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Fish body condition and recruitment success reflect antecedent flows in an Australian dryland river

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Abstract In fluctuating aquatic environments such as intermittent streams, fish condition is often highly variable due to the associated fluctuating levels of food resources. Having the physiological capacity to both metabolise and catabolise lipids, fish can survive through droughts and rapidly gain condition during flows and floods. Dryland rivers continuously cycle through periods of boom and bust due to their intermittent patterns of rainfall and flow. To help gain an understanding of how fish respond physiologically to varying antecedent flow conditions, we examined body condition measured by percent tissue water content of two generalist fish species in an Australian dryland river. We predicted that fish would be in better condition following recent flows and poorer condition when there had been no recent flows. Our expectations were met for both species with low water tissue content after high flows and high tissue water content after significant drying. It was also found that strong juvenile recruitment was also evident when body condition was high, indicating that when there are food resource spikes driven by flow pulses fish can utilise resources both to produce offspring and to store as lipid for future survival.

Keywords Fish condition · Antecedent hydrology · Flow variability · Recruitment

Introduction

Fish living in variable environments need flexible ecological traits to profit from periods of abundant food and habitat resources and to maintain populations when such resources become limited. Such traits include the physiological capacity to compartmentalise and utilise energy reserves in response to changes in background resource levels. Dryland rivers typically cycle through boom and bust productivity cycles, with the bust phase often protracted. During the boom periods, floodplains are inundated and fish are able to capitalize on the massive increase in productivity relative to low-productivity, no-flow conditions. The subsidies provided by floodplain production are used by fish to breed and grow, stored for future survival through future resource-poor periods and fuel significant in-waterhole productivity during no-flow periods [1–3]. During bust periods when resources are low, as occurs during protracted dry spells, fish must sustain themselves on low-quality food items [2] and utilise stored energy to enable them to make it through to the next boom.

It would be expected that feeding during booms on highly nutritious and abundant floodplain food sources

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would translate to a fish assemblage dominated by fish in high condition (e.g. high fat or energy reserves), thereby enhancing their ability to disperse and colonize newly inundated waterholes and reproduce in those habitats. At the other hydrological extreme, during extended drought, the health of those survivors will influence both their ability to reproduce to enable sufficient recruits to survive until the next flood, or be in a condition themselves to capitalize on flood. At such points in time, fish would be expected to be in poor condition with little stored fat. Given that intermittent streams naturally cycle through boom and bust periods, it is therefore important to understand the mechanisms that fish within these systems use to maintain viable populations. These mechanisms will involve both behavioural adaptations, such as a propensity to migrate and exploit new resources as they become available, and physiological responses, such as being able to store energy reserves in good times and metabolise these reserves during lean times to enable survival.

Fish condition is a common measure used to determine fish well-being or robustness, by assuming that, the higher the condition of a fish, the greater its energy reserves and food resources available to it, as well as implying the relative productivity of its environment [4]. Lipid reserves and their dynamics are considered to be of particular importance in deducing fish condition [5]. For most fish species the determination of either water or lipid/protein fractions serves to determine the fraction of the other [6]. In such cases, water is negatively correlated with both lipid and protein [7]. Hence, fish in good condition will have high lipid and low water content, whereas fish in poor condition will have low lipid and high water content.

In the northern Murray Darling Basin (MDB), rainfall and runoff are highly variable and unpredictable, such that many rivers exist as strings of disconnected waterholes apart from times of irregular flow. Fish living within these “dryland rivers” maintain populations through prolonged periods of zero flow (bust) by means of resistance traits and low-flow recruitment processes [1, 8]. During periods of flow (boom) they rely on connectivity among waterholes to maintain populations through movement and recruitment processes [8–11]. To gain an understanding of how resident fish respond physiologically to varying types of antecedent hydrology in such dryland rivers we examined fish condition over a period of 12 months in the Moonie River, northern MDB (see [12] for study site/region description). This period covered a range of antecedent hydrological conditions, including recent flows after an earlier wet period, significant drying and a small flow after extended dry. We examined body condition (tissue water content) of two generalist native fish species.

Based on the boom and bust ecology of fish in intermittent dryland rivers we tested the following hypothesis: fish condition will be reflective of antecedent flow conditions, whereby fish will be in better condition (lower water content) associated with recent flow and the converse with extended dry periods.

Materials and methods

The mean daily discharge at the Nindigully gauge (Fig. 1) covers a 27-month interval including the study period. Fish were first sampled in February 2006, immediately after the cessation of a small flow in the system and 6 weeks after a minor flood in late 2005 (Fig. 1). Waterholes were full (i.e. at cease to flow level) but hydrologically disconnected. The next sampling occasions were in May and September 2006 during the progression of a dry spell in the Moonie River (Fig. 1). In May, sampling occurred 3 months after the last flow event in the system. Waterholes were disconnected and drying, with an average loss of depth from full of 50 cm, due to evaporation, seepage and transpiration. By September, waterholes had been drying for 7 months, and on average, water levels in sampled pools had fallen to 80 cm below full. This dry spell continued until mid-November with water levels falling to an average of 1 m below full and some pools almost dry. The final sampling occasion, late January 2007 was during the falling arm of a small flow (maximum discharge 6.7 $m^3 s^{-1}$), the second of the season following an event in December 2006 which had filled and connected the waterholes (Fig. 1). At the time of sampling, waterholes were above ‘cease to flow’, but flow had decreased to a trickle.

The fish assemblages within each of fifteen waterholes were sampled using the same sampling protocol as per [13] to provide size–structure (fish lengths) and where possible a sub-sample of individuals for body condition analyses of two generalist species in the Moonie River waterholes [12].

The two species chosen for condition analyses were selected to represent different trophic levels in the food web. *Nematolosa erebi* (bony bream) is a moderately sized clupeid and arguably the most widespread of all dryland fish species in Australia [14]. *N. erebi* displays strong tolerance to a range of environmental extremes [14], an opportunistic reproductive strategy [11] and dietary plasticity [12], and given these adaptations, often achieves high biomass in isolated waterhole environments. This species is primarily a detritivore/algivore, consuming variable amounts of microbenthic algae, and therefore may respond significantly to changes in primary production [15].

Macquaria ambigua (yellowbelly) is a moderate to large percichthyid, commonly growing to 400–500 mm and less than 5 kg. *M. ambigua* is also widespread and abundant in isolated waterholes of Australian dryland rivers, with a suite of evolutionary adaptations that allow it to cope with

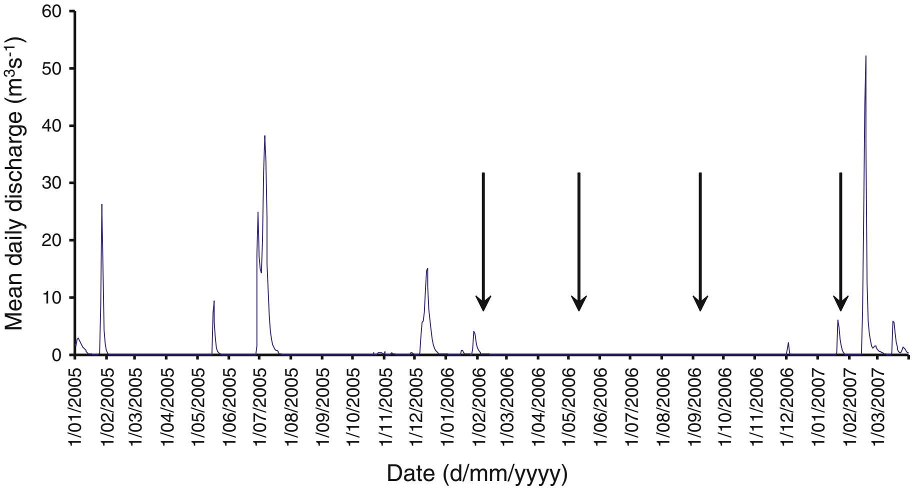

Fig. 1 Mean daily discharge at Nindigully gauge between January 2005 and March 2007. *Arrows* indicate sampling occasions of this study

a range of environmental conditions present in these types of habitats [1, 10]. This indiscriminate carnivore sits at the highest trophic position in isolated waterholes of dryland rivers and therefore is likely to show a strong response to the cascading effects of limited bottom–up production in these environments.

To gain an understanding of the potential recent histories of the fish assemblages on each occasion, we needed an indication of the potential influence on abundances due to juvenile recruitment, migration in and out of waterholes and potential die-offs within waterholes. In this way we try to get a snapshot of the potential recent changes in resource levels that fish may have been through between sampling occasions, such as poor resources leading to die-offs or spikes in resources leading to strong recruitment. To achieve this we examined the size structure (using standard length) of all individuals of both *N. erebi* and *M. ambigua* on all four sampling occasions using fyke net data from fish measured for standard length (SL) in millimetres. Fish were grouped into 25-mm increments for each size class to look for changes in size structure and abundance resulting from recruitment, potential migration and death.

Laboratory procedures

We had initially intended to retain a sub-sample up to five medium-sized *M. ambigua* and *N. erebi* individuals (between 60 and 150 mm SL) from every waterhole on all four sampling occasions, but lower than expected catches did not allow this. The numbers of fish retained (and waterholes collected from) for condition analyses across the four sampling occasions were 61 (14), 79 (14), 42 (10) and 43 (9) for *N. erebi* and 41 (13), 114 (7), 18 (12) and 78 (13) for *M. ambigua*. All samples were aggregated per sampling time, and we only undertook a temporal analysis of body condition. Retained fish were killed in an ice slurry [16] and frozen on-site for laboratory analysis in accordance with animal ethics procedures.

In the laboratory, fish were thawed, standard length was measured, and they were weighed to the nearest 0.01 g. The gonads and gut contents were removed from each fish and weighed. Final wet weights of fish (W_w) were calculated for water content analysis by subtracting gonad and gut content weight from intact fish weights. Fish were then freeze-dried in a Virtis bench-top freeze dryer at −55 °C. Following drying, fish were re-weighed to the nearest 0.01 g (W_D). Tissue water content (TWC %) was calculated as $TWC = [(W_w - W_D)/W_w] \times 100$.

Analyses

The main aim of this study is to investigate changes in fish condition through time. We expected that condition was likely to be affected by fish size [17]. So, to test the effect of time on fish condition, we used analysis of covariance (ANCOVA) with sampling occasion as a fixed effect and fish standard length as a covariate using Systat 11.00.01 for Windows [18]. To meet the assumptions of ANCOVA we tested for heterogeneity of slopes between the covariate and water content among the four sampling occasions as per [19]. Tukey honestly significant difference (HSD) post hoc tests were used to establish the nature of any differences in fish condition among each possible pair of sampling occasions. Statistical significance was accepted at $P \leq 0.05$ for all analyses.

Results

The size structure of both *N. erebi* and *M. ambigua* showed evidence of changes in the population through time (Fig. 2), most likely resulting from a combination of recruitment, movement and deaths [8].

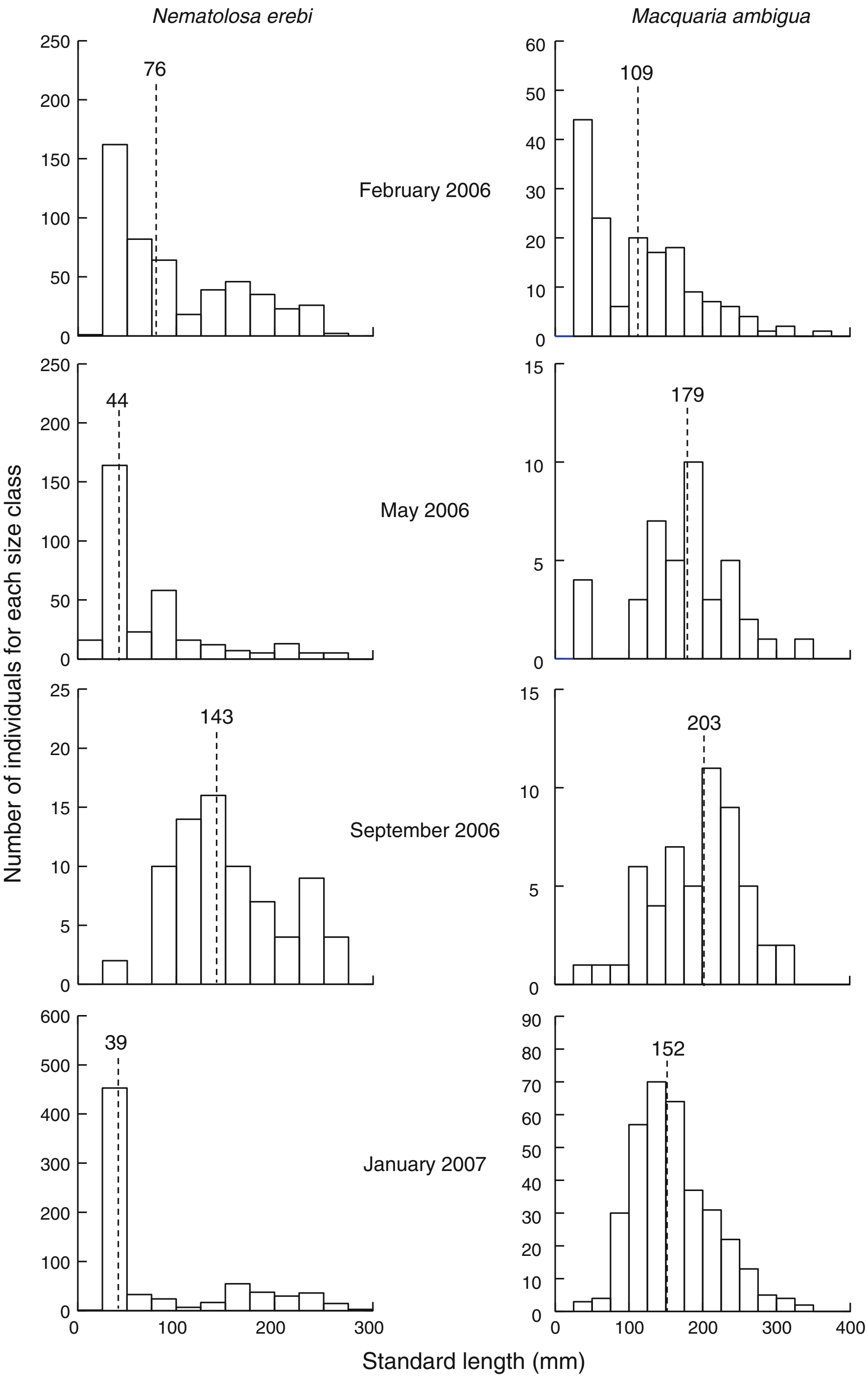

Fig. 2 Length–frequency plots for *Nematolosa erebi* (*left panel*) and *Macquaria ambigua* (*right panel*) from fifteen waterholes of Moonie River, collected on four sampling occasions using fyke net data only

The *N. erebi* population was initially dominated by juvenile fish (February 2006), with approximately 50 % of the assemblage being <100 mm SL. A new cohort of recruits were apparent in May 2006, with about 60 % of the assemblage being <50 mm SL (Fig. 2). In September 2006, the size structure had increased, with the median length increasing from 44 to 143 mm SL and approximately 65 % of fish ranging between 75 and 175 mm SL. This suggests a large die-off of the recruits that were evident in the previous sampling occasion and additionally a proportion of larger-bodied animals given the large reduction in total numbers. There was again a new cohort of fish recruits in January 2007, with approximately 65 % of fish being in the 25–50 mm size class and the median length of the assemblage being 39 mm SL.

Table 1 Summary of ANCOVA results comparing the condition (% water content) of *M. ambigua* and *N. erebi* in waterholes across four sampling occasions between February 2006 and January 2007 in the Moonie River

Dependent variable	Source	*df*	MS	*F* ratio	*P*	Significant pairwise differences
N. erebi condition	Time	3	41.54	18.68	<0.001	**1**v3, **2**v3, 3v**4**
	Length	1	138.4	62.24	<0.001	
	Error	220	2.223			
M. ambigua condition	Time	3	18.44	17.47	<0.001	**1**v2, **1**v3, **1**v4
	Length	1	163.1	154.5	<0.001	
	Error	143	1.055			

Note: Sampling occasions: 1, February 2006; 2, May 2006; 3, September 2006; 4, January 2007. For significant pairwise comparisons, bold sampling occasion indicates significantly better condition (lower water content)

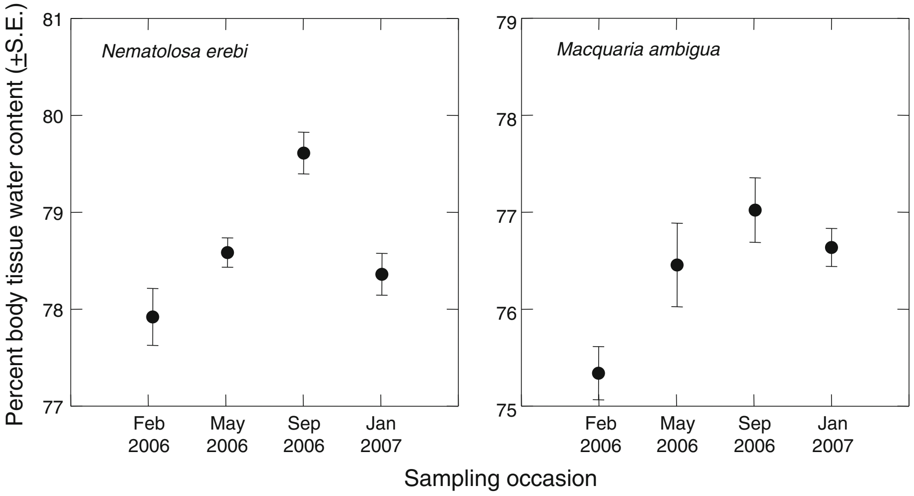

Fig. 3 Mean (±standard error, SE) of fish body condition for *N. erebi* and *M. ambigua* across four sampling occasions in Moonie River waterholes

The size structure of *M. ambigua* showed that the population was smallest in February 2006 (median 109 mm) then increased through to May (median 179 mm) and September 2006 (median 203 mm). This indicates a relatively stable assemblage through the first three sampling periods with some fish die-offs as evidenced by reduced abundances and, additionally, others growing out through that time. There was also some limited recruitment of juveniles (<100 mm SL) into the population and potentially some movement of large-bodied individuals into the sampled waterholes owing to the decrease in median length (152 mm SL) combined with an increase in total abundance from September to January 2007 (Fig. 2). Across all sampling times there tended to be a more even spread of length classes for *M. ambigua* than for *N. erebi*, except in February 2006 where about 45 % of the assemblage was <75 mm SL (Fig. 2).

Analysis of covariance revealed significant variation in TWC through time for both *N. erebi* and *M. ambigua* individuals, while standard length covaried significantly through time with TWC for both species (Table 1). Pairwise comparisons revealed that, for both species, fish condition on one sampling occasion was significantly different from all other sampling times. For *N. erebi*, fish were significantly in poorest condition (high water content) in September 2006, compared with the other three sampling times (Fig. 3). This poor condition of *N. erebi* coincided with the drying phase of the Moonie River, where waterholes had been disconnected and drying for 7 months (Fig. 1). *M. ambigua* individuals were significantly fatter (low water content) in February 2006 compared with all other sampling times. This period represents the wettest period of the study, which had followed three flow pulses.

Discussion

Our hypothesis of fish having good body condition associated with recent flow conditions and poor condition associated with extended no-flow was largely met for both species, with some small exceptions that could be explained by the trophic position of each of the two species. *N. erebi* individuals were in good condition in February 2006 followed by a decrease through the drying periods, with condition increasing again in January 2007 when fish had been sampled on the falling limb of a flow pulse (Fig. 1). Hence, our prediction that fish would be at their fattest when waterholes had recently encountered flows was strongly met for this species. Flow has also been found to be a significant driver of fish condition in other variable streams [20, 21]. Given the rapid turnover of benthic algal biofilms in these rivers [22], short-term spikes in food resources for *N. erebi* are likely to be met by algal blooms which would represent booms for these algivore/benthivores [2]. The condition of flannelmouth suckers (*Catostomus latipinnis*) has also been found to be strongly associated with flow due to increased algal productivity potential [4].

M. ambigua individuals were also in good condition in February 2006 after the three flow pulses and then subsequently declined with waterhole drying. However, unlike *N. erebi*, the condition of *M. ambigua* did not significantly improve after two small flows, one immediately before sampling in January 2007. As *M. ambigua* is a top-level predator and therefore sits higher trophically than *N. erebi*, a response in body condition to flow is likely to lag that of *N. erebi*, as there would need to be a subsequent spike in secondary production for them to gain a nutritional benefit.

In addition to observing good condition associated with flow for both species, fish recruitment also showed the same pattern. In both species, strong recruitment as evidenced by high numbers of small-bodied individuals relative to the population coincided when body water content was low (fattest fish). This suggests that the populations of both species are able both to store lipids and to expend energy on breeding in response to food resource availability driven largely by antecedent hydrology. As *N. erebi* has low ontogenetic diet variation [2], algal blooms would benefit all size classes of fish and hence would explain why these fish in particular can respond to flows quickly as occurred in both February 2006 and January 2007. Additionally, the fact that they maintained condition and had high numbers of recruits in May 2006 after some drying would suggest that algal productivity was maintained somewhat to sustain both juveniles and adults 3 months post-flow. While *M. ambigua* juveniles made up a high proportion of the population in February 2006 coinciding with high body condition, they also did have limited recruitment in January 2007, hence there must have been enough of a spike in productivity to at least enable some individuals to spawn and subsequently fuel juvenile recruitment, but not enough for them to store it as lipid.

Both species studied here have flexible spawning abilities [8, 10] and are likely to exhibit fluctuating energy (e.g. lipids) dynamics that reflect the assimilation of energy stores into their gonads to be ready to breed in quick response to favourable conditions. Alternatively, if poor conditions, such as drought, are extended, they can utilise the energy stored in their gonads to enable their longer-term survival. In contrast to the fish studied here, those in more stable environments tend to expend energy (from muscle stores) into gonad development prior to spring spawning and then assimilate energy from feeding into muscle stores to subsequently use for the next spawning season [23, 24]. Under the variable hydrological regimes of dryland rivers, fish proximate condition is likely to change over short time periods (such as weeks) in response to rapidly changing resources such as benthic algae [22].

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