Environmental Management (2012) 50:1–10
DOI 10.1007/s00267-012-9864-z

FORUM

Putting the "Ecology" into Environmental Flows: Ecological Dynamics and Demographic Modelling

Will Shenton · Nicholas R. Bond · Jian D. L. Yen · Ralph Mac Nally

Received: 9 June 2011 / Accepted: 29 March 2012 / Published online: 28 April 2012
© Springer Science+Business Media, LLC 2012

Abstract There have been significant diversions of water from rivers and streams around the world; natural flow regimes have been perturbed by dams, barriers and excessive extractions. Many aspects of the ecological 'health' of riverine systems have declined due to changes in water flows, which has stimulated the development of thinking about the maintenance and restoration of these systems, which we refer to as environmental flow methodologies (EFMs). Most existing EFMs cannot deliver information on the population viability of species because they: (1) use habitat suitability as a proxy for population status; (2) use historical time series (usually of short duration) to forecast future conditions and flow sequences; (3) cannot, or do not, handle extreme flow events associated with climate variability; and (4) assume process stationarity for flow sequences, which means the past sequences are treated as good indicators of the future. These assumptions undermine the capacity of EFMs to properly represent risks associated with different flow management options; assumption (4) is untenable given most climate-change predictions. We discuss these concerns and advocate the use of demographic modelling as a more appropriate tool for linking population dynamics to flow regime change. A 'meta-species' approach to demographic modelling is discussed as a useful step from habitat based models towards modelling strategies grounded in ecological theory when limited data are available on flow-demographic relationships. Data requirements of demographic models will undoubtedly expose gaps in existing knowledge, but, in so doing, will strengthen future efforts to link changes in river flows with their ecological consequences.

Keywords Demographic models · Environmental flows · Demographic modelling · Habitat-suitability models · Meta-species

Introduction

Competition for access to freshwater, among countries, among states and individuals, may lead to 'water wars' (Poff and others 2003; Lake and Bond 2007). Human population growth and concurrent increases in per capita rates of water use have led to considerable pressures on much of the world's major freshwater supplies (Vörösmarty and others 2000; Gleick 2003). On-going increases in irrigated agriculture and domestic water consumption has generated concerns for the sustainability of aquatic ecosystems (Dudgeon and others 2006; Vörösmarty and others 2010). Water-resource development affects not only the volume of river flows, but also patterns of flow variability, such as the timing, frequency and magnitude of flooding. These can act as important drivers of ecological processes in riverine and floodplain ecosystems, such as energy fluxes and breeding events of both terrestrial and aquatic taxa (Humphries and others 1999; Ballinger and others 2007); these problems almost certainly will be exacerbated by climate change (Palmer and others 2008). There are predictions of increasingly frequent and more severe climatic extremes in many parts of the world (Milly and others 2002; Palmer and others 2008). The condition of

W. Shenton · N. R. Bond · J. D. L. Yen · R. Mac Nally (✉)
Australian Centre for Biodiversity, School of Biological Sciences, Monash University, Caulfield East, VIC 3800, Australia
e-mail: Ralph.MacNally@monash.edu

Present Address:
N. R. Bond
Australian Rivers Institute, Griffith University, Nathan, QLD 4111, Australia

the Murray-Darling Basin in Australia exemplifies this situation, where over-extraction (for irrigated agriculture and for domestic use) has reduced river flows and the frequency of floodplain inundation, leading to hypersaline conditions in the lower river system that may lead to ecosystem collapse if not addressed (Kingsford 2009; Mac Nally and others 2011).

Water-resource planning frequently seeks to optimize the distribution of water among competing uses, including the maintenance of ecosystems and the services they provide, through estimates of ‘environmental flow requirements’ (Hamstead and others 2008). Environmental flow specifications are now an integral part of water management policy in more than 30 countries (King and Brown 2006). Frameworks used in environmental flows planning typically apply a standard ‘building-block’, or bottom-up, approach to assessment (Arthington and Pusey 2003). These methods examine the historical frequency, timing and duration of components of streamflow (e.g., baseflows, overbank flows, pulses etc.) and link these to physical and ecological processes. Frameworks for strategic environmental flows planning should also address the roles of extreme weather events and future changes in hydrological variability.

Hydrological and habitat-based environmental flows methodologies (EFMs) have brought together hydrologists, ecologists and geomorphologists to develop conceptual and quantitative models linking aspects of the natural flow regime to pertinent physical and ecological processes (Arthington and others 2006). The result is a transparent planning process for specifying environmental flows and for informing how water resources ought be shared between consumptive and environmental needs (Richter and others 2003). Aspects of these approaches have been maligned for paying little or no heed to ecological theory (Lancaster and Downes 2010). The method does not help to forecast rates of decline and recovery of populations from severe events, such as drought (Bond and others 2008). In contrast, demographic modelling has been used effectively to address these threats (Beissinger 1995).

In this review, we identify the shortcomings of current EFMs and discuss how these might be addressed. The method we use examines EFM through the ‘lens of ecology’ rather than from the usual hydrological perspective. For example, although the use of past ‘natural variability’ is arguably a good predictor of future function (Landres and others 1999), in the face of a changing climate and an increasing likelihood of more frequent extreme events, these hydrological futures may not resemble hydrological pasts. Underlying assumptions usually are based on the analysis of historical flows, but the derived summary statistics often do not adequately represent the influence of the sequence of previous (antecedent) conditions. The potential for temporal effects, such as lagged and non-linear responses to particular flow conditions, also needs to be considered in more depth.

EFMs and Water-Resource Planning

EFMs were initially developed to address the effects of dams and flow regulation on river biota (Tharme 2003). Early approaches to water allocation, such as the Tennant method (Tennant and Bitterman 1975), assumed that only a fixed percentage of the mean flow is needed to maintain a healthy stream environment (Jowett 1997). This simple approach did not provide adequate ecological protection for rivers and led to the development of EFMs based on the ‘natural flow paradigm’ (Petts 1996; Poff and others 1997). The natural flow paradigm encompasses the full range of natural intra- and inter-annual variation of hydrological regimes that are thought to be critical for sustaining biodiversity and the ecological function of aquatic ecosystems (Richter and others 1997). Adoption of the natural flow paradigm in EFMs has resulted in the concept becoming an integral part of managing riverine ecosystems (Poff and others 1997; Lytle and Poff 2004).

Several environmental flow assessment approaches have been developed that support water-resource planning, and that build on the notion of a ‘natural flow’ (Tharme 2003; Arthington and others 2006). The four main types of EFMs are: (1) hydrological; (2) hydraulic rating; (3) habitat simulation or rating; and (4) holistic methodologies (Tharme 2003). Environmental flow assessment methodologies can be grouped into two broad categories: (a) prescriptive; and (b) interactive (King and Brown 2006). The prescriptive approach to environmental flows is the traditional approach to EFMs and often specifies a set of flow recommendations believed to best satisfy ecological objectives (Gippel and others 2009). Interactive approaches provide formal risk assessments by presenting a range of flow scenarios, each having different probabilities of arising and severities of their consequences (King and others 2005).

There is a schism between the planning and prescription of ecologically desirable/acceptable flow regimes and the dynamics of freshwater ecosystems. To establish the viability of riverine populations requires explicit consideration of how key ecological processes, such as recruitment and survival, are determined by the dynamics of flow (Anderson and others 2006).

Limiting Assumptions in EFMs

EFMs are based on key assumptions that constrain and limit their relevance. Our intention is not to undermine the existing approaches because bottom-up methods have pragmatic merit in prescribing environmental flows, particularly in regulated rivers. Rather, we highlight some of the developmental steps that could improve EFMs and place them within a framework for ecologically sustainable water management.

We focus on two key assumptions underpinning EFMs:

1) A reliance on summary statistics derived from natural flows; and
2) Models of habitat suitability provide a proxy for actual population dynamics.

Corollaries follow from these assumptions that have important implications for developing decision support systems for water resource planning. These include:

1) The use and employment of historical data understate the importance of extreme events and ignore the potential for process non-stationarity (i.e., the future is not well predicted by the past); and
2) EFMs do not address the temporal nature of population dynamics of stream biota, especially in relation to the necessary sequences of events and cues used by the biota to stimulate and govern life-history events.

Historical Flows, Summary Statistics and EFMs

Most approaches for determining environmental flows rely on the analysis of historical time-series flows data—either modeled or from gauged information. A standard approach is to examine the historical frequency, timing and duration of flow events (Poff and others 1997). Such time series generally are assumed to be representative of the full range of flow conditions that might occur in the future (i.e., patterns of variability). This assumption has two limitations: (a) the typically atemporal nature of analyses; and (b) the short period of the historical flows record.

Atemporality

Atemporality arises from a reliance on statistical summaries and measures of central tendencies of the flow regime (i.e., mean or median annual flows, period between overbank flows etc.) even though both variability and unpredictability are defining features of hydrological regimes (e.g., Resh and others 1988). In most regional or global comparisons of river regimes, flow variability has been described by statistics that include coefficients of variation (CV) of daily and maximum and minimum mean annual flows (Jowett and Duncan 1990). Such summary data then are linked to hydraulic investigations, and conceptual ecological models are used to identify the particular flow components or magnitudes that may be pivotal in maintaining the integrity of ecological *assets* (i.e. the natural values being considered; Saintilan 2010). For example, the initial steps of the DRIFT methodology (Arthington and others 2003) involve the preparation of hydrological data and the derivation of summary statistics that are linked to cross-sectional river features; ecologically significant scenarios then are inferred. Once a particular flow component (e.g., overbank flows) has been identified as critical, analysis of the historical frequency and the maximum historical interval between such events are coupled with information on the life-history and demography of a species to determine the frequency with which such flows are required under the regulated regime.

The critical issue regarding water allocation to protect river ecosystems is the temporal scaling of flows because ecological responses to flow variation can occur over timescales of hours to years (Biggs and others 2005). Therefore, the use of summary statistics from historical flow analysis is not adequate to capture biotic dynamics. A typical example of a standard atemporal analytical tool used in environmental flow analysis is the flow-duration curve (FDC) (Vogel and Fennessey 1995), which pays no heed to the sequences of flows and flood frequency. Average recurrence intervals do not incorporate variability and predictability in the timing of events. King and Brown (2006) discussed the difficulty in translating information in the form of FDCs into effects on the river ecosystem in response to flow changes. A consequence of this method is that flow recommendations often are unrepresentative of ecologically significant flow dynamics. Even where interannual variability is built into environmental flow recommendations, existing habitat-based models do not allow the size, structure or condition of populations to be tracked through time in response to the variability that is imposed or arises.

Extreme Events, Process Stationarity and EFMs

Historical time series of flows are comparatively short (typically < 100 years), and so, fail to capture two climate-driven processes that could compromise strategic environmental flows decisions, namely, extreme weather events and process stationarity. The use of short historical time series almost certainly will give poor estimates of extreme hydrological events (Stewardson and Gippel 2003). Other issues arise when historical time-series are used to evaluate tradeoffs between environmental and consumptive uses (e.g. software tools such as IQQM) (Simons and others 1996). The assumption that historical flows are indicative of future flows can lead to risks of shortfalls in water availability should an historically unprecedented sequence of dry years occur (Cai and Cowan 2008). The recent drought in Australia—the ‘Big Dry’ (Jones 2012)—left water managers with few options to address water scarcity (Lester and others 2011). While this drought was by far the longest in the historical gauging record, palæoclimatic data shows that such events have occurred over the past 1500 years (Tibby and Tiller 2007) and might have been considered in scenario analyses.

The influence of relatively rare events, such as floods and droughts, and their temporal sequences, has ecologically significance (Parsons and others 2005). Extreme events play a critical role in structuring aquatic ecosystems through their effect on fish populations, which may require years to recover from a single extreme flow event (Hickey and Diaz 1999; Douglas and others 2003). Droughts and floods have marked effects on the size- or age-structure of populations, assemblage composition and diversity, and on ecosystem processes (Lake 2000; Lake 2003). Prolonged drought conditions may require several ‘wetter’ years to allow populations to recover to pre-drought densities with a low risk to long-term viability (Beissinger 1995). However, such events, and the potential lagged responses of population trajectories, are rarely considered in published studies on environmental flows, but have been modelled for native vegetation models (Lytle and Merritt 2004; Vesk and Dorrough 2006).

The reliance on historical time series implies climatic stationarity, that is, that any variable (e.g., annual stream flow) has a time-invariant probability density function whose statistical properties can be estimated from the historical record (Milly and others 2008). Given a changing climate, stationarity in the hydrological variability of river systems can no longer be assumed. Therefore, stationarity is not defensible in water-resource risk assessment and planning and an alternative is needed (Milly and others 2008). Similar arguments apply in the planning of environmental flows, where recent unprecedented drought and floods in parts of Australia (Cai and Cowan 2008; Cai and others 2009), coupled with projected changes in climate, call into question the use of metrics derived from historical time-series.

Habitat-Suitability Models: Static Models of Dynamic Ecosystems

Habitat-suitability models are the cornerstone of EFMs. The use of habitat-suitability modelling has been criticized for being expensive to build and to implement, for having relevance at only small spatial scales, for paying insufficient attention to uncertainty, and for focusing on specific taxa (Lancaster and Downes 2010; Lester and others 2011). These models describe the habitat requirements of different species (or life stages), often as a function of hydrological and hydraulic criteria. Historical flow time-series data then are used in conjunction with these models to examine the extent to which habitat requirements are met (Petts 2009). For example, PHABSIM (Annear and others 2002) is an oft-used technique for developing a rating curve that relates total available habitat area to river discharge. This rating curve is then combined with a flow-duration curve to produce a habitat-duration curve. Physical habitat and habitat-preference models treat many dynamic factors as external forcing functions and ignore crucial intraspecific feedbacks in populations (Anderson and others 2006). Therefore, habitat-based models that emphasize linkages among components of the river environment cannot fully inform EFMs. While models used in EFMs are sometimes spatially explicit (e.g., in examining inundation patterns of floodplain vegetation), few are temporally explicit, notwithstanding that changes in temporal variability are the major effects of river regulation.

Several of the tools that have recently been applied to support environmental flow allocation decisions are especially poor at dealing with temporal dynamics. Bayesian network models have proven attractive at incorporating elicited expert opinion into EFMs (Shenton and others 2010), but these are inherently poor at capturing temporal feedbacks (Marcot and others 2006). While such static assessments of habitat suitability have been useful in predicting relative abundances in small reaches of stream (e.g., based on pool volumes), their fundamental limitation is that they do not model populations per se or the processes that govern those populations, such as rates of fecundity, recruitment and mortality (*vital rates*) (Lancaster and Downes 2010). Habitat-suitability models are unable to predict actual population states at any point in time. Even when extended to include multiple life-stages of an aquatic organism, these models are not well suited to capture the temporal lags and interdependencies that occur in population dynamics (Lancaster and Downes 2010).

Freshwater ecologists long have advocated shifting the focus of management from provision of habitat for target species to preserving the viability of the riverine ecosystem (Poff and others 1997). However, habitat-rating curves still are used frequently to translate the natural flow series into a measure of how habitat availability varies through time, or how frequently particular ecological processes are ‘switched on’ (Horne and others 2010). There is an assumption that the dynamics of distributions of habitat suitability provide a proxy for dynamics of the population or ecological process of interest. This assumption is unlikely to be valid for many processes because of non-linear dynamics, lags and internal feedbacks, and an inability to incorporate antecedent conditions. One should focus on directly modelling the ecological response rather than a necessary but not sufficient surrogate (habitat) (Anderson and others 2006).

Ecological Dynamics and Demographic Modelling for EFMs

Achieving viable and self-sustaining riverine populations requires methods and tools that couple flows and population dynamics. At best, current EFMs might use existing data or expert opinion to characterize just which flow components are needed to sustain or restore populations (Fig. 1a). These associations often are driven by ad hoc observations or opinions of experienced workers over years rather than from numerical correlations. Poff and Zimmerman (2010) suggested that good quantitative evidence for the impacts of flow alteration are relatively rare, even though longer-term studies of population variability in rivers implicate flow extremes in driving population cycles (Milner and others 2003).

It is also likely that one particular flow component evokes different responses in two (or more) life-history stages of a species (Fig. 1b), which would confound efforts to detect changes in simple indicators such as abundance. That one flow component may have negative effects on the potentially breeding cohort yet be a necessary element for the survival of sub-adult stages. These relationships have to be established before one can develop useful demographic models for a population.

Ecological response models that explicitly consider temporal dynamics are needed. In the long-term, process-oriented ecological models will be better suited to guide flow-regime decisions because they can generate dynamic responses across scales and levels of biological organization (Anderson and others 2006). Some classes of models, such as Markov-chain models that are often used to model demographic processes (Todd and others 2005), are well suited to the explicit modelling of temporal dynamics.

Demographic modelling is the simulation of population change using mathematical models that can address some of the ecologically relevant shortcomings of contemporary EFMs. Demographic modelling often is done using matrix population models (Caswell 2001), which are used in population biology to link individual life stages to population dynamics (Hodgson and Townley 2004). These are a standard tool in assessing the viability of structured populations (Morris and Doak 2002), and have been applied to a wide range of ecological problems and for many species, especially for population viability analysis (Fieberg and Ellner 2001; Morris and Doak 2002).

Population projection matrices are constructed from the vital rates of an organism from demographic data collected over years. For example, matrix population models have been used to explore the effects of altered flood timing and rainfall patterns on riparian vegetation (Lytle and Merritt 2004; Smith and others 2005), and the effects of flow regulation of flathead catfish *Pylodictis olivaris* (Sakaris and Irwin 2010). These models have been used to examine the effects of other anthropogenic stressors such as cold-water pollution (Todd and others 2005) and trout habitat

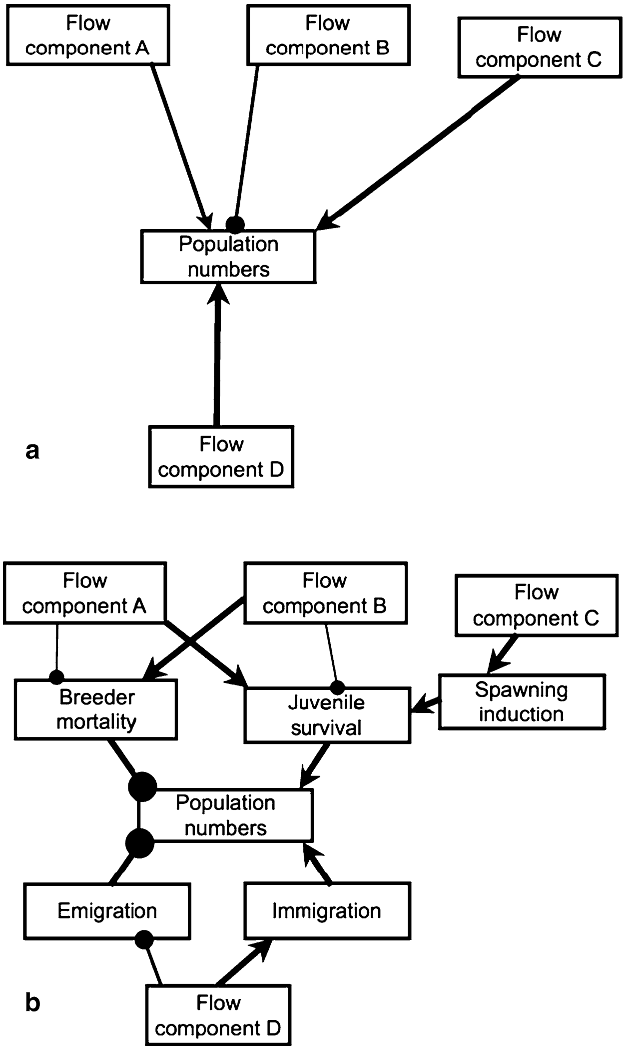

Fig. 1 Hypothetical population dynamics of a riverine animal species, where population numbers through time is the response variable. **a** A common expert-elicited version of the relative influences of four flow components (e.g., magnitude of largest spring fresh, base-flow in the driest period, etc.) on population numbers. **b** A version of population dynamics in the influences of flow components on the four fundamental determinants of population dynamics (mortality of potential breeders, recruitment, emigration and immigration) are made explicit. Some flow components may have reinforcing effects on depressing the population (e.g., Flow component B, which increases breeder mortality and reduces juvenile survival) while others may have positive effects one determinant and negative ones of the other(s). Symbols: filled circles indicate depressing effects, arrowheads indicate increasing effects and width of lines and circle size indicates magnitudes

fragmentation (Letcher and others 2007). These applications have shown the potential for demographic modelling to represent the dynamic responses of populations to different hydrological regimes, including explicit scenarios of temporal sequences of 'good' and 'bad' conditions. Demographic modelling, which is capable of handling time explicitly, confers significant advantages over the more widely used habitat-suitability models — whether these are statistical or mechanistic — for EFMs.

Demographic models are structurally straightforward but are 'data hungry' (Morris and others 2002; Xu and others 2010). Model formulation and parameterization require the consideration of spatial population structure and the potential roles of immigration and emigration and internal dynamics to determine population trajectories (Schlosser and Angermeier 1995). While such complexities might be viewed as hindrances to model development, an alternative is to treat the model-development process as structured learning (Burgman 2000) in which model formulation and subsequent sensitivity (the degree to which population dynamics are affected by small changes in each demographic parameter) and elasticity analyses (the effect of a *proportional* change in the vital rates on population growth) can help to identify important knowledge and data gaps (Schodelbauerova and others 2010).

A Way Forward: Guilds and Demographic Simulation

Conservation biologists have bemoaned that poor data cause difficulties in parameter estimation, which in turn leads to unreliable estimates of risk (Brook and others 2000). Beissinger and Westphal (1998) reviewed the use of demographic models for endangered species management and recommended that population viability analysis (PVA) be used to evaluate *relative*, rather than *absolute*, extinction risk. A lack of high-quality data need not impede the utility and application of demographic modelling if a broader definition of an ecological asset is used—the ecological '*guild*'. An ecological guild is a group of species that exploits the same class of environmental resources in a similar way (Root 1967). It has long been recognized that groups of species behave in a sufficiently similar manner and can be classed as a common group (Mac Nally 1983). Life history guilds also have been used (Winemiller and Rose 1992; Van Winkle and others 1993). The use of guilds is a central technique in managing groups of species with similar traits because functionally similar species are likely to respond in a similar way to specific disturbances (Mac Nally and others 2008). The guild structure of an ecosystem often is more stable in time than its species composition (Aarts and Nienhuis 2003). In the context of EFMs, a guild can be defined as a set of species that responds in a similar manner to changing hydrology and geomorphology of riverine ecosystems (Welcomme and others 2006). The guild approach provides an operational unit linking individual species characteristics with the assemblage as a whole and provides an effective bridge linking ecological knowledge of in-stream assemblages to flow (Noble and others 2007).

Once species have been classified into appropriate flow-response guilds (Merritt and others 2010), a further abstraction is needed to translate existing studies of extant species in a guild into a '*meta-species'* (Archibald 1994). A meta-species is a notional construct that is representative of each guild, the vital rates being an amalgam of species-specific knowledge derived from analysis and existing literature. The meta-species concept is a vehicle to combine different sources of data into plausible estimates of growth, survival and mortality (with uncertainties), given the best available data, although the goal is the incorporation of long-term datasets (Doak and Morris 1999).

To demonstrate the use of demographic modelling to EFMs, we briefly outline the process and some simulation results (Fig. 2); a full description of the framework and an application to climate change is detailed elsewhere (Yen and others in review). A meta-species was constructed for Murray cod *Machullochella peelii* Mitchell, a member of the 'mode 1' guild (Humphries and others 1999). Members of this guild include the Trout cod *M. macquariensis* Cuvier and River blackfish *Gadopsis marmoratus* Richardson. Vital rates were represented as probability distributions and estimated using published values for any species within the guild (Humphries and others 1999; Growns 2004; Todd and others 2005) along with

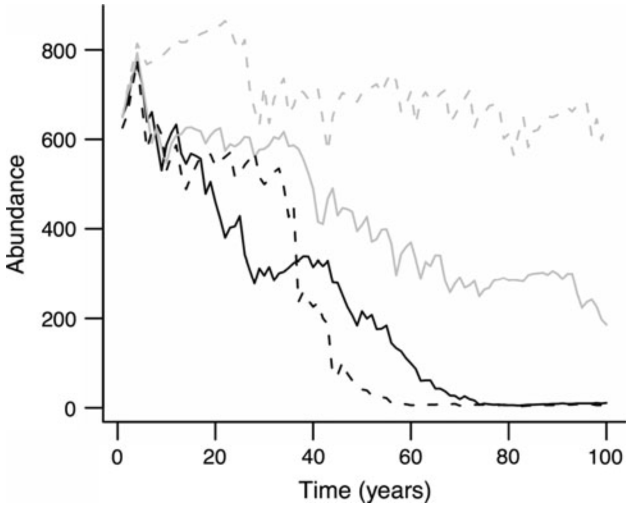

Fig. 2 Simulation results for Murray cod for four different scenarios. Grey line represents regulated flows and black lines are natural flows. Solid lines are long droughts; dashed lines are short droughts and high variability in drought/flood years. The lines are median population size

information on general guild characteristics. As an example, fecundity estimates from the literature ranged from 3500 (± 1500 SD) (Todd and others 2005) to 25 000 (± 10 000 SD) (Growns 2004) and on the order of 10^3–10^4 (Humphries and others 1999). We represented this as a lognormal distribution with a mean of 15 000 and standard deviation of 10 000. A stage-based demographic model was based on a pre-breeding census and implemented in a Bayesian Markov chain Monte Carlo (MCMC) framework, which allowed stochasticity to be incorporated into parameter estimates (Yen and others in review). The Bayesian MCMC approach included demographic stochasticity and density dependence (Yen and others in review). Demographic models then are linked to flow scenarios using 'flow-response functions', which convert a flow time series into a series of vital rate scaling values from zero to one. A hidden Markov model is used to generate time series of flow events under four different flow scenarios—regulated (short and long drought sequences) and natural (short and long drought sequences) flows. The abundance of Murray cod tends to decrease greatest under natural flows with long periods of drought (Fig. 2); cod abundance is maintained under regulated scenarios that incorporate flood and droughts. Such results are consistent with the evidence for Murray cod persistence with respect to flow conditions given that the lifecycle of the fish is relatively flow insensitive, often being described as a 'main channel specialist' (i.e., most common in the highest-order rivers), although they are sensitive to hypoxia in flows stress. However, the important aspect of the simulation results relevant to EFMs is the ability to incorporate temporal sequences of drought and variability within a stochastic framework that can be used to support scenario-based decision making regarding temporal sequences of floods and drought and their effects on population persistence. Such modelling currently is rare in EFMs.

Synthesis

Scientists should broaden their repertoire of methods used in EFMs to include tools that implicitly model flow-ecology dynamics. Effective environmental flow decisions require an improved capacity to evaluate the full range of potential flows that may occur in the future, including the previously unobserved extreme flows that are predicted for climatically altered flow regimes. We identified several shortcomings in existing and widely used approaches to EFMs. These include the use of relatively short historical time-series and summary statistics based on habitat-suitability models. Such an approach to environmental-flows planning leads to an exclusion of rare, but not unexpected, flow-related events such as extreme floods and long-term droughts. That approach also fails to reflect the dynamic and context-dependent response of biotic populations to patterns of flow variability.

These shortcomings reflect a major divide between current EFMs and progress made in the broader ecological community in which modelling to estimate the abundance and persistence of populations under management scenarios has evolved rapidly. Examples are fisheries and conservation biology, where stock-recruitment models and population viability analysis are core tools used in guiding management actions (Morris and others 2002). There are several key features that define current best-practice (Morris and others 2002). First, the models must address the ecological end-points of interest (e.g., population size, or persistence time). This characteristic is surprisingly rare among EFMs because most EFMs model surrogates, such as the suitability or extent of habitat. Second, population dynamics are governed by not only external drivers, such as flow variability, but also by internal feedbacks, such as density dependence in population growth rates (Dennis and others 2006); feedback mechanisms need to be incorporated into the model structure. It is the failure of habitat-suitability models to efficiently capture these feedbacks that has attracted strong criticism (Anderson and others 2006; Lancaster and Downes 2010). Third, model parameters are often difficult to estimate, so that models must reflect the uncertainty in parameter estimates. The incorporation of this uncertainty is the cornerstone of stochastic simulation models (Lande and others 2003). Good modelling practice requires the use of sensitivity analysis to evaluate the relative influence of different parameters and hence the consequences of different sources of uncertainty for model predictions (Todd and others 2005). Requirements for considering parameter uncertainty include not just the internal parameters in the model but also uncertainty in the scenarios being modelled, an issue we discuss in relation to the generation of flow scenarios for water resource planning. It is not difficult to find examples of population models that fulfil all of these 'best-practice' criteria in the wider ecological literature, but examples explicitly from the field of environmental flows assessment are comparatively rare, although there are some good examples (Sakaris and Irwin 2010).

Future methods are needed to capture the dynamics of freshwater ecosystems in ways that can translate alternative flow regimes into estimates of population response, which, in turn, can guide water-allocation trade-offs (Grafton 2010). This is especially important for highly variable or periodic environments subject to floods and droughts because these events have strong legacy effects on populations for long periods (Parsons and others 2005; Magalhaes and others 2007). Demographic modelling potentially can satisfy these criteria, but will be constrained in the short-term by a lack of suitable long-term datasets from which to derive reliable parameter estimates. Nevertheless, there are standard approaches based on analysis of cohort data that provide avenues for making these estimates (Guy and Brown 2007); the establishment of long-term monitoring programs to collect this information is a high priority (Lindenmayer and Likens 2009).

The adoption of a guild-based demographic modelling framework may provide an appropriate intermediate, bridging step to couple conventional hydrological models with population-process based models, and help to integrate modelling and empirical data gathering—a need often espoused as part of adaptive environmental management (Gregory and others 2006). Practitioners in the field, including those funding environmental flows assessments, may regard recommendations such as ours as falling within the research domain rather than that of practical EFMs (Anderson and others 2006). However, marrying high-end research with pressing management actions is essential if EFMs are to pass the growing scrutiny they will attract as water-scarcity grows over the coming decades.

Acknowledgments The (Australian) National Water Commission and the Victorian Water Trust funded the work undertaken in the paper through the project: *Farms, Rivers and Markets: A Whole-of-System Approach for Doing More with Less Water*, funding for which was obtained largely due to the leadership of John Langford. Assistance was rendered to us by the 'ecology team' of that project, which included Andrew Western, Ben Gawne, Mike Stewardson, Darren Neilson, Nathan Ning, and Geoff Vietz. Additional support came from a grant from the Australian Research Council, DP120100797. We also thank Sam Lake, Paul Reich, Jim Thomson and Shaun Cunningham for helpful insights into the work. This is contribution No. 246 from the Australian Centre for Biodiversity, Monash University.

References

Aarts BGW, Nienhuis PH (2003) Fish zonations and guilds as the basis for assessment of ecological integrity of large rivers. Hydrobiologia 500:157–178

Anderson KE, Paul AJ, McCauley E, Jackson LJ, Post JR, Nisbet RM (2006) Instream flow needs in streams and rivers: the importance of understanding ecological dynamics. Frontiers in Ecology and the Environment 4:309–318

Annear TC, Hubert W, Simpkins D, Hebdon L (2002) Behavioural and physiological response of trout to winter habitat in tailwaters in Wyoming, USA. Hydrological Processes 16:915–925

Archibald JD (1994) Metataxon concepts and assessing possible ancestry using phylogenetic systematics. Systematic Biology 43:27–40

Arthington AH, Pusey BJ (2003) Flow restoration and protection in Australian rivers. River Research and Applications 19:377–395

Arthington AH, Rall JL, Kennard MJ, Pusey BJ (2003) Environmental flow requirements of fish in lesotho rivers using the drift methodology. River Research and Applications 19:641–666

Arthington AH, Bunn SE, Poff NL, Naiman RJ (2006) The challenge of providing environmental flow rules to sustain river ecosystems. Ecological Applications 16:1311–1318

Ballinger A, Lake PS, Mac Nally R (2007) Do terrestrial invertebrates experience floodplains as landscape mosaics? immediate and longer-term effects of flooding on ant assemblages in a floodplain forest. Oecologia 152:227–238

Beissinger SR (1995) Modeling extinction in periodic environments—everglades water levels and snail kite population viability. Ecological Applications 5:618–631

Beissinger SR, Westphal MI (1998) On the use of demographic models of population viability in endangered species management. Journal of Wildlife Management 62:821–841

Biggs BJF, Nikora VI, Snelder TH (2005) Linking scales of flow variability to lotic ecosystem structure and function. River Research and Applications 21:283–298

Bond NR, Lake PS, Arthington AH (2008) The impacts of drought on freshwater ecosystems: an Australian perspective. Hydrobiologia 600:3–16

Brook BW, O'Grady JJ, Chapman AP, Burgman MA, Akcakaya HR, Frankham R (2000) Predictive accuracy of population viability analysis in conservation biology. Nature 404:385–387

Burgman MA (2000) Population viability analysis for bird conservation: prediction, heuristics, monitoring and psychology. Emu 100:347–353

Cai W, Cowan T (2008) Evidence of impacts from rising temperature on inflows to the Murray-Darling Basin. Geophysical Research Letters 35:L07701

Cai W, Cowan T, Raupach M (2009) Positive Indian Ocean Dipole events precondition southeast Australia bushfires. Geophysical Research Letters 36:L19710

Caswell H (2001) Matrix population models: construction analysis and Interpretation. Sinauer Associates Inc., Massachusetts

Dennis B, Ponciano JM, Lele SR, Taper ML, Staples DF (2006) Estimating density dependence, process noise, and observation error. Ecological Monographs 76:323–341

Doak DF, Morris W (1999) Detecting population-level consequences of ongoing environmental change without long-term monitoring. Ecology 80:1537–1551

Douglas MR, Brunner PC, Douglas ME (2003) Drought in an evolutionary context: molecular variability in Flannelmouth Sucker (*Catostomus latipinnis*) from the Colorado River Basin of western North America. Freshwater Biology 48:1254–1273

Dudgeon D et al (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews 81: 163–182

Fieberg J, Ellner SP (2001) Stochastic matrix models for conservation and management: a comparative review of methods. Ecology Letters 4:244–266

Gippel CJ, Cosier M, Markar S, Liu CS (2009) Balancing environmental flows needs and water supply reliability. International Journal of Water Resources Development 25:331–353

Gleick PH (2003) Global freshwater resources: soft-path solutions for the 21st century. Science 302:1524–1528

Grafton Q (2010) How to increase the cost-effectiveness of water reform and environmental flows in the Murray-Darling Basin. Agenda 17:17–40

Gregory R, Ohlson D, Arvai J (2006) Deconstructing adaptive management: criteria for applications to environmental management. Ecological Applications 16:2411–2425

Growns I (2004) A numerical classification of reproductive guilds of the freshwater fishes of south-eastern Australia and their application to river management. Fisheries Management and Ecology 11:369–377

Guy CS, Brown ML (eds) (2007) Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda

Hamstead M, Baldwin C, O'Keefe V (2008) Water allocation planning in Australia—current practices and lessons learned waterlines occasional paper No 6, April 2008 National Water Commission, Canberra

Hickey JT, Diaz GE (1999) From flow to fish to dollars: an integrated approach to water allocation. Journal of the American Water Resources Association 35:1053–1067

Hodgson DJ, Townley S (2004) Linking management changes to population dynamic responses: the transfer function of a projection matrix perturbation. Journal of Applied Ecology 41:1155–1161

Horne A, Stewardson M, Freebairn J, McMahon TA (2010) Using an economic framework to inform management of environmental entitlements. River Research and Applications 26:779–795

Humphries P, King AJ, Koehn JD (1999) Fish, flows and flood plains: links between freshwater fishes and their environment in the Murray-Darling River system, Australia. Environmental Biology of Fishes 56:129–151

Jones RN (2012) Detecting and attributing nonlinear anthropogenic regional warming in southeastern Australia. Journal of Geophysical Research D: Atmospheres 117

Jowett IG (1997) Instream flow methods: a comparison of approaches. Regulated Rivers-Research & Management 13:115–127

Jowett IG, Duncan MJ (1990) Flow variability in New-Zealand rivers and its relationship to in-stream habitat and biota. New Zealand Journal of Marine and Freshwater Research 24:305–317

King J, Brown C (2006) Environmental flows: striking the balance between development and resource protection. Ecology and Society 11:26

King J, Brown C, Sabet H (2005) A scenario-based holistic approach to environmental flow assessments for rivers. River Research and Applications 21:579

Kingsford RT (2009) Managing Australia's scarce water resources for the environment. Pacific Conservation Biology 15:4–6

Lake PS (2000) Disturbance, patchiness, and diversity in streams. Journal of the North American Benthological Society 19:573–592

Lake PS (2003) Ecological effects of perturbation by drought in flowing waters. Freshwater Biology 48:1161–1172

Lake PS, Bond NR (2007) Australian futures: freshwater ecosystems and human water usage. Futures 39:288–305

Lancaster J, Downes BJ (2010) Linking the hydraulic world of individual organisms to ecological processes: putting ecology into ecohydraulics. River Research and Applications 26:385–403

Lande R, Engen S, Saether BE (2003) Stochastic population dynamics in ecology and conservation. Oxford University Press, Oxford

Landres PB, Morgan P, Swanson FJ (1999) Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications 9:1179–1188

Lester RE, Webster IT, Fairweather PG, Young WJ (2011) Linking water-resource models to ecosystem-response models to guide water-resource planning—an example from the Murray—Darling Basin, Australia. Marine & Freshwater Research 62:279–289

Letcher BH, Nislow KH, Coombs JA, O'Donnell MJ, Dubreuil TL (2007) Population response to habitat fragmentation in a stream-dwelling brook trout Population. PLoS ONE 2(11):e1139

Lindenmayer DB, Likens GE (2009) Adaptive monitoring: a new paradigm for long-term research and monitoring. Trends in Ecology & Evolution 24:482–486

Lytle DA, Merritt DM (2004) Hydrologic regimes and riparian forests: A structured population model for cottonwood. Ecology 85:2493–2503

Lytle DA, Poff NL (2004) Adaptation to natural flow regimes. Trends in Ecology & Evolution 19:94–100

Mac Nally R (1983) On assessing the significance of interspecific competition to guild structure. Ecology 64:1646–1652

Mac Nally R, Fleishman E, Thomson J, Dobkin DS (2008) Use of guilds for modeling avian responses to vegetation change in the Intermountain West (USA). Global Ecology and Biogeography 17:758–769

Mac Nally R, Baker PJ, Cunningham SC, Horner GJ, Thomson JR (2011) Dynamics of Murray-Darling floodplain forests under multiple water stressors—the past, present and future of an Australian icon. Water Resources Research

Magalhaes MF, Beja P, Schlosser IJ, Collares-Pereira MJ (2007) Effects of multi-year droughts on fish assemblages of seasonally drying Mediterranean streams. Freshwater Biology 52:1494–1510

Marcot BG, Steventon JD, Sutherland GD, McCann RK (2006) Guidelines for developing and updating Bayesian belief networks applied to ecological modeling and conservation. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 36:3063–3074

Merritt DM, Scott ML, Poff NL, Auble GT, Lytle DA (2010) Theory, methods and tools for determining environmental flows for riparian vegetation: riparian vegetation-flow response guilds. Freshwater Biology 55:206–225

Milly PCD, Wetherald RT, Dunne KA, Delworth TL (2002) Increasing risk of great floods in a changing climate. Nature 415:514–517

Milly PCD, Betancourt J, Falkenmark M, Hirsch RM, Kundzewicz ZW, Lettenmaier DP, Stouffer RJ (2008) Climate change—stationarity is dead: whither water management? Science 319:573–574

Milner NJ, Elliott JM, Armstrong JD, Gardiner R, Welton JS, Ladle M (2003) The natural control of salmon and trout populations in streams. Fisheries Research 62:111–125

Morris WF, Doak DF (2002) Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates Inc., Massachusetts

Morris WF, Bloch PL, Hudgens BR, Moyle LC, Stinchcombe JR (2002) Population viability analysis in endangered species recovery plans: past use and future improvements. Ecological Applications 12:708–712

Noble RAA, Cowx IG, Goffaux D, Kestemont P (2007) Assessing the health of European rivers using functional ecological guilds of fish communities: standardising species classification and approaches to metric selection. Fisheries Management and Ecology 14:381–392

Palmer MA, Liermann CAR, Nilsson C, Florke M, Alcamo J, Lake PS, Bond N (2008) Climate change and the world's river basins: anticipating management options. Frontiers in Ecology and the Environment 6:81–89

Parsons M, McLoughlin CA, Kotschy KA, Rogers KH, Rountree MW (2005) The effects of extreme floods on the biophysical heterogeneity of river landscapes. Frontiers in Ecology and the Environment 3:487–494

Petts GE (1996) Water allocation to protect river ecosystems. Regulated Rivers-Research & Management 12:353–365

Petts GE (2009) Instream flow science for sustainable river management. Journal of the American Water Resources Association 45:1071–1086

Poff NL, Zimmerman JKH (2010) Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. Freshwater Biology 55:194–205

Poff NL, Allan JD, Bain MB, Karr JR, Prestegaard KL, Richter BD, Sparks RE, Stromberg JC (1997) The natural flow regime. BioScience 47:769–784

Poff NL, Allan JD, Palmer MA, Hart DD, Richter BD, Arthington AH, Rogers KH, Meyers JL, Stanford JA (2003) Fiver flows and water wars: emerging science for environmental decision making. Frontiers in Ecology and the Environment 1:298–306

Resh VH, Brown AV, Covich AP, Gurtz ME, Li HW, Minshall GW, Reice SR, Sheldon AL, Wallace JB, Wissmar RC (1988) The role of disturbance in stream ecology. Journal of the North American Benthological Society 7:433–455

Richter BD, Baumgartner JV, Wigington R, Braun DP (1997) How much water does a river need? Freshwater Biology 37:231–249

Richter BD, Mathews R, Wigington R (2003) Ecologically sustainable water management: managing river flows for ecological integrity. Ecological Applications 13:206–224

Root RB (1967) Niche exploitation pattern of blue-gray gnatcatcher. Ecological Monographs 37:317

Saintilan NOI (2010) Ecosystem response modelling in the murray-darling basin. CSIRO, Australia

Sakaris PC, Irwin ER (2010) Tuning stochastic matrix models with hydrologic data to predict the population dynamics of a riverine fish. Ecological Applications 20:483–496

Schlosser IJ, Angermeier PL (1995) Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. Evolution and the Aquatic Ecosystem: Defining Unique Units in Population Conservation 17:392–401

Schodelbauerova I, Tremblay RL, Kindlmann P (2010) Prediction vs. reality: can a PVA model predict population persistence 13 years later? Biodiversity and Conservation 19:637–650

Shenton W, Hart BT, Brodie J (2010) A Bayesian network model linking nutrient management actions in the Tully catchment (northern Queensland) with Great Barrier Reef condition. Marine & Freshwater Research 61:587–595

Simons M, Podger G, Cooke R (1996) IQQM—a hydrologic modelling tool for water resource and salinity management. Environmental Software 11:185–192

Smith M, Caswell H, Mettler-Cherry P (2005) Stochastic flood and precipitation regimes and the population dynamics of a threatened floodplain plant. Ecological Applications 15:1036–1052

Stewardson MJ, Gippel CJ (2003) Incorporating flow variability into environmental flow regimes using the flow events method. River Research and Applications 19:459–472

Tennant WA, Bitterman ME (1975) Blocking and overshadowing in 2 species of fish. Journal of Experimental Psychology 104:22–29

Tharme RE (2003) A global perspective on environmental flow assessment: emerging trends in the development and application of environmental flow methodologies for rivers. River Research and Applications 19:397–441

Tibby J, Tiller D (2007) Climate-water quality relationships in three Western Victorian (Australia) lakes 1984–2000. Hydrobiologia 591:219–234

Todd CR, Ryan T, Nicol SJ, Bearlin AR (2005) The impact of cold water releases on the critical period of post-spawning survival and its implications for Murray cod (*Maccullochella peelii peelii*): a case study of the Mitta Mitta River, southeastern Australia. River Research and Applications 21:1035–1052

Van Winkle W, Rose KA, Winemiller KO, DeAngelis DL, Christensen SW, Otto RG, Shuter BJ (1993) Linking life history theory, environmental setting, and individual-based modeling to compare responses of different fish species to environmental change. Transactions of the American Fisheries Society 122:459–466

Vesk PA, Dorrough JW (2006) Getting trees on farms the easy way? lessons from a model of eucalypt regeneration on pastures. Australian Journal of Botany 54:509–519

Vogel RM, Fennessey NM (1995) Flow duration curves.2. A review of applications in water-resources planning. Water Resources Bulletin 31:1029–1039

Vörösmarty CJ, Green P, Salisbury J, Lammers RB (2000) Global water resources: vulnerability from climate change and population growth. Science 289:284–288

Vörösmarty CJ et al (2010) Global threats to human water security and river biodiversity. Nature 467:555–561

Welcomme RL, Winemiller KO, Cowx IG (2006) Fish environmental guilds as a tool for assessment of ecological condition of rivers. River Research and Applications 22:377–396

Winemiller KO, Rose KA (1992) Patterns off life-history diversification in North American fishes: implications for population regulation. Canadian Journal of Fisheries and Aquatic Sciences 49:2196–2218

Xu CL, Letcher BH, Nislow KH (2010) Size-dependent survival of brook trout *Salvelinus fontinalis* in summer: effects of water temperature and stream flow. Journal of Fish Biology 76:2342–2369

Yen J, Shenton W, Bond NR, Spring DA, Mac Nally R (in review) Identifying robust water-management strategies in variable climates: a Bayesian demographic modelling approach