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Modelling population responses to flow: The development of a generic fish population model

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ABSTRACT

Many fish species are dependent upon flows to trigger breeding, facilitate high recruitment of offspring, and to maintain adult survival rates. Understanding how fish populations respond to different flow regimes is important in regulated waterways as subtle changes in regimes have the potential to influence both fish breeding and survival. In this paper, we describe an age-structured population response model that explores how quantitative changes in the flow regime can lead to changes in fish population size and structure through time. We use three large bodied fish species (golden perch, Murray cod and the invasive common carp) from the mid Murray River near Barmah-Millewa Forest to explore the possible responses to the observed flow regime over a 30-year period. The model links flow volumes, seasonality, temperature and rates of fall to the fecundity and survival rates for the different fish species to project population change through time.

1. Introduction

Many freshwater fish species are reliant upon particular flow conditions to trigger breeding and to facilitate survival of both adults and their offspring (Mims and Olden, 2012b). River regulation affects the timing, frequency and magnitude of flows and the resulting flow regime has the potential to change both fish population structure and species diversity (Bunn and Arthington, 2002; Humphries et al., 2007; Poff and Zimmerman, 2010). In Australia's highly regulated Murray-Darling Basin, the Basin Plan (Murray-Darling Basin Authority, 2012) establishes objectives to optimise social, economic and environmental outcomes arising from the use of Basin water resources in the national interest. To manage regulated rivers effectively for environmental outcomes, we need to understand and assess how different aspects of an ecosystem respond to different flow regimes. Fish represent one component of a complex ecosystem and are a target outcome under the Basin Plan. Methods that allow us to assess changes in fish populations can provide useful inputs into the decision-making process for water managers.

Modelling can be an important tool in understanding how systems respond to change (Beissinger et al., 2006; Jeschke and Strayer, 2008; Addison et al., 2013) and can be used in management to provide transparency by maintaining consistency between assessments (Noon and McKelvey, 1996; Addison et al., 2013). While many ecological modelling approaches exist, population response modelling, incorporating aspects of species ecology and life history, is considered an important modelling tool in river management (Shenton et al., 2012). For fish, population response modelling provides a number of benefits, these include: (1) explicitly representing temporal processes, including the environmental time series; (2) improved understanding of the time lags associated with fish growth, and; (3) development, and allowing extrapolation of long-term changes from what is known from short-term processes and responses (Crone et al., 2011; Shenton et al., 2012).

To improve understanding of how different drivers impact on populations requires associating different vital rates with specific environmental variables. Creating associations between these different vital rates with realistic temporal patterns of the environmental variables is referred to as environmental-state methods. This approach has been successfully used across a variety of plants (Crone et al., 2011) and animals (Beissinger, 1995; Sakaris and Irwin, 2010). For fish, Yen et al. (2013) undertook a similar approach for the assessment of fish population response to flow conditions in the Broken River. Yen et al. (2013) used input environmental time-series based upon Markov-chain transition probabilities. The Marcov states represent conditional hydrological states under plausible future flow scenarios. This approach overcomes the assumptions that past environmental conditions are going to be representative

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of future conditions, explicitly accounts for environmental variability and autocorrelation within the time-series and enables an assessment of uncertainty associated with future predictions in environmental conditions (Bearlin et al., 2002; Shenton et al., 2012). We build upon these methods and provide a population response model that incorporates and considers multiple flow attributes including flow volumes, timing and temperature of a daily flow time series. Daily flow and temperature files are used directly as model inputs allowing scenario analysis to be undertaken with relative ease and the model to be used within an integrated assessment framework based upon river system or basin modelling.

Within the Australian context, the Murray-Darling Basin contains fish species with a wide range of ecological and life history characteristics (Humphries et al., 1999; Baumgartner et al., 2014). A number of fish population models have been developed to understand species responses for Murray-Darling Basin fish species including the Murray cod (Todd et al., 2005; Yen et al., 2013), trout cod (Todd et al., 2004), carp gudgeon (Perry and Bond, 2009; Yen et al., 2013), golden perch (Yen et al., 2013) and common carp (Brown and Walker, 2004; Forsyth et al., 2013). These models utilise different variations on population modelling including purely stochastic viability assessments, environmental-state methods, continuous time models and individual based models. These model types are founded on different modelling principles, different ecological conceptualisations of the system and also require different data for parameterisation, but ultimately explore how each species responds to environmental drivers.

In this paper, we describe the development and parameterisation of an environmental-state population response model that incorporates flow and water temperature as environmental input variables for modelling fish populations. While flow is recognised as an important driver for population processes, co-occurring warm temperature and high flows are recognised as important in providing suitable environmental conditions for enhancing fish population response (Rolls et al., 2013). Enhanced population responses can occur through increased spawning or survival associated with the suitable environmental conditions including timing and magnitude of flows. Linking fish demographic processes to environmental variables allows us to explore how different flow regimes influence different fish species with different ecological and life history characteristics. To assess the robustness of the model we have parameterised the model for Murray cod, golden perch and common carp and used observed time series data from down-stream of Yarrawonga Weir (located upstream of Barmah-Millewa Forest) to demonstrate the different responses to flow conditions. The model parameterisation draws on a diverse range of data sources presented in the peer-reviewed literature and uses the different ecological traits of these species to provide a mechanism for evaluating the likely population structure associated with different periods of the historical environmental time series. The goal of this paper is to describe a model that can be used in broader hypothesis testing about how different fish species respond to different environmental conditions.

2. Materials and methods

2.1. Study site

We selected a section of the Murray River downstream of Yarrawonga Weir and upstream of the township of Echuca in south-eastern Australia as our demonstration reach. This reach includes the Barmah-Millewa floodplain (including Barmah and Millewa forests) hereafter referred to as the mid-Murray region. The mid-Murray river has been identified as an important regional source of fish recruitment, and has been the focus of the number of studies on fish ecology (Brown et al., 2003; King et al., 2007, 2009; Macdonald and Crook, 2014). Flows in the mid-Murray are regulated due to Yarrawonga weir and Hume Dam controlling flow throughout most of the year. River flows increase when water is delivered for seasonal agricultural production from upstream storages and in association with natural flooding events. While river regulation can change many aspects of the flow regime, changes in the timing and magnitude of flood events are among the most significant for maintaining ecological integrity (Poff et al., 1997). These changed flow conditions create a disjunct between the current and the historical flow regimes of the river and can have implications for ecological processes and species (Poff and Zimmerman, 2010; Mims and Olden, 2012a). Within the mid-Murray river region around Barmah-Millewa Forest, water releases for the environment have been primarily targeted at river red gum floodplain communities and water bird breeding sites. This is in part due to a comparatively higher level of understanding of the flow requirements of both water birds and river red gums (King et al., 2009; Koehn et al., 2014).

2.2. Fish species

2.2.1. Golden perch

Golden perch are broadly recognised as 'flow dependent specialists' and are considered sensitive to characteristics of the flow regime for triggering breeding responses (Humphries et al., 1999; Lintermans, 2007; Vilizzi, 2012; Baumgartner et al., 2014). While this species spawns under a broad range of flow conditions including rising river flows, fluctuations around discharges at steady bank full flows and floodplain inundation, flow is considered important for triggering breeding (King et al., 2009; Zampatti and Leigh, 2013b; Koehn et al., 2014). Golden perch are a highly fecund species with gravid females having in excess of 300 000 eggs (Growns, 2004; Yen et al., 2013), and accordingly, larval and juvenile survival rates are considered to be low. Females of the species can reach maturity at 3 years and have a maximum longevity of approximately 25 years (Growns, 2004; Yen et al., 2013).

2.2.2. Murray cod

The Murray cod is an iconic species of the Murray-Darling Basin (MDB) and is listed as a vulnerable species under the Commonwealth Environment Protection and Biodiversity Conservation Act 1999. Studies of Murray cod provide strong evidence that the species does not require either high flows or changes in river discharges to initiate spawning events (Humphries, 2005; Koehn and Harrington, 2006; Vilizzi, 2012). However, recruitment pulses and increased abundance of young-of-year have been associated with years with favourable flow conditions (Ye et al., 2000; Kearney and Kildea, 2001; King et al., 2009). The mechanisms driving high survival to recruitment in Murray cod are not fully understood, however nutrient exchange and increases in the complexity have been put forward as plausible explanations (King et al., 2009; Koehn et al., 2014).

The Murray cod is a large, highly fecund and long-lived species with females of the species able to reach maturity at 4–5 years and have a maximum longevity of up to 60 years (Todd et al., 2005). Both the Murray cod and the Golden perch are recognised as in-channel specialists that do not directly utilise the inundated floodplain for either spawning or rearing. Additionally, individuals of both Murray cod and golden perch also make migrations of considerable distance upstream to spawn (Humphries et al., 1999; King et al., 2003; Mallen-Cooper and Stuart, 2003; Leigh and Zampatti, 2013).

2.2.3. Common carp

The introduced common carp are now ubiquitous throughout