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Lifetime movement history is associated with variable growth of a potamodromous freshwater fish

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Abstract

1. Directional or stabilising selection should drive the expression of a dominant movement phenotype within a population. Widespread persistence of multiple movement phenotypes within wild populations, however, suggests that individuals that move (movers) and those that do not (residents) can have commensurate performance.

2. The costs and benefits of mover and resident phenotypes remain poorly understood. Here, we explore how the presence and timing of movements are correlated with annual somatic growth rates, a useful proxy for performance because it is easily measured and rapidly reflects environmental changes.

3. We used otolith growth measurements and stable isotope analyses to recreate growth and among-reach movement histories of a partially migrating, long-lived freshwater fish, golden perch *Macquaria ambigua*. We compared the association between movement and growth at two temporal scales: 1) short-term (annual) differences in growth, in the years preceding, during, or following movement; and 2) long-term (lifetime) differences in growth.

4. Overall, 59% of individuals performed at least one among-reach movement, with these individuals subsequently more likely to move repeatedly throughout their lives. Movers grew faster than residents, with this difference most pronounced in the juvenile and early adult stages, when most movements occurred. Annual growth did not, however, change immediately prior to or following a specific movement event. Among-individual variation in growth was initially higher for residents than movers but decreased with age, at a faster rate for residents than movers, such that levels conformed after five years of age.

5. Our results indicate that lifetime movement is linked to faster growth in the early years of a fish's life. These faster growing movers are likely to be larger at a given age, leading to numerous potential benefits. However, the persistence of resident phenotypes suggests that there is likely a cost-benefit trade off to moving. The presence of multiple movement phenotypes may contribute to the resilience of populations by buffering against natural and anthropogenically exacerbated environmental variability.

Key words: bet hedging, dispersal, golden perch, Murray-Darling Basin, otolith microchemistry, partial migration, populations, trade-offs.

Introduction

The persistence of alternate movement tactics within a population suggests that each can have context-dependent fitness benefits (Lundberg, 1987; Jenni & Schaub, 2003). It is well documented that some individuals within a population move, often over large distances, for processes such as reproduction and feeding. Conversely, others move little and establish defined home ranges within which they remain and complete their life cycle (Parker & Stuart, 1976; Chapman, Brönmark, Nilsson & Hansson, 2011). The phenomenon of intrapopulation variation in movement is known as partial migration (Chapman et al., 2012). Moving individuals can escape density-dependent suppressors such as disease and predation (Mueller et al., 2011; Forsman, 2015; Schindler, Armstrong & Reed, 2015), and can have increased likelihood of encountering more favourable conditions at critical life history stages (Thériault, Bernatchez & Dodson, 2007). Resident individuals that remain within one location, may have increased reproductive output and survival, and avoid the risk of encountering locations with poorer environmental conditions (Grayson, Bailey & Wilbur, 2011; Grist et al., 2017). Despite these potential outcomes for residents, the individual-specific benefits of movement or residency are poorly understood for many species.

The costs and benefits of alternative movement tactics are likely to be particularly pronounced in variable and unpredictable environments. For freshwater fish inhabiting rivers with highly variable flows, individuals face a trade-off between moving to access potentially better resources (with increased mortality risk during migration (Furey et al., 2016)) or staying in a habitat where they may have a greater probability of persisting but with, for example, increased competitive stress (Olsson, Greenberg, Bergman & Wysujack, 2006). Spatial and temporal variation in environmental conditions could select for divergent movement phenotypes within and among populations such that movers are genetically distinct to residents (Verspoor & Cole, 1989). Individuals may therefore have an innate preference for movement or residency and use that tactic throughout their life, regardless of the environmental circumstance and body condition (Brodersen et al., 2014). Conversely, the expression of an individual’s movement phenotype might be a plastic response to environmental experience (Wysujack, Greenberg, Bergman &

Olsson, 2009) or predicted future conditions (Skov et al., 2011). Movement plasticity could negate the need for individuals to possess a broad tolerance to environmental conditions as they just move somewhere better when conditions become unfavourable. If movement is innate, then moving individuals may need to possess a broad tolerance to environmental stress as they will move regardless of conditions while their resident counterparts may become adapted to local conditions (Ghalambor, McKay, Carroll & Reznick, 2007). Selection should favour certain phenotypes in different environments, however, this may depend on the success of the decisions made by individuals moving among locations (Clobert, Le Galliard, Cote, Meylan & Massot, 2009).

Somatic growth is positively associated with individual performance and it can be strongly influenced by, and reflect variation in, environmental conditions. Indeed, growth has been successfully used to investigate both annual and long-term adaptive consequences of different fish movement phenotypes (Gillanders, Izzo, Doubleday & Ye, 2015; Roberts et al., 2019). The growth of individuals that move (movers) or stay (residents) can be influenced in three key ways: 1) spatial and temporal variability in resource quality and quantity; 2) the level of competition for available resources at a given location (Amundsen, Knudsen & Klemetsen, 2007) and 3) the energetic costs associated with movement. Movers could maximise their growth by attempting to maximise the time spent in resource rich areas, but in so doing risk incurring energy costs from moving and ending up in similar or worse locations (Forseth, Nesje, Jonsson & Hårsaker, 1999; Barraquand & Benhamou, 2008). Below a threshold of resource encounter probability, the benefits associated with tracking resource pulses dissipates and individuals are better off residing in a patch that may have only moderate resource quality (Mason & Fortin, 2017). Conversely, individuals in a high quality environment are likely to have received a locally driven growth benefit which, in turn, could increase swimming capacity or stored energy reserves that are needed to undertake large movements or to avoid more intense biological interactions associated with spikes in productivity (Beckman, Larsen, Lee-Pawlak & Dickhoff, 1998; Brodersen, Nilsson, Hansson, Skov & Bronmark, 2008). Whether these well-provisioned individuals move to seek better quality habitat depends on their capacity to perceive the surrounding environment and previous environmental selection (McMahon & Matter, 2006).

Movement ‘decisions’ are often considered adaptive (Dodson, Aubin-Horth, Theriault & Paez, 2013), but this not necessarily the case. For example, poorly performing individuals may not have the energy reserves required to complete large movements and must therefore remain (Rideout, Rose & Burton, 2005). In contrast, residents can be competitively dominant and force other individuals to move from a potentially productive habitat (Cutts, Metcalfe & Taylor, 1999). Individuals that are undertaking a large-scale movement may get interrupted (e.g. by a high flow or barrier), halting their movement and forcing individuals to remain in an undesirable location, return, or move in a different direction (Branco, Amaral, Ferreira & Santos, 2017). Movers that are forced into a location or those that choose to remain resident will be disadvantaged if they miss out on resource rich environments that are exploited by movers (Roberts et al., 2019).

Variation in growth among individuals can give insight into the processes driving movement decisions (Gillanders, Izzo, Doubleday & Ye, 2015). In variable environments, movers may maintain exposure to consistently higher quality environmental conditions by tracking resource pulses and aligning movements with seasonal peaks in food abundance and optimal temperatures (Crook et al., 2020), increasing their average growth rate and decreasing annual variability in growth. In comparison, residents in variable environments are often exposed to large seasonal variation in temperature and river flows (Strange, 2012). Exposure to such variable conditions might manifest in residents having slower growth on average, perhaps with very fast growth in years when conditions are good, resulting in increased variability in growth (Hilderbrand & Kershner, 2004). Residents may also inhabit high quality habitat and, therefore, benefit from remaining and allocating energy into activities such as home range protection and reproduction (Cutts, Metcalfe & Taylor, 1999; Crook, 2004). Lastly, it is possible that the frequency of movers is initially high in a cohort, and despite gaining the benefits of moving among higher quality habitats, these phenotypes may suffer high mortality rates due to increased energy expenditure and exposure to predation or capture (Chapman et al., 2011; Alos, Palmer & Arlinghaus, 2012).

In this study, we explored the relationship between movement and growth of a large-bodied (up to 760 mm length), long-lived (up to 26 years) Australian potamodromous fish species, golden perch *Macquaria ambigua* (Mallen-Cooper & Stuart, 2003; Lintermans, 2007). Golden perch are found throughout the Murray-Darling Basin (MDB) in south-eastern Australia and some individuals have a high propensity to move large distances (Reynolds, 1983; Koehn & Nicol, 2016). We analysed the growth and movement information naturally archived in otoliths to explore the links between movement and growth rate. We characterised the repeatability of movement by individual fish, and the correlations between movement and annual growth rate, and movement and variability in annual growth among individuals. Our analysis of average growth considered two complementary hypotheses: 1) annual growth will be sensitive to annual movement variation, whereby it will be maximised in the years preceding or following movement or depleted in the year of movement; and 2) lifetime movement history is correlated with annual growth expression, whereby movers gain a cumulative growth advantage over their lifetime compared to residents.

Materials and Methods

Study region

The Murray-Darling Basin (MDB) covers 1,073,000 km^2 of eastern Australia and comprises two major rivers: the Murray (2,530 km in length) and the Darling (2,740 km in length) (Lintermans, 2007). This study focused on four river reaches in the southern MDB: The lower Murray River (downstream of the junction of the Murray and Darling Rivers, ~820 km), the mid Murray River (between the junction of the Murray and Darling Rivers, and the junction of the Murray and Goulburn Rivers, ~980 km), the upper Murray River (between the junction of the Murray and Goulburn Rivers and Yarrawonga weir, ~230 km), and the lower Darling River (between the junction of the Murray and Darling Rivers, and the main Menindee Weir, ~510 km) (Fig. 1). These river reaches were used to define movements of golden perch, by correlating the unique water chemistry in each reach with the chemical composition in fish otoliths.

Sample collection and preparation

We sourced 213 sectioned golden perch otoliths from previous studies that sampled Murray Darling Basin rivers in 2014-2017 (Zampatti et al., 2015; Zampatti et al., 2018)(Table 1). A 400 to 500 µm thick transverse section was taken from each otolith, which was then mounted onto a glass slide using a thin layer of resin, with 20 to 50 otolith sections per slide depending on otolith size.

Age, growth, and movement history

We took a digital image of each otolith section using a Canon (Canon Inc, Tokyo, Japan) EOS 60D digital camera attached to a dissecting microscope at 25× magnification. The age of each fish was estimated by counting the opaque zones on the dorsal side of each otolith, from the primordium (when the fish was born) to the outer edge (when the fish died). To estimate annual otolith growth rates, we measured the distance between the outer edges of each opaque zone using Image Pro Plus software (v.6.3, Media cybernetics, Maryland, USA). The first growth increment was excluded because its width can vary due to factors not associated with annual growth, such as spawning date and difficulties identifying the location of the otolith core.

We used annual otolith increment measurements and length-at-capture and age-at-capture data to back-calculate fish length at each age. The relationship between otolith growth and fish growth is not always linear across individuals in a population (Fey, 2001). We therefore used the biological intercept method of back calculation to account for individual variation and non-linearity of the otolith and fish length relationship (Campana, 1990). The length and otolith radius data from a juvenile golden perch (age = 2, length = 95 mm) was used as a the biologically determined intercept in the back-calculation equation. Length-at-age was thus calculated by:

$$L_a = L_c + (O_a - O_c) \times (L_c - L_i) \times (O_c - O_i)^{-1}$$

where L_a is the length of a fish at age a, back-calculated from the otolith measurement at age a, L_c and O_c are fish length and otolith radius at time of capture

c, and L_i and O_i are the length and otolith radius at the biological intercept (Campana & Jones, 1992).

Our otolith samples had been previously analysed for strontium isotope ratios ($^{87}Sr/^{86}Sr$) using laser ablation – inductively coupled mass spectrometry (LA-ICP-MS) (Zampatti et al., 2015). Dissolved $^{87}Sr/^{86}Sr$ in water can provide a geographically unique marker in fish otoliths, making them appropriate for movement history reconstruction and this method has been successfully implemented previously in the MDB and elsewhere (Kennedy, Klaue, Blum, Folt & Nislow, 2002; Crook et al., 2013; Sturrock et al., 2015). Each otolith was ablated along a transect from the primordium to the outer edge with the $^{87}Sr/^{86}Sr$ values compared to river water $^{87}Sr/^{86}Sr$ across the MDB, as per Zampatti et al. (2015). $^{87}Sr/^{86}Sr$ profiles represent four distinct river reaches in the southern MDB: the lower Darling River ($^{87}Sr/^{86}Sr$ = ~0.7075), the lower Murray River (~0.7080 – 0.7160), the mid Murray River (~0.7160 – 0.7190), and the upper Murray River (~0.7190) (Fig. 2) (Zampatti et al., 2015).

Statistical analyses

We used three sets of linear mixed effects models to investigate the repeatability of individual movement behaviour, the ages when movement occurred, and the association between movement and annual growth of golden perch. In this study, we define *movement* as a transition in otolith $^{87}Sr/^{86}Sr$ corresponding to movement between any two of the four chemically distinct river reaches in the southern MDB.

For each set of models, we used model selection to identify the highest-ranking random-effects and fixed-effects structures. First, we used restricted maximum likelihood estimation (REML) to fit models with different combinations of random intercepts and slopes, and ranked these models using Akaike's Information Criterion corrected for small sample size (AICc). Second, we used the highest-ranked random-effects model to compare models with different combinations of fixed predictors. Last, we refitted the highest-ranked full model (fixed and random effects) with REML to produce unbiased parameter estimates (Zuur, Ieno, Walker, Saveliev & Smith, 2009).

We calculated conditional and marginal R^2 values for the highest-ranked models, based on the proportion of variation in annual growth explained by fixed effects (marginal) or fixed and random effects (conditional) (Nakagawa, Schielzeth & O'Hara, 2013). We fitted models using the lme4 package (Bates et al. 2015) in the program R (v3.6.2) (R Core Team, 2020) and compared them using the AICcmodavg package (Mazerolle, 2015).

Movement analysis

We used a generalised mixed effects model to investigate the probability of fish movement in a particular year as a function of its age, using data from movers only. The binary response variable was equal to one if a fish moved in a given year and zero otherwise. We assumed a Bernoulli likelihood and used a logit link function. We included a random intercept for fish identity to account for repeated observations per fish and considered a second random-effects structure that additionally included a random slope for age to allow for differences in age-dependent movement probability. Using the highest-ranked random effects structure, we then compared an intercept-only model to models with linear and linear plus quadratic age effects.

We used a second generalised mixed effects model to investigate the repeatability of individual movement expression. We compared three models with different fixed- and random-effects structures, representing three types of repeatability (Biro & Stamps, 2015). The first model included an overall model intercept and a random intercept for fish identity, representing no ontogenetic change in movement phenotypic expression (*agreement repeatability*). The second model included an age fixed effect and a random intercept for fish identity, representing common changes in phenotypic expression among individuals as they age (*consistency repeatability*). The third model included an age fixed effect and a random age slope for fish identity, representing individual differences in the ontogeny of movement expression (*conditional repeatability*). We calculated repeatability (*r*) scores (the proportion of variance in movement behaviour that is accounted for by differences among individuals), using the rptR package based on 1000 parametric bootstraps from the highest-ranked model (Stoffel, Nakagawa, Schielzeth & Goslee, 2017).

Growth analysis

The correlations between movement and annual growth were assessed using a series of linear mixed effects models. These models included each fish's age at observation (age) and age-at-capture, interactions between age and the movement predictor, and a suite of random effects. We accounted for non-independence of increments formed within the same fish (fish identity), and of increments that were formed in the same year by different fish (year). We included a random slope for movement (predictors described below) and location of capture to allow for the effects on annual growth to differ among movement types and among locations where individuals were captured. Finally, we included natal origin and cohort in a nested random intercept structure to account for non-independence of increments formed in the same year (cohort) and same river reach (natal origin) caused by any among-system differences in early life conditions. The general model form was:

growth ~ age × movement predictor + age-at-capture + (age I fish identity) + (age I year) + (movement predictor I capture location) + (age I cohort : natal origin).

We developed two sets of movement predictors to test hypotheses about the links between movement and annual growth. The first set contained three lifetime movement predictors, which were used to determine whether persistent individual phenotypic differences are associated with differences in annual growth (Table 2). *Movement type* described whether an individual moved between any of the four reaches at least once in its life. *Movement type – maturity* described when in its lifetime an individual moved. *Total movements* described the total number of movements each individual fish made throughout their life. The second set contained five annual movement predictors which explored immediate changes in growth occurring prior to or following a movement (Table 2). *Moving year* identified each growth increment as occurring when the fish moved or stayed. *Moving year – lagged* distinguished the year following movement from all other years. *Moving year – pre* distinguished the year prior to movement from all other years. *Pre and post movement* distinguished increments that were formed until the first movement from all years following that movement. *Pre and post movement – lagged* distinguished increments that were formed until the year following movement from all subsequent years. A null model including only random effects was also included in this comparison. We also recreated the lifetime movement analysis using only individuals greater than 5 years old to test for potential biases in our analysis that might arise from some individuals being captured at a relatively young age not having the opportunity to undertake a movement. This is outlined in the supporting information documents.

Finally, we calculated the coefficient of variation (CV) of growth among individuals at a given age from the best lifetime movement model. We developed a mixed effects model with growth CV as the response variable and an interaction between age and the best lifetime movement predictor (Movement type). We weighted the model by sample size, as there were many more measurements at younger ages than at older ages.

Results

Age, growth, and movement history

We measured a total of 1,323 otolith growth increments from 213 golden perch collected from four reaches of the southern MDB. The mean age-at-capture was 7.21 years (range = 2–25 years), and the mean number of lifetime movements was 0.76 (range = 0–4 movements). There were 126 fish that moved at least once, and 87 fish that did not make any among-reach movements at the resolution of our Sr data.

Movement analysis

Golden perch movement was best described by the inclusion of both linear and quadratic age predictors, with higher probabilities of movement in the first eight years of life, decreasing with age and flattening after approximately 15 years (Fig. 3). The best random-effects structure for the movement analysis included a random intercept for fish identity (ΔAICc to random slope model = 2.3). Movement behaviour was repeatable (95% confidence intervals do not span zero), differing among individuals and as they aged (conditional repeatability; $r = 0.102$, CI = 0.025 – 0.501).

Growth analysis

Golden perch growth was best described by the inclusion of an interaction between age and the *Movement type* predictor (Table 3), which designated whether a fish moved within its life or not (mover or resident), with growth of movers greater than residents, particularly at young ages (2–8 years) (Table 4, Fig. 4). This was the highest-ranking lifetime movement model and was substantially better than the second highest-ranking null model (ΔAICc > 10) (Table 3). Annual movement predictors did not improve model fit compared to the null model. There was, however, weak evidence of an interaction between age and the moving year predictor that suggested that growth of older fish increased in moving years (Table 4, Fig. 5). All models included the best random effects structure that included an age effect that differed among individuals, years, cohorts, and natal origins (ΔAICc to next best model = 35). The best fixed-effects structure for the base model included both age and age-at-capture. The age-at-capture term revealed that individuals that were captured at younger ages had faster growth than those caught at older ages.

The recreation of the lifetime movement analysis using only data from individuals captured at greater than five years of age produced results qualitatively the same as those using the full data set. Again, the *Movement type* predictor was the highest-ranking model, with movers growing at a faster rate than residents over the first eight years of life. The results are outlined in supplementary tables 1 and 2, and supplementary figure 1.

The analysis of the coefficient of variation (CV) of growth revealed a detectable interaction between age and movement type ($F_{3,32} = 16.32$, $p < 0.01$): among-individual differences in growth of residents was more variable than that of movers between the ages of two and five (Fig. 6). However, as fish became older, the growth CV of both movement types decreased, with the growth CV of residents decreasing at a faster rate than movers. After the age of approximately ten years old, the growth CV of resident fish became less than moving fish, however the confidence intervals were overlapping, indicating that there was no observable difference at later ages (Fig. 6).

Discussion

We identified that movement phenotypes influenced average annual growth and among-individual variation in growth of golden perch. Fish that made at least one among-reach movement in their lifetime had higher age-specific annual growth rates during their first eight years compared to those that did not. Among-individual growth variation (CV) was higher for residents than movers earlier in life but this difference reversed after five years of age, indicating that at young ages when movement was more likely to occur, movers may track relatively stable environmental conditions while residents are exposed to more variable conditions. Our observation of repeatable movement behaviours and faster annual growth in movers than residents in their first eight years suggests that among-individual movement variation is reflective of a behavioural personality, which could be underpinned by genetic differences caused by selection or the canalisation of behaviour induced by early life experience (Coates, Hale & Morrongiello, 2019; Debes, Piavchenko, Erkinaro & Primmer, 2020).

The presence of multiple movement phenotypes may provide a mechanism to buffer populations against the risks of fluctuating resource availability (Schindler, Armstrong & Reed, 2015). In highly variable environments, such as those experienced by golden perch (Puckridge, Sheldon, Walker & Boulton, 1998), movers may benefit by tracking relatively stable environmental conditions. By remaining in a single location, residents may be exposed to good conditions in some years and poor conditions in others, which may influence survival (Acker et al., 2021). Golden perch have been observed occupying, but also shifting home ranges on the scale of kilometres (Crook, 2004). Our results suggest that these home range shifts might be occurring on much larger scales than previously observed, perhaps partly due to our capacity to detect movement in young fish that are not usually tagged (Mallen-Cooper, 1996).

Although faster annual growth of moving individuals has been observed in populations with variable movement expression (Robillard, Casselman, McLaughlin & Mackereth, 2011; Chapman et al., 2012), the presence of residents indicates that there must be benefits of both movement types. We detected large proportions of both movers and residents in our data (59% and 41%, respectively), which would not be expected if movers were consistently advantaged. In our study system, the benefits of movement likely accumulate over multiple years, as movers repeatedly select higher quality locations, rather than manifesting at annual time scales, which would reflect a more plastic movement response to local environmental conditions (Olsson, Greenberg, Bergman & Wysujack, 2006). The commensurate benefits for residents are unstudied but could include increased reproductive output or long-term survival (Shaw & Levin, 2011; Buchan, Gilroy, Catry & Franco, 2020).

Differences in among-individual variation in growth might reveal the processes driving movement decisions. For example, growth variation of resident golden perch was greater than that of movers in the first five years, which was also when movements were most likely to occur. Our observation of an annual growth advantage in movers might indicate that these individuals experience more stable environmental conditions, thereby reducing the variation in growth among individuals (McMahon & Matter, 2006). Conversely, young residents may experience a relatively more spatially and temporally variable local environment or be exposed to differential intraspecific competition compared to older residents, thus increasing among-individual growth variation (Hilderbrand & Kershner, 2004; Morrongiello, Sweetman & Thresher, 2019). The decline and convergence in growth variation of both movement types (Brönmark, Skov, Brodersen, Nilsson & Hansson, 2008; Réale et al., 2010) with age supports this proposition, as older fish make fewer movements and thus behave more similarly to older residents inhabiting a presumably acceptable home range. There is some evidence that the trend of the CV pattern reverses later in life. It is plausible that the selective mortality of some resident individuals expressing extreme growth phenotypes could occur, which in turn would reduce among-individual variation in growth. There was a negative effect of age-at-capture on annual growth, indicating that individuals that were captured at young ages had faster growth than those captured at older ages, which could suggest that there is selective mortality of fast-growing individuals. However, additional models that identify the interactions between age-at-capture and movement are required to examine these hypotheses. Furthermore, due to the confidence intervals overlapping and the small sample size of growth measurements at these ages, we suggest that the downward trend of resident growth variation is likely driven by growth variation between two to five years of age. It is also possible that slow-growing movers experience high mortality after reproducing at young ages (Kuparinen, Hardie & Hutchings, 2012), which may reduce the variation in growth of our captured individuals and result in our sample of movers being biased towards individuals with fast growth. Likewise, the onset of sexual maturity and subsequent trade-off between energy allocation to reproduction and growth may also contribute to decreasing growth variation (Jørgensen & Fiksen, 2006).

Growth of juvenile fish is more responsive to environmental variation than that of adults because surplus energy is converted directly into somatic growth, whereas energy is allocated to both growth and reproduction in adult fish (Day & Taylor, 1997). Ontogenetic changes in food resources may therefore contribute to declines in annual growth variation over time (Tonkin et al., 2017). Like many fishes, the early life stages of golden perch typically prey on small invertebrates (Arumugam & Geddes, 1986), with the availability of these food resources responding rapidly to local environmental conditions (Jenkins & Boulton, 2003). Larger and older golden perch feed at a higher trophic position, with their main prey being macroinvertebrates, insects and small fish, which are less influenced by fluctuating environmental conditions than individuals at lower trophic positions (Ebner, 2006; Baumgartner, 2007). Understanding ontogenetic changes in growth variation will require more-detailed knowledge of how the frequencies of environmental signals (e.g. variation in flow and temperature) change as they are integrated through trophic levels (Di Lorenzo & Ohman, 2013).

There are, however, limitations in the spatial resolution of the $^{87}Sr/^{86}Sr$ analysis. There are only four unique $^{87}Sr/^{86}Sr$ signatures currently identified for the main river reaches of the Murray and Darling rivers (not including tributaries), which limits the spatial resolution at which movements can be observed with this method. Additionally, individuals that undertake among-reach movements and return within short time scales are not detected by our analysis. Golden perch have been observed undertaking many small to medium range movements, which may not be represented in our data set (O'Connor, O'Mahony & O'Mahony, 2005; Zampatti, Leigh, Bice & Rogers, 2018). Prospective movers may also be restricted by barriers (Harris, Kingsford, Peirson & Baumgartner, 2017) or captured at a young age before being able to make a movement rendering them to be subsequently identified as residents or with less movements than they may have undertaken if they were not captured. However, this censoring issue would have created more variation in the association between growth and movement, as both residents and potential movers had the same classification. The fact that we found a strong link between young fish growth and movement provides further evidence of the robustness of the association. To provide further evidence for our results, we reproduced the lifetime movement analysis, using only individuals greater than five years of age. The results were consistent with the current analysis and are presented in the supporting information. The development of methods to extract more finely resolved movement information over individual lifetimes would potentially clarify the effects of fine-scale movements on growth, providing new insights into the short-term costs and benefits of movement (Crook et al., 2013).

In many regulated river systems such as the MDB, there has been considerable focus on the management of river flows and connectivity to improve fish populations (Baumgartner, Zampatti, Jones, Stuart & Mallen-Cooper, 2014; Koehn et al., 2014). Research supporting these management programs has generally focused on the effects of river flows on reproduction and recruitment (Tonkin et al., 2019), barriers to movement and gene flow (Jager, Chandler, Lepla & Van Winkle, 2001; Katopodis, 2005), and the birthplace and subsequent dispersal of larval individuals (Bradbury, Campana & Bentzen, 2008). There has been less focus, however, on the presence of variable movement traits within populations, and the sensitivity of these to remedial actions, which can affect population persistence (Hale, Morrongiello & Swearer, 2016). Given increasingly variable environmental conditions in river systems worldwide (Neave, McLeod, Raisin & Swirepik, 2015), it seems plausible that the presence of different movement types within populations will bolster the resilience of populations to episodic disturbances (Schindler, Armstrong & Reed, 2015).

Tables and figures

Table 1. The total number, age range, birth year, and size range of fish collected from the four locations across the MDB.

Capture location	Number of fish	Age range (years)	Birth year range	Size range (mm)
Lower Murray River	99	2-19	1997-2014	134-464
Mid Murray River	55	2-17	1997-2014	240-515
Upper Murray River	47	3-25	1991-2013	273-513
Lower Darling River	12	2-6	2008-2012	95-419

Table 2. Lifetime and annual movement predictors used in mixed effects models. The first column is the name of each movement predictor. The second column is a description of each predictor. The third column described the type of value that represents each predictor. The fourth column is a hypothesis about how the movement predictor may influence fish growth.

Predictor	Description	Values (n_i = number of individuals, n_m = number of measurements)	Growth hypothesis
Lifetime predictors			
Movement type	Whether a fish moved at least once during its life (e.g. Fish a. and b. in Fig. 2 are a resident and a migrant respectively).	Resident (n_i = 87, n_m =529), Mover (n_i = 126, n_m = 794).	Annual growth of migrant fish is greater than annual growth of resident fish. Migrant fish move amongst productive environments, while resident fish remain in a location with good or bad conditions.
Movement type - maturity	The timing of any movement within a fish's life cycle. Movement may have occurred when a fish was a juvenile (0-3 years for males, 0-4 for females (Mallen-Cooper & Stuart, 2003), an adult, both life stages ("full migrant"), or not at all.	Resident (n_i = 87, n_m =529), Juvenile Mover (n_i = 100, n_m 543), Adult Mover (n_i = 10, n_m =90), Full Mover (n_i = 16, n_m =161).	Annual growth of full migrants is greater than partial migrants (adult or juvenile migrants). Annual growth of partial migrants is greater than residents. Individuals that move more, consistently locate productive habitats.
Total movements	Total number of movements made by each fish between river stretches. (e.g. Fish a. and b. in Fig. 2 have moved a total of 0 and 2 times respectively).	0 (n_i = 87, n_m = 529), 1 (n_i = 98, n_m = 541), 2 (n_i = 22, n_m = 173), 3 (n_i = 4, n_m = 54), 4 (n_i = 2, n_m = 26).	Annual growth is greater for fish that moved a larger number of times. Individuals that move more, consistently locate productive habitats.
Null model	No movement predictor	Null	Annual growth is explained by age, age-at-capture, and random

			effects.
Annual predictors			
Moving year	Growth increments were classified as moving years or staying years depending on whether movement occurred in that year.	Moving year (n_m = 88), Staying year (n_m = 1,235).	Annual growth is reduced in the year in which fish moved compared to years when fish did not move. Movement results in increased energy expenditure in that year. Individuals may also move in response to poor conditions in their location, resulting in a growth decrease.
Moving year - lagged	Moving year data were lagged one year to understand the lasting influences of movement on growth in the following year.	Previous year moving (n_m = 56), Staying year (n_m = 1,267).	Annual growth is greater in the year following a movement event compared to all other years. Movement has resulted in fish locating a more productive environment, thus receiving a growth benefit in years following movement. Individuals that move in response to poor conditions in their location, may locate a better environment, resulting in an immediate growth increase.
Moving year - pre	Moving year data were preceded one year to understand the influences on growth that precipitated movement	Next year moving (n_m = 88), Staying year (n_m = 1,235).	Annual growth is greater in the year preceding a movement event, compared to growth in all other years. Increased growth in years prior to movement results in increased energy reserves for movement to occur in the following year.
Pre or post movement	Increments were classified as either pre or post movement depending on when movement occurred throughout a fish's life.	Pre-movement (n_m = 589), Movement (n_m = 88), Post movement (n_m = 646).	Annual growth is initially reduced in the year of movement and increased in all years following movement. Individuals spend energy resources moving to locate a new productive environment, thus receiving a growth benefit in the following years.

Pre or post movement – lagged	Pre or post movement data were lagged to understand the lasting influence of moving in the following year.	Pre-movement (n_m = 643), Post movement (n_m = 680).	Annual growth is greater in the year after a movement event, and in all years following. Moving fish gain an ongoing growth benefit from locating an environment with increased productivity.
Null model	No movement predictor	Null	Movement is explained by age, age-at-capture, and random effects.

Table 3. Best fitting models of golden perch annual growth including an age interaction with lifetime and annual movement predictors after AIC comparison. Columns are degrees of freedom (df), AICc value, differences in AICc (ΔAICc), AIC weight, and marginal and conditional R2 values.

Movement predictor	df	AICc	ΔAICc	AIC weight	Cond R^2	Marg R^2
Lifetime models						
Movement type	18	197.99	0	0.99	0.922	0.818
No movement predictor	14	207.99	10.00	0.01	0.926	0.803
Movement type - maturity	29	214.70	16.72	0	0.921	0.830
Total movements	36	226.20	28.21	0	0.919	0.821
Annual models						
No movement predictor	14	207.99	0	0.54	0.924	0.802
Moving year	18	210.04	2.05	0.19	0.925	0.802
Pre or post movement	23	211.55	3.56	0.09	0.923	0.812
Moving year - pre	18	211.87	3.88	0.08	0.924	0.801
Moving year - lagged	18	212.21	4.23	0.07	0.924	0.802
Pre or post movement lagged	18	213.49	5.50	0.03	0.925	0.802

Table 4. Parameter estimates with 95% confidence intervals from the highest-ranking models describing golden perch growth.

Model	Parameter	Estimate (lower and upper CI)
Movement type	Intercept	3.569 (3.475 – 3.688)
	Age	-1.094 (-1.189 – -0.992)

	Age-at-capture	-0.212 (-0.296 – -0.129)
	Movement type	-0.082 (-0.139 – -0.021)
	Age × Movement type	0.159 (0.079 – 0.242)
Null Model	Intercept	3.517 (3.398 – 3.638)
	Age	-1.039 (-1.131 – -0.942)
	Age-at-capture	-0.210 (-0.299 – -0.124)
Moving year	Intercept	3.528 (3.401 – 3.650)
	Age	-1.053 (-1.148 – -0.952)
	Age-at-capture	-0.191 (-0.284 – -0.103)
	Moving year	0.050 (-0.066 – 0.170)
	Age × Moving year	0.018 (-0.068 – 0.114)

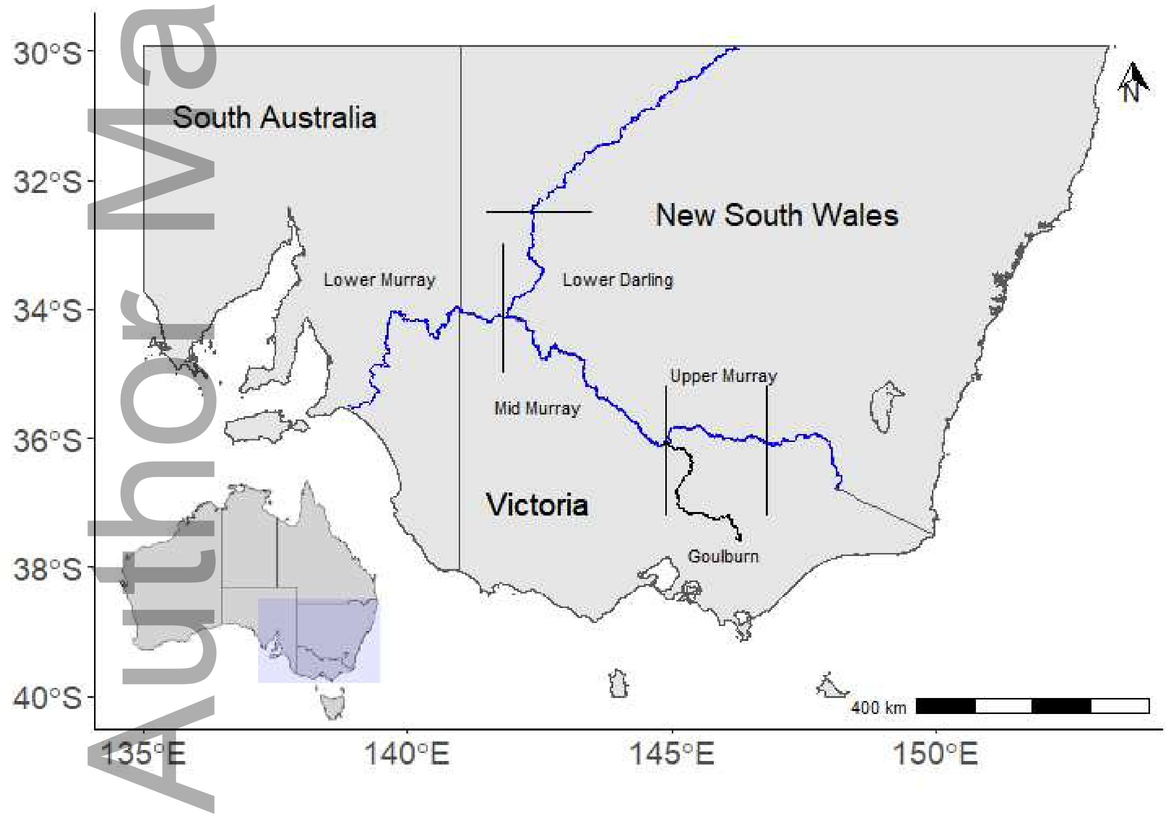

Figure 1. Map of the southern Murray-Darling Basin in south-eastern Australia. The black lines indicate where Sr data has identified breaks in water chemistry and thus delineate our study reaches which are labelled.

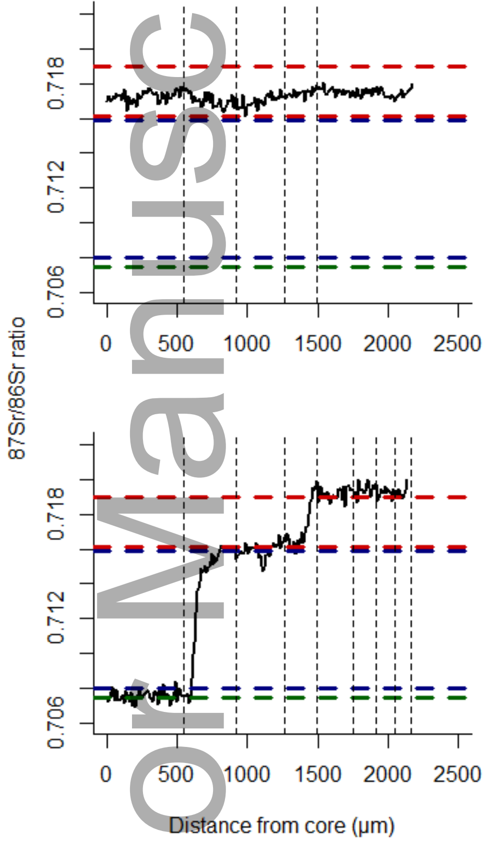

Figure 2. Examples of strontium isotope ratio (Sr^{87}/Sr^{86}) transects from two fish. The solid black line is the Sr isotope ratio across a transect of an otolith. The horizontal dashed lines show the chemical delineation for water from the Darling River (green), the Lower Murray River (between blue lines), the mid Murray River (between red lines), and Upper Murray River (above top red line). The vertical dashed black lines are the location of the annuli on the otolith section. The individual in the top panel has stayed in the Mid-Murray River, and the individual in the bottom panel moved from the Darling River into the Mid-Murray River as a one-year-old, then into the Upper-Murray River as a three-year-old.

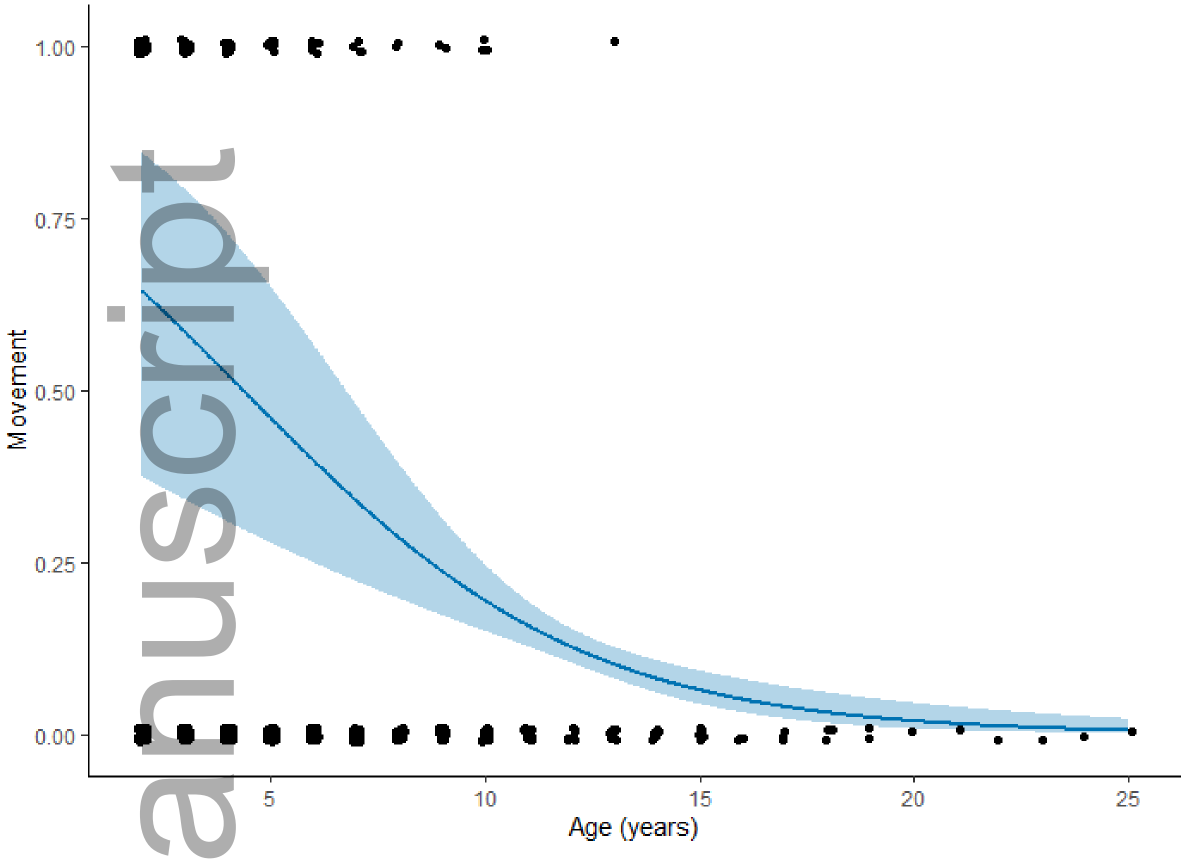

Figure 3. Predicted movement of golden perch as a function of age. The y-axis represents the probability that fish moved at each age, where 1 = movement and 0 = residency. Shaded

areas represent 95% CI. Black circles are the raw movement data per year.

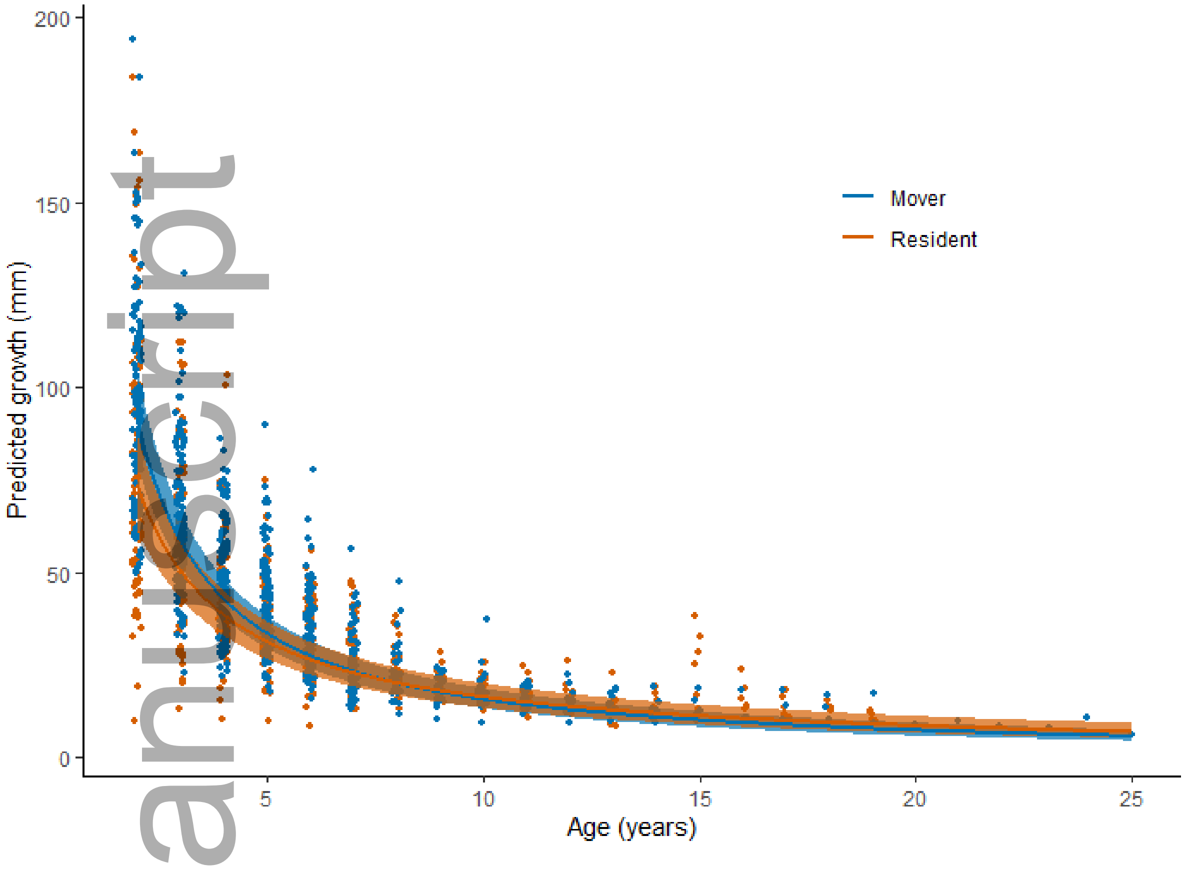

Figure 4. Predicted annual growth (mm of length) of golden perch. The blue line is growth of moving fish, and the orange line is growth of resident fish. Shaded areas represent 95% CI. Blue and orange circles are the mover and resident raw growth data, respectively.

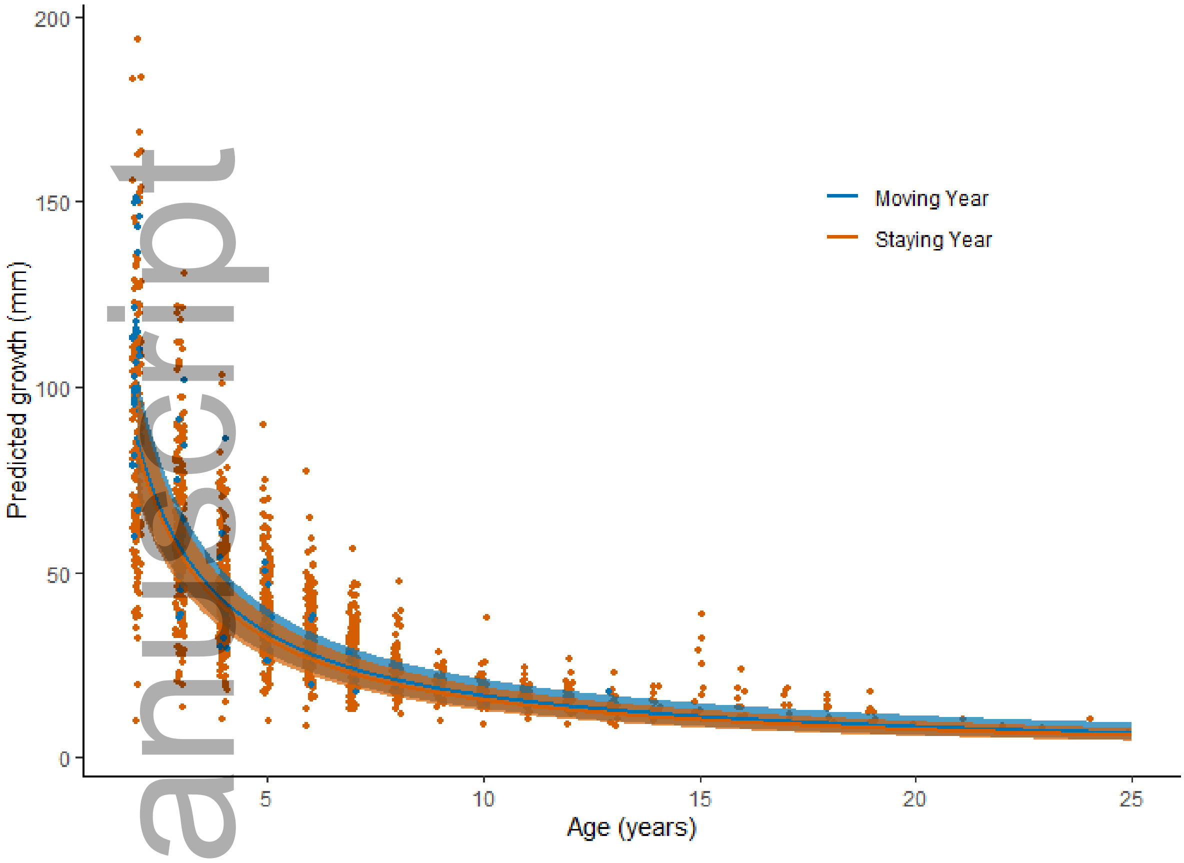

Figure 5. Predicted annual growth (mm - length) of golden perch. The blue line is growth in years when movement occurred, and the orange line is growth in years when no movement occurred. Shaded areas represent 95% CI. Blue and orange circles are the moving year and staying year raw growth data, respectively.

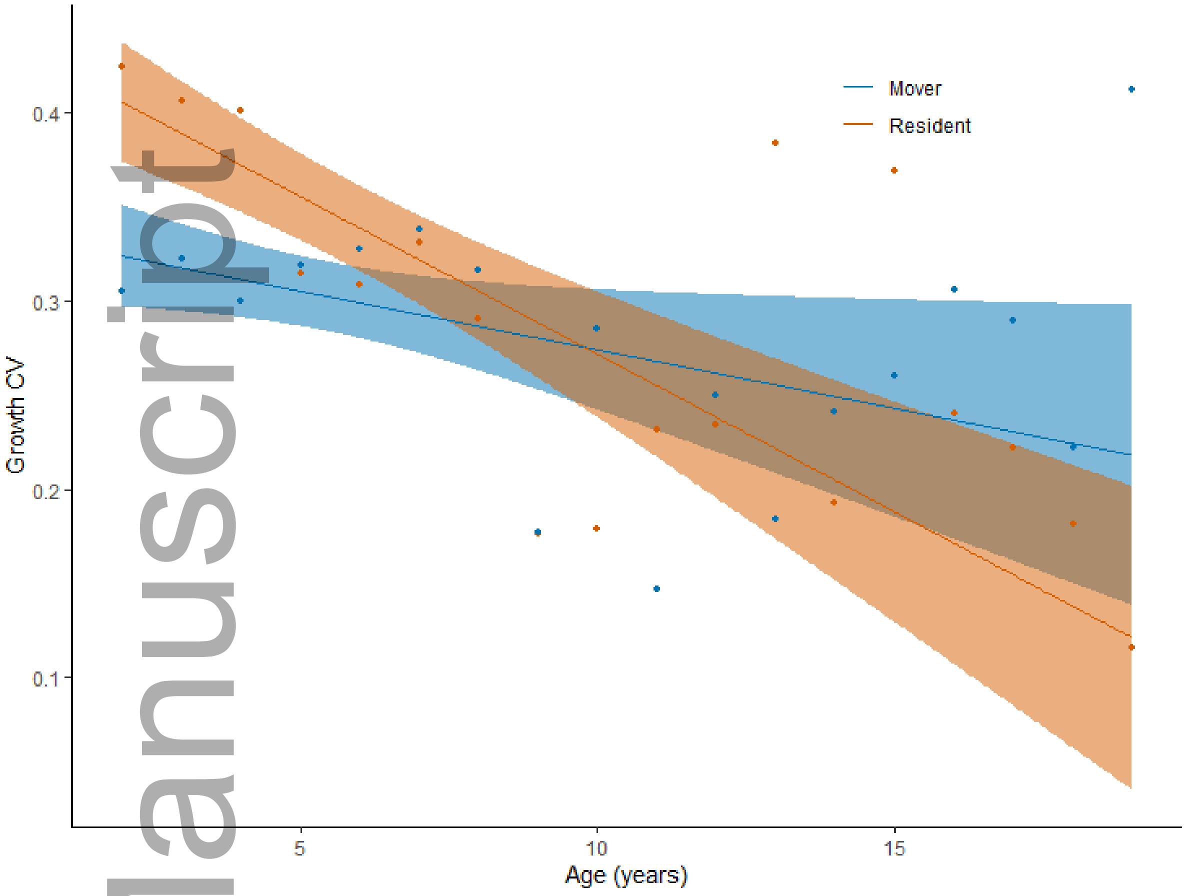

Figure 6. Age dependent CV of growth of golden perch. The blue line is growth of moving fish, and the orange line is the growth of resident fish. Shaded areas represent 95% CI. Blue and orange circles are the mover and resident raw growth CV data, respectively.

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Conflict of Interest

All authors declare no conflict of interest.

Authors' contributions

JB, JM JY, and JK conceived the ideas and designed methods; AS collected and prepared the samples; BZ, ZT, and JT analysed and interpreted water and otolith samples and provided guidance on the movement ecology of golden perch; JB completed the otolith growth measurements; JB, JM, and JY lead the statistical analysis; JB, JM, JY, and JK led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

Supplementary methods and results are appended as supplementary information to the online version of this article. All data are available at https://doi.org/10.26188/14122688. Data used in this study are provided specifically for purposes of reproducibility.

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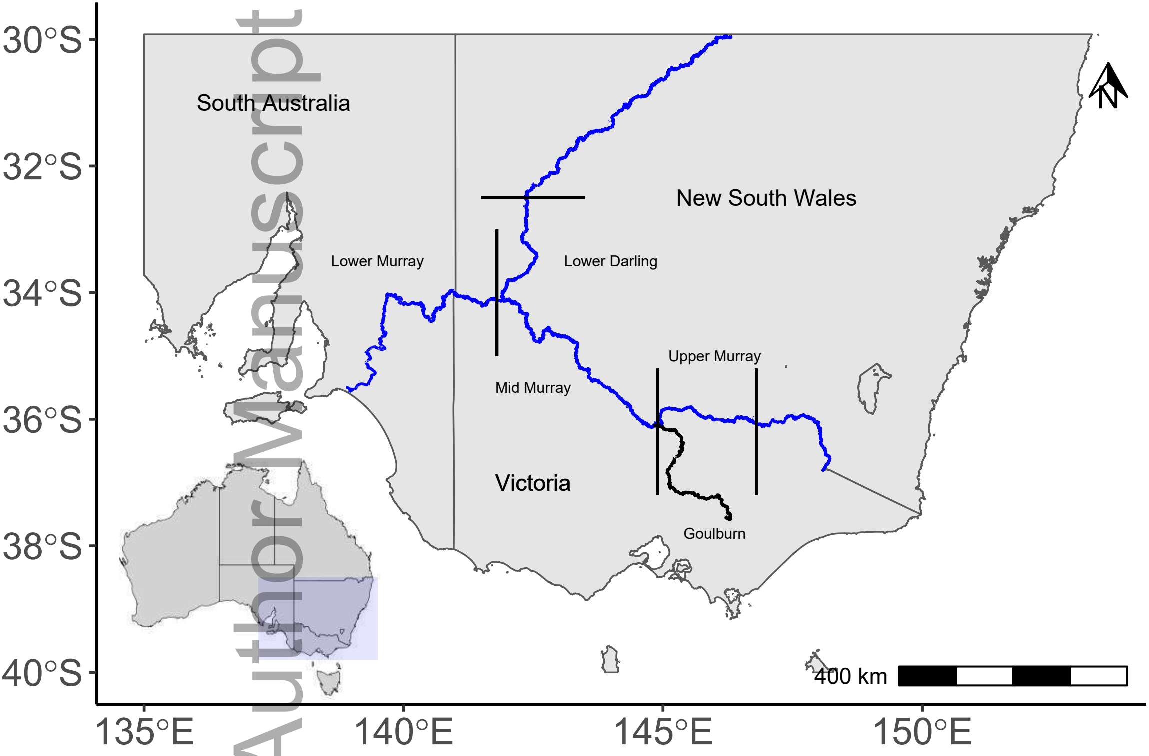
30°S
32°S
34°S
36°S
38°S
40°S
135°E
140°E
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South Australia
New South Wales
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Lower Murray
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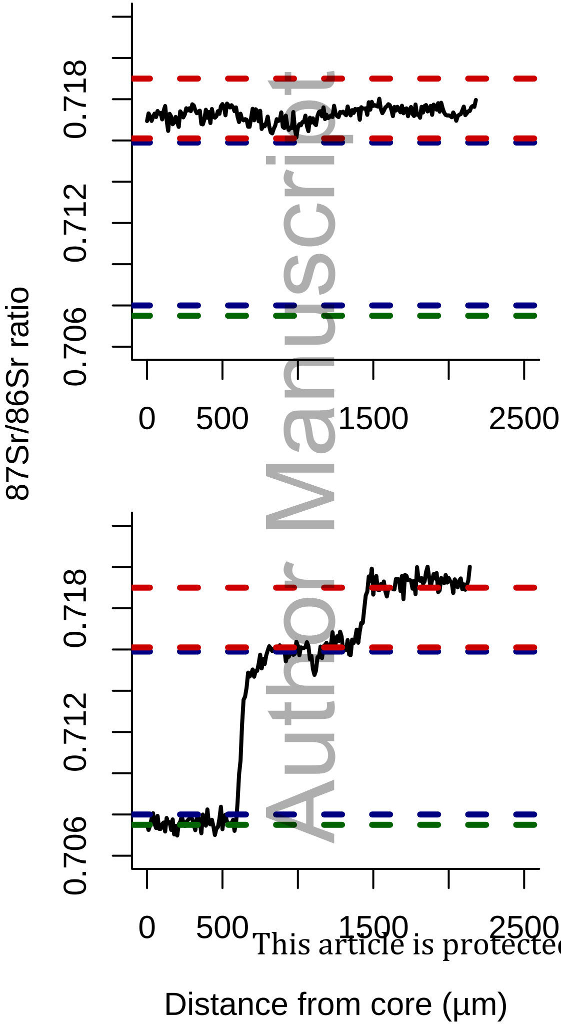
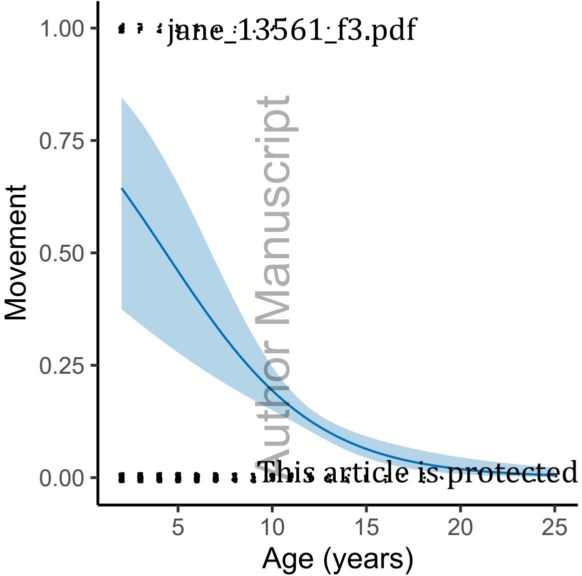
Mid Murray
Upper Murray
Goulburn
N
400 km


87Sr/86Sr ratio
0.706
0.712
0.718
0
500
1500
2500
0.706
0.712
0.718
0
500
1500
2500
Distance from core (µm)


1.00
0.75
0.50
0.25
0.00
Movement
5
10
15
20
25
Age (years)

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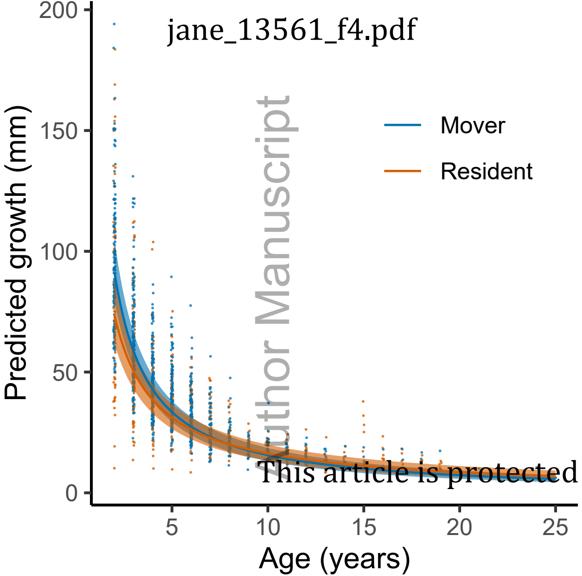

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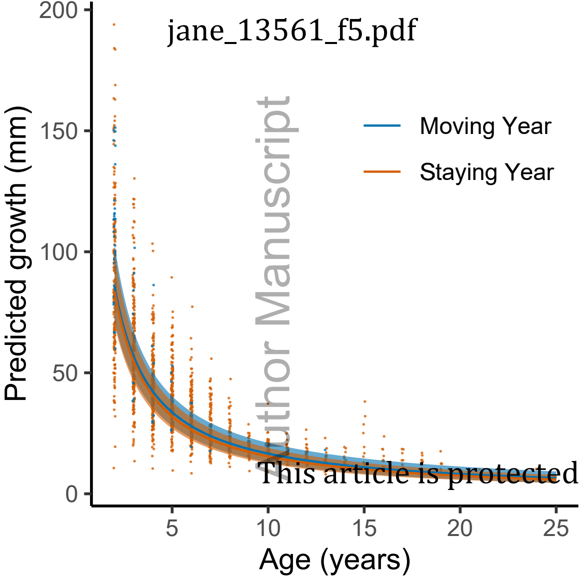

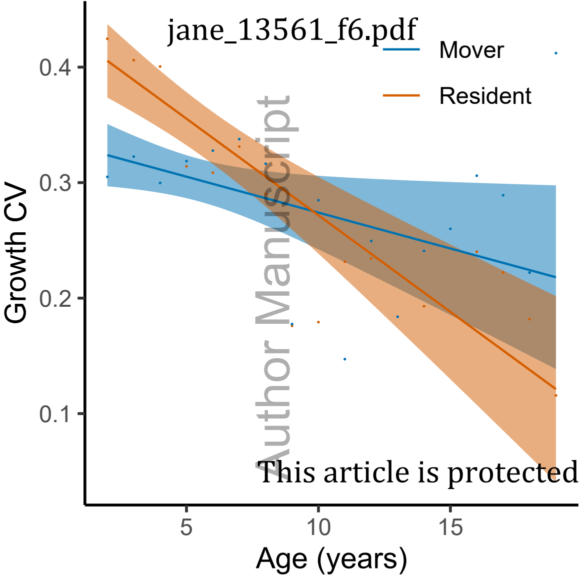
Mover
Resident
Growth CV
0.4
0.3
0.2
0.1
5
10
15
Age (years)