and habitat use ([Butler and Rowland 2009](#); [Ebner et al. 2014](#)). Other evolving options are worth exploring to further understand ecological processes, such as floodplain productivity ([Rees et al. 2020](#)), including the use of bulk and compound-specific tracers, stable isotopes and fatty and amino acids to investigate productivity, food web resources, trophic requirements, fish condition and trophic ecology (e.g. [Jardine et al. 2020](#); [Twining et al. 2020](#)). The continued development and adoption of these and other technologies will provide more holistic knowledge to inform management actions across a range of spatial and temporal scales.

Improvements to monitoring

The quantification of catch effectiveness metrics for species by different sampling methods (expressed as detection or capture probability; [Bearlin et al. 2008](#); [Ebner et al. 2008](#); [Lyon et al. 2014a](#)) strengthens the ability of monitoring data to estimate population abundances ([Gwinn et al. 2019](#)) and to assess the presence or recruitment status of rare species ([Lintermans 2016](#)). Currently many large-scale environmental or threatened species monitoring programs (e.g. the Sustainable Rivers Audit; [Davies et al. 2008, 2010](#)) do not adequately consider this (but see [Harris and Gehrke 1997](#), chapter 1; [Lintermans and Robinson 2018](#)). Rare fish species or those with low detectability may be undersampled in general or non-targeted surveys ([Ebner et al. 2008](#); [Lintermans and Robinson 2018](#); [Wedderburn 2018](#); [Scheele et al. 2019](#)). In addition, some habitats (e.g. wetlands)

are often entirely overlooked or sampled with inappropriate techniques or effort. The need for targeted, robust monitoring (i.e. not just generic river monitoring) is now recognised and recommended to assess the status of threatened species' populations (Scheele *et al.* 2019), as well as to provide data to judge the success of recovery actions (Lintermans 2013c).

The need for Indigenous knowledge

The objective of this paper was to collate published data as a basis for population models; however, a collation of Indigenous knowledge would be an important addition to this compendium and provide an additional perspective on native fish population restoration. If undertaken by traditional owners, this would increase ecological knowledge (e.g. Dargin 1976), respect cultural values (e.g. Ginns 2012; Jackson *et al.* 2014; Jackson and Moggridge 2019; Moggridge *et al.* 2019) and provide a traditional ecological management viewpoint for restoration (Trueman 2012b; Pascoe 2017). This knowledge, along with other historical information (e.g. Trueman 2012a), would also inform natural native fish population abundances and correct post-European settlement perspectives that have occurred due to based shifting baselines (lack of recognition of gradual changes from natural conditions; Humphries and Winemiller 2009).

Threat assessment and priority restoration actions

A holistic approach is required to mitigate key threats to fishes and rehabilitate populations in the MDB (Lintermans 2013a). Many common and well-understood threats were confirmed as high priorities for attention. Reduced movement pathways through barriers to longitudinal and lateral connectivity, altered flow seasonality, loss of refugia, loss of both lotic and lentic habitats, alien species, decreased water quality and losses of aquatic vegetation are examples of such key threats. Most of these threats have long been recognised (Cadwallader 1978). Some have been partially addressed (e.g. fish passage in the Murray River; Barrett and Mallen-Cooper 2006; Baumgartner *et al.* 2014b), but others, such as cold water pollution (Lugg and Copeland 2014; but see Michie *et al.* 2020), alien species control (e.g. carp, redfin, eastern gambusia; Lintermans 2013a) and undershot weirs (Baumgartner *et al.* 2006), remain as future challenges. The more recently recognised threats, such as loss of early fish life stages to irrigation pumps (Baumgartner *et al.* 2009; Boys *et al.* 2012, 2013a, 2013b) and infrastructure diversions (King and O'Connor 2007), appear significant but require quantification of their effect on populations.

Some threats were found to exhibit regional differences. For example, recreational fishing regulations and harvest rates are not uniform across the MDB. Combined with regional growth rate variations, these are likely to have different effects on population structures (Nicol *et al.* 2005). In the NMDB, loss of refugia, loss to pumps, movement pathways and barriers to longitudinal connectivity are considered principal threats, whereas altered flow seasonality and loss of aquatic vegetation are considered more prominent in the more regulated SMDB. Some historical, widespread threats, such as river desnagging and cold water releases (which can have severe effects in particular river reaches), may now have less of an impact due to the poor status of remaining populations (Lugg and Copeland

2014). Remediation of these issues provides proven opportunities to increase fish populations (Todd *et al.* 2005; Sherman *et al.* 2007; Gray *et al.* 2019; Lyon *et al.* 2019; Michie *et al.* 2020). Water extraction is a widespread threat that can be especially damaging to vital refuge habitats during low flows (Bond *et al.* 2015). Floodplain harvesting (retaining overbank flood flows using water diversion and storage structures) was considered an acute issue in the NMDB, resulting in the loss of floodplain wetland habitats, loss of connectivity to those habitats (floodplain channels), reduced flooding and downstream flows and restricted useable floodplain area (Thoms *et al.* 2005). Climate change poses risks to most species (Balcombe *et al.* 2011; Morrongiello *et al.* 2011; Pratchett *et al.* 2011) and was considered likely to exacerbate (but not supersede) the existing flow-related threats associated with river regulation and water extraction (McMahon and Finlayson 2003; Koehn *et al.* 2011).

Application of this knowledge to management

Although access to a comprehensive, contemporary knowledge base increases confidence in ecological decision making (Stoffels *et al.* 2018; Koehn *et al.* 2019a), it is also important to facilitate effective use of that knowledge. The detailed technical aspects of the biology, ecology and life-history processes (Tables 4–12) readily inform restoration actions for each individual species, support management decisions or can parameterise tools such as population models. Indeed, the knowledge collated for this paper has already supported published population models (Todd and Lintermans 2015; Todd *et al.* 2017) and been used to inform ecological outcomes from environmental flow delivery in the MDB (Koehn *et al.* 2014c). However, more 'collective' use of this knowledge can increase our conceptual understanding of how to manage species and ecosystems. In the following section, we describe case studies illustrating the use of the collated knowledge and outputs from workshop discussions to inform management. The case studies relate to: (1) species-specific management; (2) the timing of key ecological events; (3) population processes; and (4) managing flows for native fish (designed hydrograph).

Case study 1: species-specific management

The detailed knowledge highlights some striking ecological differences between closely related species that are often managed concurrently. Some management responses prefer to deal with groups of 'similar' species (a grouping approach) rather than addressing the different needs of a larger number of individual species. Grouping can be useful in a management context because it allows more 'similar' species to be assigned to a 'guild', where membership depends on the ecological traits selected or management actions being considered (e.g. Winemiller and Rose 1992; Humphries *et al.* 1999; Gowns 2004; Baumgartner *et al.* 2014a; Mallen-Cooper and Zampatti 2015). Managing a group of 'similar species' often appeals under resource-constrained management conditions, where development and implementation of fewer actions can occur, rather than more actions for numerous individual species. Although this may achieve efficiencies for water delivery, we must ensure that ecological outcomes are maximised. However, individual native fish species have a range of different environmental requirements, life histories, habitat preferences, trophic positions,

Table 13. Comparison of the ecological differences between trout cod and Murray cod, as well as management implications
Knowledge derived from Tables 4 and 5

Trout cod, in relation to Murray cod	
Ecological differences	Management implications
<ul style="list-style-type: none"> • Overall smaller distribution and abundance • All life stages prefer perennial lotic habitats, whereas adult Murray cod can tolerate large lentic habitats • Timing of spawning may be earlier but can overlap • Less fecund • More limited movements and rates of dispersal • Higher dependencies on structural woody habitat • Use structural wood situated in faster waters further from the bank • Higher site fidelity and smaller home range • Grow to a smaller size • More aggressive 	<ul style="list-style-type: none"> • Higher conservation risk • Restoration of perennial, higher-velocity, lotic habitats of greater importance • May also be protected by incidental recreational capture by fishing closures for Murray cod • Slower population recovery rates; more reliant on stocking for recovery • Slower rates of colonisation; more limited use of fish passage • Greater importance of reinstatement of structural woody habitat • More susceptible to main-channel wood realignment; needs more midstream habitat placement; more reliant on flowing waters • Reinstated habitat patches for adults should be closer together • Can use smaller habitat patches; more susceptible to predation • Higher susceptibility to capture and hence catch-and-release stress and mortality

predator defences and metabolic rates, all of which influence the specific niche of any given species (Winemiller *et al.* 2015). Thus, there are inherent assumptions and risks associated with the oversimplification of species' needs. Although there is an argument to group species into guilds for ease of management, a more plausible argument could be made to manage species individually so as to maximise benefits to them, this being especially so if they are threatened. There is no 'one-size-fits-all' approach to fish and flows (Poff *et al.* 1997; Yen *et al.* 2013).

Two very closely related species often considered ecologically 'similar', namely the Murray cod and trout cod (both being described as habitat and river channel specialists), exhibit significant ecological differences (Table 13), despite them being within the same genera and being so closely related that they can hybridise. For example, trout cod have a much smaller distribution than Murray cod, they may spawn earlier and they have lower fecundity; the two species also have different microhabitat preferences, movements, temperature tolerances and maximum lengths. These differences contributed to trout cod being at a significantly greater conservation risk than Murray cod. Transferring knowledge from the 'better-known' Murray cod to manage trout cod may have critical implications for recovery management decisions because there are clearly significant species-specific ecological differences that have allowed the Murray cod to persist while trout cod declined. For example, based on a nuanced understanding of habitat preferences, instream woody habitat reconstruction (i.e. resnagging; Lyon *et al.* 2014b, 2019) should occur further from the bank and in faster water if remediation outcomes are targeted at trout cod rather than Murray cod (Koehn and Nicol 2014). In addition, due to lesser dispersal rates for trout cod, such habitat patches should be constructed closer together and in closer proximity to existing habitat patches (Koehn *et al.* 2008, 2009; Koehn and Nicol 2016). Evidence from resnagging programs suggests that the dispersal and subsequent population recovery times are slower for trout cod than Murray cod (Lyon *et al.* 2019; Raymond *et al.* 2019).

Case study 2: timing of key ecological events

Consideration of the temporal occurrence and extent of key biological events is critical to successful ecosystem management, both for removing threats (e.g. loss to pumps and water diversions during peak periods of egg or larval drift) and supporting ecological processes (e.g. reinstating spawning or movement cues). In addition, other operational works that may affect fishes (e.g. water level lowering) should be undertaken at the appropriate times of the year. To raise awareness of these issues and to inform management scheduling, Fig. 9 provides a calendar of key biological events for the nine species considered here.

Case study 3: population processes

Understanding the temporal and spatial scales of ecological processes that drive population dynamics for species enables researchers and managers to better predict the likelihood and progression of success following implementation of restoration actions. To illustrate this, we provide examples of how these processes operate differently across the life-history strategies of three species from this study (southern pygmy perch, Murray cod and golden perch; Fig. 10). The different ages of maturity and fecundities of these three species affect their reproductive output and recruitment into adult populations; thus, it is necessary to account for the size of the original spawning stock, the survival of all life stages and the contribution of each life stage to population outcomes. It is important to consider the wider impact of reproductive output and recruitment across the whole range, especially for widespread species. For example, the suggested minimum spatial scale to manage highly mobile species such as golden perch is >500 km (see Fig. 8; Table 6); for Murray cod it may be <50 km (Table 4) and for southern pygmy perch (Table 10) it may be at the local site scale (e.g. within a wetland or creek reach; <1 km). However, it must be recognised that local populations often occur within a hierarchy of habitats and larger distributions, which can be enhanced by broader-scale ecological functions (such as productivity and

	Month											
	J	A	S	O	N	D	J	F	M	A	M	J
Murray cod												
Spawning season			■	■		■	■					
Eggs and larvae			■				■					
Juvenile movements												
Adult movements		■	■	■	■	■	■	■	■	■	■	■
Trout cod												
Spawning season				■	■							
Eggs and larvae				■	■							
Juvenile movements						■						
Adult movements				■	■	■						
Golden perch												
Spawning season		■	■	■					■	■	■	■
Eggs and larvae		■	■	■					■	■	■	■
Juvenile movements			■	■	■	■	■	■	■	■	■	■
Adult movements			■	■	■	■	■	■	■	■	■	■
Silver perch												
Spawning season				■	■			■	■	■		
Eggs and larvae				■	■			■	■	■		
Juvenile movements											■	
Adult movements				■	■	■	■	■	■	■		
Macquarie perch												
Spawning season				■	■	■						
Eggs and larvae				■	■	■						
Juvenile movements*												
Adult movements			■	■	■	■						
Freshwater catfish												
Spawning season			■	■						■	■	
Eggs and larvae			■	■						■	■	
Juvenile movements			■	■	■	■						
Adult movements			■	■	■	■	■					
Southern pygmy perch												
Spawning season			■	■		■	■					
Eggs and larvae			■	■		■	■					
Juvenile movements*												
Adult movements*												
Murray hardyhead												
Spawning season				■	■				■	■		
Eggs and larvae				■	■				■	■		
Juvenile movements*												
Adult movements*												
Olive perchlet												
Spawning season				■	■	■						
Eggs and larvae				■	■	■						
Juvenile movements*												
Adult movements			■	■	■	■	■	■	■	■	■	■

Fig. 9. Calendar indicating the timing (by month) for the occurrence of key biological attributes for each fish species. Knowledge obtained from Murray–Darling Basin (MDB) literature, recent data and studies and the opinions of regional species experts. Dark grey shading indicates ‘core periods’ (in the southern and northern MDB); light grey shading extends these ‘core periods’ for longer temporal ranges for some key biological aspects and species in the northern MDB. Asterisks indicate unknown movements (see Table 2).

connectivity). Therefore, monitoring needs to be undertaken at the appropriate scale for each species, because what happens in one region may provide benefits elsewhere (e.g. golden perch spawning may result in the recruitment of juveniles into populations downstream).

The production and use of conceptual models for all MDB species would enable managers to synthesise issues related to individual species’ life cycle, threats and population dynamics

for recovery. We chose not to produce figures for all nine species, and indeed believe it is a useful process for managers to complete prior to considering restoration options. Regardless, the similarities and differences among the other species in this paper should be considered, especially in light of the ecological differences exemplified in Table 13 for Murray cod and trout cod. It should be noted that models in this compendium were constructed from current knowledge and species’ distributions.

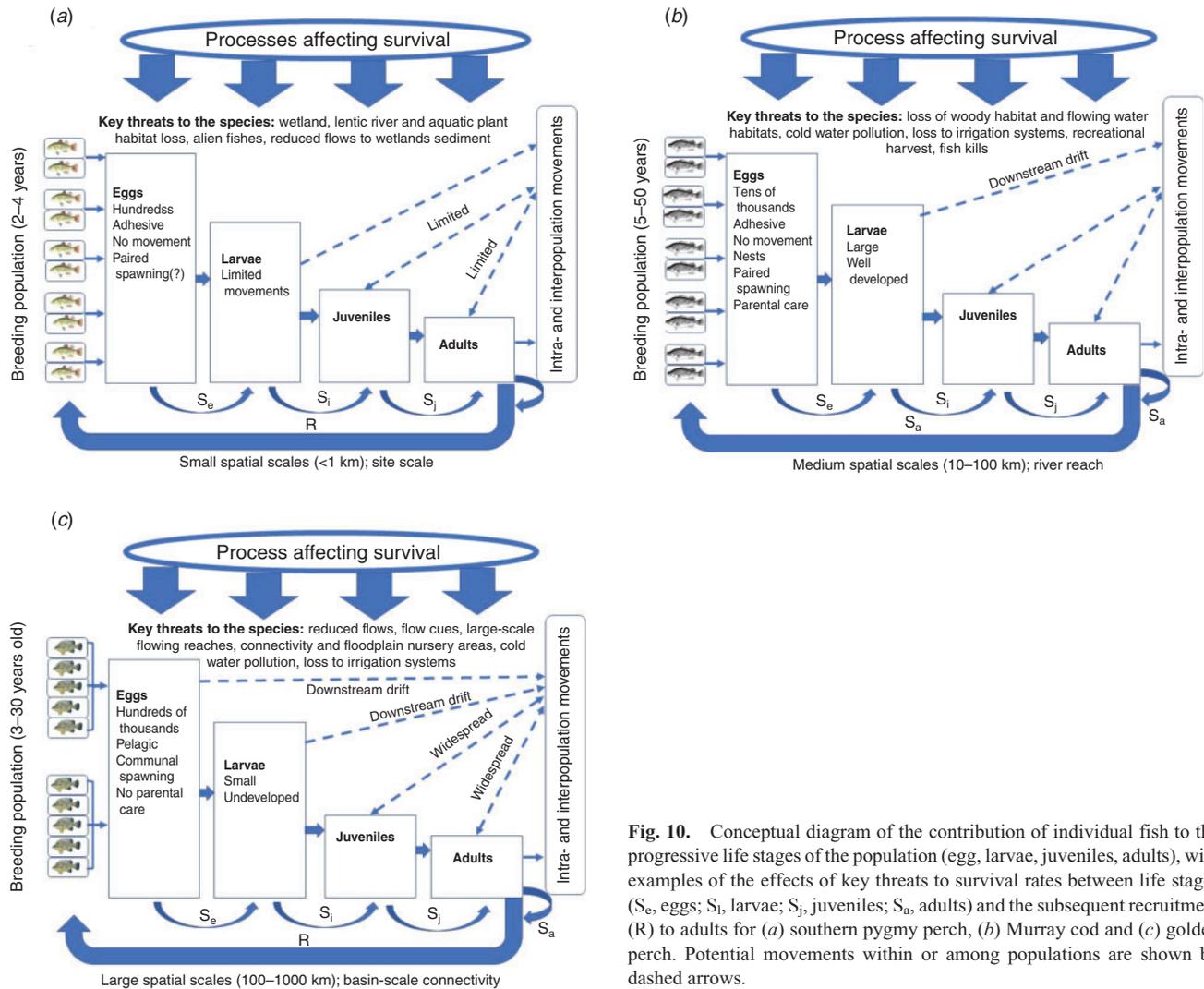


Fig. 10. Conceptual diagram of the contribution of individual fish to the progressive life stages of the population (egg, larvae, juveniles, adults), with examples of the effects of key threats to survival rates between life stages (S_e , eggs; S_l , larvae; S_j , juveniles; S_a , adults) and the subsequent recruitment (R) to adults for (a) southern pygmy perch, (b) Murray cod and (c) golden perch. Potential movements within or among populations are shown by dashed arrows.

Hence, they may have been constrained by historical reductions in range and habitat occupancy, and should be updated as more knowledge becomes available.

Case study 4: managing flows for native fish

One approach for the effective delivery of environmental flows to improve fish outcomes is to design hydrographs that reflect aspects of the natural flow regime associated with key biological events (Poff *et al.* 1997; Stuart *et al.* 2019). For riverine species, flow recommendations aimed at achieving native fish outcomes must consider the suite of drivers that flows create within an appropriate spatial scale (i.e. a river reach; interconnected valleys for golden perch). This is in acknowledgment that aquatic biota do not respond to discharge *per se*, but to the conditions that it creates, such as connectivity, water velocity, turbulence, depth and the availability of key habitats (Mallen-Cooper and Zampatti 2018). Because flow discharge is the currency of water management, unfortunately this concept of

hydraulic complexity and change is often missed. As flow is delivered as discharge, most recommendations are expressed in this language ($ML\ day^{-1}$), although increasingly more detailed flow plans do use mechanistic links between river flows and some of the ecological drivers or processes they influence (e.g. cues to movement; e.g. Victorian Environmental Water Holder 2020). Some such links to the flow are well established (e.g. height to fill for wetlands), whereas others, such as areas of particular water velocity or turbulence, are not (Mallen-Cooper and Zampatti 2018). Despite the loss of lotic habitats being widely acknowledged as altering biodiversity in rivers (Walker 2006), quantitative studies that link the interaction of discharge, hydraulics and biotic processes are lacking in the MDB (Davies *et al.* 2014). The updated knowledge collated here is used to provide a specific case study of a conceptual hydrograph for the SMDB that includes some key components of hydraulic diversity important for three species, namely the Murray cod, a riverine nesting species, and golden perch and silver perch, which are pelagic spawners,

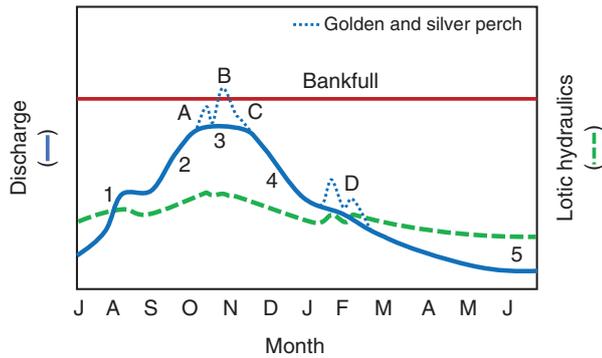


Fig. 11. A conceptual flow regime for the mid-southern Murray–Darling Basin (MDB) that uses ecological knowledge to incorporate two key components of the natural flow regime, namely an annual spring pulse and permanent lotic hydraulics, into a functional flow to enhance life-cycle processes. This designed hydrograph also includes winter base flows for fish survival, spring pulses for fish migration and spawning and a slow summer recession for fish growth and juvenile colonisation. Under current regulated conditions, the annual spring pulse and permanent lotic conditions have been lost or greatly reduced, both spatially and temporally. This flow regime restores these hydrological components and can be added at a variety of spatial scales, depending on fish life-history requirements. Ecological objectives and benefits for Murray cod (1–5), golden and silver perch (A–D) and other species are given in Table 14.

indicating the likely benefits to these and other species (Fig. 11; Table 14). These species all require lotic habitats (identified as a key habitat loss in regulated rivers; Table 3), which could be achieved with increased flows or a combination of flow and weir lowering or removal (Bice *et al.* 2017; Mallen-Cooper and Zampatti 2018). Wetland specialist species would require a different emphasis for their hydrograph, which may describe hydraulic characteristics such as wetland depth, area and persistence, partial wetting and the spatial connective links to the river.

Delivering a designed hydrograph with flow components that meet each species' life stage requirements, including spawning, survival of the various life stages (and hence recruitment) and movements, can contribute to beneficial population outcomes. The present example is focused over a reasonably short spatial scale (river reach) in the SMDB, where the common environmental flow mechanism is the delivery of water from an upland storage (which should be at a natural temperature). Other management options can protect important flow components from water extraction, such as pumping, diversion and floodplain harvesting (capture of overbank flows). This is particularly applicable in the NMDB, where there is less capacity for stored water to be delivered for the environment and greater extraction of flows from the river. 'Designed' hydrographs (*sensu* Acreman *et al.* 2014) can be used to inform flow management, including the use of modified irrigation flows to provide benefits to fishes. Note that this conceptual hydrograph (Fig. 11) is designed for the SMDB, and careful implementation is needed for any individual river reach, with the spatial scale, magnitude and timing of flow and hydraulic components adjusted to suit that reach and fish community.

On the basis of our review, we suggest that efforts should be made to further incorporate a range of key ecological concepts into management and recovery actions, including survival of all life stages and their recruitment through to adults (see Fig. 4), movements of all life stages and spatial management cognisant of the riverscape scales of life-history processes (e.g. Fig. 8), quantification of flow–ecology relationships that link volumetric recommendations (e.g. discharge) to the specific drivers they are trying to influence (e.g. water velocity, habitat area, connectivity; Mallen-Cooper and Zampatti 2018), the use of stochastic population models to explore outcomes from a number of possible management actions (e.g. Todd *et al.* 2017), the coordination of flow management over appropriate spatial and temporal scales to meet population requirements (e.g. year to year; decadal flow sequences) and the need to undertake accurate population assessments (Lyon *et al.* 2019) that include abundance, diversity, distribution and structure (age and size) and account for factors affecting populations, such as recreational harvest, larval mortality and stocking (see Todd and Koehn 2009).

Integrated restoration management

The multijurisdictional nature of the MDB, together with the broad distribution and movements of many fishes, necessitates integrated management through multiagency coordination of environmental flows and other actions to restore populations (Murray–Darling Basin Authority 2011; Koehn and Lintermans 2012; Stuart and Sharpe 2017; Reid *et al.* 2019; Baumgartner *et al.* 2020). Flow management occurs at spatial scales ranging from individual sites to the entire MDB, over time frames of 1–10 years (Stewardson and Guarino 2018; Koehn *et al.* 2019a). Collaborations between managers and researchers are most fruitful when they integrate knowledge such as species' requirements and appropriate timing and spatial and temporal scales into restoration management actions (Gibbons *et al.* 2008). This is particularly so in the complex space of delivering environmental flows, and further efforts in this regard can only improve environmental outcomes.

Examples of previous successful collaborations for Australian restoration programs include the Sea to Lake Hume Lake Hume Murray Fishway Program (Baumgartner *et al.* 2014b), the MDB Native Fish Strategy (Koehn and Lintermans 2012, Koehn *et al.* 2014b), coordinated and well-designed conservation stocking regimes (Bearlin *et al.* 2002; Todd *et al.* 2004), recovery plans (Trout Cod Recovery Team 2008a, 2008b; National Murray Cod Recovery Team 2010a, 2010b; Koehn *et al.* 2013) and improved, multi-State stocking and size regulations for Murray cod recreational fisheries management (Rogers *et al.* 2010; Koehn and Todd 2012; Lintermans 2013c). Ecological modelling can be used to evaluate the likely outcomes of various combinations of management options (Koehn and Todd 2012; Todd *et al.* 2017), and these will be most successful if the models integrate contemporary ecological knowledge with up-to-date rainfall, flow, climate patterns and climate change predictions (Neave *et al.* 2015).

To help managers integrate knowledge and priorities into decisions, a stepwise framework for restoration is presented in Table 15. This is supplemented by a case study example for Murray cod management in the mid-Murray River system. In this

Table 14. Description of flow components for a designed environmental flow hydrograph for the mid-southern Murray–Darling Basin (SMDB) with corresponding ecological or hydraulic objectives (Fig. 11) for Murray cod (flow components 1–5) and golden perch and silver perch (flow components A–D) and the benefits to these and other species

Note that this is conceptual for a river with reversed seasonality in the SMDB and the references provide context rather than direct support. Asterisks indicate key knowledge gaps. Further research is required to identify direct flow or hydraulic–ecology relationships within individual river reaches. Timing and spatial scales should be adjusted for different regions and species life-history requirements. ARI, Arthur Rylah Institute for Environmental Research

Flow components and timing (for SMDB)	Ecological or hydraulic objective	Primary species	Benefits to other species	Context references
1. Annual late-winter to early spring in-channel rise in discharge to inundate benches by mid-October	Inundate dry banks, benches, spawning and feeding habitats, create productivity, provide diversity of lotic (>0.3 m s ⁻¹) habitats at spatial scale >5 km*, provide cue for fish movement	Murray cod	All species present	Humphries (2005); Koehn and Harrington (2006); Koehn <i>et al.</i> (2009); Koster <i>et al.</i> (2014); Bice <i>et al.</i> (2017)
2. Spring rise in discharge with no rapid water level drops	Enable selection of spawning habitats, provide appropriate lotic hydraulic conditions for nesting species and avoid rapid level drop to prevent nest abandonment*	Murray cod	Golden perch, silver perch, Macquarie perch	Rowland (1998a); Mallen-Cooper and Zampatti (2018); Stuart <i>et al.</i> (2019); Koster <i>et al.</i> (2020)
3. Littoral inundation for primary and secondary productivity in spring and summer	Increase in-stream productivity to suitable food resources for larval and juvenile fish survival, growth and condition in hydraulically diverse habitats	Murray cod	All species present	Francis and Sheldon (2002); Jenkins and Boulton (2003)
4. Slow flow recession with no rapid water level drops in summer	Allow for larval drift, avoid stranding of fish and enable juveniles to disperse among habitats	Murray cod	Golden perch	Baumgartner <i>et al.</i> (2014b); Tonkin <i>et al.</i> (2017b)
5. Permanent winter base flow	Maintain lotic habitats to improve over-wintering survival of juvenile fish*	Murray cod	All species present	Lieschke <i>et al.</i> (2016)
A. Late spring and summer in-channel fresh event	Provide cue for pelagic spawning; increase spatial extent and continuity of lotic habitats; provide in-channel productivity pulse	Golden perch, silver perch	All species present	King <i>et al.</i> (2009a); Zampatti and Leigh (2013a, 2013b); Koster <i>et al.</i> (2017); Tonkin <i>et al.</i> (2019a)
B. Inundate connected floodplains in spring	Provide access for larval and juvenile fish to productive floodplain feeding and growth habitats; access for other wetland species	Golden perch, silver perch	All species present	Lyon <i>et al.</i> (2010); Sharpe (2011); Tonkin <i>et al.</i> (2017c, 2019a); Stuart and Sharpe (2020)
C. Slow late summer to autumn recession of floodplain habitats with access for dispersal of young fish	Provide access for juvenile fish to permanent riverine habitats; provide floodplain productivity benefits to the main river channel	Golden perch, silver perch	All species present	Stuart and Sharpe (2020)
D. Small summer to autumn flow spikes	Movement cues to assist dispersal and recolonisation of fish from nursery habitats along main river stem and tributaries	Golden perch, silver perch	Bony herring <i>Nematalosa erebi</i>	Mallen-Cooper (1999); Mallen-Cooper and Stuart (2003); W. Koster, ARI, unpubl. data

example, the key ecological elements necessary for maintaining Murray cod populations were identified (Table 15) and an assessment was undertaken for each river reach to highlight the key limiting elements (Table 16). Although some key elements or components pose ‘threshold’ effects (e.g. low base flows, rise and fall rates, cold water pollution) that can be population limiting (e.g. by reducing recruitment; Fig. 11), once these are restored, other actions (e.g. habitat improvement) can be successfully implemented (Table 16). Some threats occur widely across river reaches (e.g. recreational fishing), whereas others, such as cold water pollution, only apply downstream of major storages. Some effects will be more easily remedied than others. For example,

extensive river reaches (≥1000 km) of the lower Murray and Barwon–Darling rivers were converted from lotic to lentic environments by the imposition of weirs and reduced flows (Maheshwari *et al.* 1995; Walker 2006; Mallen-Cooper and Zampatti, in press) Remediation of hydraulic effects occurring within these reaches is unlikely from a generically designed hydrograph or by changes to river flows alone. A combination of integrated actions, such as weir removal or lowering in combination with flow restorations, may be required (Bice and Zampatti 2015; Bice *et al.* 2017; Mallen-Cooper and Zampatti 2018). A further summary perspective on broader restoration actions for MDB fishes is provided in Koehn *et al.* (2020)

Table 15. An integrated framework for restoration, supplemented by a case study example of how this could be applied to Murray cod in the connected Murray River

CPUE, catch per unit effort; CWP, cold water pollution; SHW, structural woody habitat; TBD, to be determined; TL, total length

Restoration process	Case study for Murray cod in the connected Murray River
(1) Set restoration objective, identify and work with stakeholders	(1) Increase Murray cod adult population (>550 mm TL) by 20% (TBD) with corresponding angler CPUE increase within 10 years
(2) Formulate a species conceptual ecological model	(2) Murray cod is a large, long-lived, river channel specialist that requires flowing (lotic) waters for effective recruitment (survival of young) and prefers structural habitats, such as large woody debris or rocks. Expect slow (5- to 10-year) recovery at river reach scale
(3) Identify key ecological (including hydrological and hydrodynamic) requirements	(3) Key ecological requirements: flowing water habitats, SWH or rocks, spawning water temperatures >16°C
(4) Identify key threats	(4) Key threats: loss of flowing water (lotic) habitats in weir pools (over 1000 km in the lower Murray River), cold water releases, low winter flows with loss of overwinter lotic refugia in some highly regulated tributaries, limited SWH, angler take and catch–release mortality, fish kills, damage to larvae through weirs, loss into irrigation channels and pumps
(5) Identify knowledge gaps	(5) Key knowledge gaps: unknown settlement and nursery habitat of 0+ fish (i.e. larvae, fry), early life stage survival rates unknown, depth of nests and thresholds of water level drops to prevent nests being abandoned unknown, effects of large weirs (especially undershot) in rivers on larvae unknown
(6) Formulate a management model; identify key management levers and constraints	(6) Water delivery regime (irrigation, water transfers, environmental, spatial scale) recreational angling, habitat restoration
(7) Qualify and update knowledge; identify key knowledge gaps and uncertainties	(7) Add recent work; interview scientists for present thinking and refinements of conceptual models; revisit National Recovery Plan
(8) Develop a restoration plan; identify and prioritise key actions, options, timing, sequence, costs etc.	(8) Priority restoration options: restore lotic habitats at the appropriate spatial scale; remediate CWP; add SWH; implement winter base flows for lotic refugia, especially for juveniles (0+ fish); develop a hydrological plan with designed hydrograph; educate anglers on catch and release best practise; replace undershot with overshot weirs; screen pumps and channel outlets; 5- to 10-year plan in annual steps
(9) Set evaluation outcome targets	(9) Targets: detection of new recruits, population growth (<550 mm TL) over 5 years, increased fish into the fishery (>550 mm TL) over 10 years, predict likely population and CPUE outcomes using a population model
(10) Operationalise restoration plan and implement actions	(10) Undertake and document actions
(11) Monitor and report outcomes; adaptive management cycle, refine models and targets	(11) Use existing regional monitoring programs, supplement at local scale; add scientific and angler monitoring; report outcomes; continue adaptive management cycle

The need for access to research results, scientific concepts and assessments is essential to support major environmental restoration programs underway within the MDB (Murray–Darling Basin Authority 2011). The knowledge presented in this paper partially meets this need, yet additional methods of communication are required to facilitate knowledge transfer to decision makers and the public (e.g. communication plans, knowledge brokers, video clips etc.). In addition to further knowledge to inform policy and management, managers require timely advice during the planning and implementation of management actions, based on robust research and monitoring. The uptake of research is greatest when projects incorporate a specific knowledge transfer component (Koehn *et al.* 2019a), where dialogue and collaborative relationships between researchers and managers can improve ecological outcomes (Gibbons *et al.* 2008; Cvitanovic *et al.* 2015).

Conclusion

Given the poor and declining status of native fish populations in the MDB, there is an urgent need for restoration policy, management and community actions; we cannot just manage for the status quo. We need to build resilient fish populations able to withstand and recover from the multitude of human-induced

impacts and disturbances. There is a need for an integrated approach to address flow- and non-flow-related stressors, which requires ready access to contemporary knowledge. This paper offers direction and scientific support to maximise restoration outcomes by providing an accessible compendium of up-to-date ecological knowledge. A conceptual ecological understanding of the nine key fish species provides a basis from which recovery management can be planned. Assessing the potential effects of threats to these species guides the prioritisation of restoration actions. Identification of key knowledge gaps highlighted the need for continued investment in knowledge generation and dissemination. The compendium format publishes the current ecological knowledge synthesis, together with a bibliography of the associated primary literature, in a format accessible to a range of readers (e.g. students, researchers, natural resource managers and funders) that may be involved in native fish population recovery in the MDB. The species-specific approach supports nuanced management, with information provided on multiple species and life stages at a variety of spatial scales to inform the processes needed to ensure population recovery. This approach is applicable to many other fishes, regions and integrated restoration programs, both in Australia and worldwide.

Table 16. A river reach assessment of the key elements for maintaining Murray cod populations in the connected Murray River (* or tributary) downstream of Lake Hume
 ✓✓, existing; ✓, partially present (present in some years or areas); ×, not present, needs a restoration action

Key ecological elements for maintaining Murray cod populations	Murray River reach									
	Lake Hume–Lake Mulwala	Lake Euston	*Edward–Wakool	Lower Murray River	*Lower Goulburn River	*Lower Murrumbidgee River	*Loddon–Campaspe rivers	*Mullaroo Creek		
Natural temperature regime	×	✓✓	✓✓	✓✓	✓✓	✓✓	✓	✓✓	✓✓	✓✓
Flowing water (>5 km)	✓✓	✓✓	✓✓	×	✓✓	✓✓	✓✓	✓✓	✓✓	✓✓
Permanent winter base flow	✓✓	✓✓	✓	✓✓	✓✓	×	✓✓	✓✓	✓✓	✓✓
No rapid drops during spawning season	✓	✓	✓	✓✓	×	×	×	✓✓	✓✓	✓✓
Large woody debris	✓	✓	✓✓	✓	✓✓	✓✓	✓	✓✓	✓✓	✓✓

Conflicts of interest

Lee J. Baumgartner is an Associate Editor of *Marine and Freshwater Research*. Despite this relationship, he did not at any stage have Associate Editor-level access to this manuscript while in peer review, as is the standard practice when handling manuscripts submitted by an editor to this Journal. *Marine and Freshwater Research* encourages its editors to publish in the Journal and they are kept totally separate from the decision-making process for their manuscripts. The authors declare that they have no further conflicts of interest.

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