



Multi-species response to rapid environmental change in a large estuary system: A biochronological approach



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ABSTRACT

The sensitivity of species to environmental change is dependent on their ecological requirements (i.e. specialist v. generalist), and hence likely to be species-specific. Identifying species level variation in environmental sensitivity informs assessments of community vulnerability and assists in developing adaptive management strategies. We investigated species-specific sensitivity in fish to understand the vulnerability of differing life histories and ecological requirements to rapid environmental alteration (i.e. drought). Biochronologies of fish growth, based on increment widths in otoliths, were analysed using a mixed modelling approach. We assessed multi-decadal responses in fish growth to environmental variation in the terminal system of Australia's largest river, for three long-lived fish species with differing life histories and ecological requirements: a freshwater specialist and two estuarine generalists. Biochronologies were between 20 and 38 years long, spanned a decade of severe drought and showed considerable inter-annual variation in growth. Precipitation influenced the growth of the obligate freshwater specialist, *Macquaria ambigua ambigua*. Temperature and salinity influenced the growth of the two estuarine generalists: *Argyrosomus japonicus* (estuarine opportunist) and *Acanthopagrus butcheri* (estuarine dependent), respectively. These results suggest that generalisations about how species respond to environmental change may mask species-specific responses to dependent on the constraints of their ecological requirements (i.e. specialist v. generalist). These findings also highlight the importance of considering the diversity of life history strategies that inhabit an ecosystem when developing conservation and management strategies.

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1. Introduction

Species respond to environmental change by shifting distributional patterns, altering phenological cycles and physiology (Parmesan 2006). Yet, when environmental alteration occurs at rates that exceed the capacity of species to respond, those species

may be at risk to localised extinctions (Rountrey et al., 2014). However, it may be inappropriate to assume that all species will respond in a similar manner to a shared stressor, since the capacity of species to alter their biological processes will in part be dependent on their ecological requirements (e.g. specialist v. generalist). Therefore, environmental sensitivity is likely to be species-specific (Roessig et al., 2004; Cheung et al., 2009; Last et al., 2011), with specialised species considered more vulnerable to change (Swihart et al., 2003; Thuiller et al., 2005; Dawson et al., 2011). We define 'environmental sensitivity' as the degree of modification that a species will undergo in response to changing environmental conditions. 'Sensitive' species will drastically alter their distributional range or biological processes (i.e. growth), and conversely, 'insensitive' species will display a minor shift in their distribution or biology when exposed to environmental fluctuation. Identifying and understanding how specialisation affects the environmental sensitivity of

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species informs assessments of vulnerability and assists in developing adaptive management strategies (Brander 2007; Rowland et al., 2011).

The environmental sensitivity of species has largely been defined in terms of changes in species distributions (VanDerWal et al., 2013; Rountrey et al., 2014), with distributional shifts widely demonstrated in a range of fish species (e.g. Perry et al., 2005; Last et al., 2011). Populations can also alter their biological processes in response to environmental change (e.g. growth, reproduction and productivity: Roessig et al., 2004; Doney et al., 2012), which may occur over relatively rapid (decadal) time scales (see Scheffer et al., 2001; Folke et al., 2004). Relative shifts in biological parameters, such as growth rates or population abundance, can be measured through time using ecological time series. These time series provide context for individual or population level responses to environmental change, as well as informing predictive modelling (Jackson et al., 2001). In the absence of direct measurements of ecological data, proxies may be used to provide indirect measures of change through time, with tree-rings and bivalve shells augmenting time series over decadal and centennial time scales (e.g. Black 2009; Black et al., 2014). Otolith biochronologies are based on variation in growth increment widths and provide a proxy of somatic fish growth by quantifying the direction (i.e. either positive or negative) and magnitude of inter-annual deviations in the net growth of many individuals through time (Thresher et al., 2007; Morrongiello et al., 2012; Rountrey et al., 2014). Given that otolith biochronologies allow the relative influences of biological, temporal and environmental factors on population growth to be partitioned (Morrongiello et al., 2012), the sensitivity of a species to one or more key environmental parameters may be explored (Rountrey et al., 2014).

We investigated species-specific sensitivity in otolith growth (width of growth increments) of fish species from the terminal system of Australia's largest river, the River Murray lakes and estuary. Three endemic Australian fish species were selected, with contrasting ecological requirements and life history strategies: *Macquaria ambigua ambigua* (Richardson 1845) (freshwater obligate; completing their life cycle in freshwater), *Acanthopagrus butcheri* (Munro, 1949) (estuarine dependent; spawning in estuaries, but found in marine and fresh waters), and *Argyrosomus japonicus* (Temminck and Schlegel 1843) (estuarine opportunist; regularly entering estuaries via coastal waters) (Brookes et al., 2015; Potter et al., 2015). The latter two species were considered 'generalists' due to their ability to use a range of salinity habitats in a species-specific manner (Ye et al., 2013; Brookes et al., 2015), whereas the flow-dependent freshwater obligate *M. ambigua ambigua* was regarded as a 'specialist' species (Humphries et al., 1999). We quantified inter-annual variation in the width of annual otolith growth increments as a proxy of somatic growth, including a period that encompassed the lowest recorded rainfall in southeast Australia (van Dijk et al., 2013). We hypothesized that the specialist species would show greater growth response compared to the more generalist species, implying a greater degree of environmental sensitivity. Our approach also identified specific environmental correlates of growth, which were expected to differ among species due to their differing environmental requirements and life history strategies.

2. Materials and methods

2.1. Study site and sample collection

The River Murray lakes and estuary ecosystem forms the interface between the River Murray and the Indian Ocean, and prior to

the construction of multiple barrages in 1940 included freshwater rivers, brackish lakes and marine lagoons. After barrage construction, the River Murray lakes became a predominantly freshwater system, and the remnant estuary is now restricted to the area below the barrages (Ferguson et al., 2013). Southeast Australia experienced a decadal period (1997–2010) with the lowest recorded rainfalls on record, known as the Millennium Drought (van Dijk et al., 2013), which resulted in a shift in the environmental conditions within the River Murray lakes and estuary over a short time period (i.e. months). These shifts include, reductions in lake and lagoon water levels and the subsequent loss of habitat, a reduction in freshwater derived nutrients, and hypersaline conditions (Mosley et al., 2012; Brookes et al., 2015).

2.2. Otolith preparation and increment interpretation

Fish were collected for two research projects undertaken by the South Australian Research and Development Institute (Aquatic Sciences) in the River Murray lakes and estuary and coastal waters adjacent to the Murray Mouth (Table 1). Fish were obtained (i) using multi-panel gill nets (stretched mesh sizes: estuary, 40, 50, 70, 113 and 153 mm); (ii) from stock assessment surveys of commercial net catches collected for the purposes of stock assessment or fish condition monitoring (stretched mesh sizes: freshwater, > 50 mm; estuary, > 115 to ≤ 150 mm; marine, > 120 mm); and (iii) from recreationally line caught fish.

Otolith preparation was similar for all species and sampling periods. Otoliths were embedded in epoxy resin and thin-sectioned through the primordium. Sections were mounted onto microscope slides for increment interpretation under a stereo-microscope with a transmitting light source. Otolith increment widths were measured using the Image Pro-Plus v6.0 software package (Media Cybernetics Inc.). For all species, an annual increment was defined as a pair of translucent and opaque bands. Increment widths were measured along a standardised growth axis from the otolith primordium to the marginal edge, with measurements taken from the outer edges of the opaque bands. *Argyrosomus japonicus* and *M. ambigua ambigua* increments were measured by one reader (CI) and *A. butcheri* by a second, single reader (ZAD). The first year of growth and the marginal increment were excluded from the analyses for all samples, as these increments may not represent a complete growth season. All otoliths used in this study had previously been aged by highly experienced otolith readers, and the ages provided allowed us to verify our increment counts.

For all species, the annual periodicity of growth increment formation had been previously validated (Table 1), enabling the development of annually resolved biochronologies as well as facilitating matching of growth time series among individuals collected at different times. In addition, allometric relationships between otolith and somatic growth have been estimated for these species (Table 1). Since somatic growth and otolith growth are proportional, we assumed that otolith increment widths provided a suitable proxy for somatic growth, and all subsequent reference to 'growth' pertains to otolith growth.

Species-specific growth years were based on the timing of increment formation (Table 1), with *Year* categorised as the start of the year of formation (e.g. for increment spanning 1999/2000 calendar years: $Year = 1999$). Individual growth increments were assigned a *Year* through counting back relative to the date and age of capture (following Weisberg et al., 2010). To ensure detection of an adequate temporal signal, annual growth years represented

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