

Dispersal direction, geographic location and river discharge all influence juvenile growth of a freshwater fish

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Abstract

1. Seeking out appropriate habitat or food resources is one of the key reasons why animals move. Despite the benefits of movement, some individuals in a population remain resident or express alternative movement phenotypes. Movement, however, is energetically costly and can result in resources being diverted away from growth and reproduction. The presence of multiple movement phenotypes within populations suggests that each can have commensurate levels of performance depending on the underlying environmental conditions.
2. Here we explore the context-dependent costs and benefits of upstream and downstream juvenile dispersal in a large river system. We expect that if the energetic costs of moving (upstream against a current or downstream with a current) exceed any benefits to growth, then residents (who do not move) will have faster growth. Alternatively, movement costs may be offset if individuals move to more favourable environments, resulting in dispersers benefiting with faster growth.
3. We used biological information naturally archived in the otoliths of a potamodromous fish, golden perch *Macquaria ambigua*, to quantify how movement phenotypes affect growth across individuals exposed to spatiotemporally varying environmental conditions.
4. We found that juvenile growth differed considerably among dispersal phenotypes (resident, upstream, downstream, stocked): in general, surviving wild-spawned downstream and upstream dispersers and hatchery-stocked fish all grew faster than individuals that remained resident within their natal reach. Further, juvenile growth was sensitive to local environmental conditions and had carryover effects from an individual's natal-year. Juvenile growth of all dispersal phenotypes was higher in years with below average natal-year summer discharge (when fish are ~2–3 months old), likely because of increased concentrations of food resources. In contrast, the effects of natal-year spring discharge (around the time individuals were spawned) were dependent on dispersal direction, with positive effects for

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downstream dispersers and upstream dispersers, and negative effects for resident individuals.

5. Our results suggest that an individual's growth can benefit from early-life movement, although the magnitude of this effect depends on local environmental conditions and the direction travelled. Our study reinforces the importance of heterogeneous and connected riverscapes that foster a diversity of individual growth responses.

KEYWORDS

bet hedging, dispersal, freshwater, otolith microchemistry, partial migration, phenotypic diversity, river regulation

1 | INTRODUCTION

The persistence of among-individual variation in the expression of dispersal phenotypes (e.g. movers or resident) suggests that different life history tactics can have commensurate performance benefits under relevant environmental conditions (Lundberg, 1987). In many species, significant rates of presumably adaptive dispersal away from the natal environment occurs in the juvenile phase (Forseth et al., 1999; Rotics et al., 2016). For example, individuals may seek new locations with more abundant and better-quality resources or actively move away from natal sites when resources become limited (Charnov, 1976). Similarly, individuals can benefit by moving away from areas of high competition (Nathan et al., 2008). Despite the benefits of movement, an individual's 'decision' to undertake juvenile dispersal is likely to incur considerable energetic and physiological costs (Noren et al., 2006). Conversely, individuals that remain in their natal habitat can experience reduced predation rates and do not risk inadvertently moving to a poorer quality location (Chapman et al., 2011; Patchett et al., 2018).

Spatiotemporal variation in environmental conditions can favour populations and species comprised of a mix of individuals that remain and disperse (Schindler et al., 2015). Individuals that remain may gain a growth, survival or reproduction benefit when local environmental conditions are favourable. When local conditions deteriorate, those individuals that have dispersed elsewhere to more favourable environments instead gain a performance advantage. When conditions are variable or unpredictable, variation in the expression of movement phenotypes can thus increase the probability of species persistence at the landscape scale and represents a form of dispersal bet-hedging (Mathias et al., 2001; Starrfelt & Kokko, 2012).

Movement costs can be exacerbated by external forces such as wind or water currents (Bonte et al., 2012; Halsey, 2016). Therefore, the benefits of dispersal away from the natal environment are conditional on the direction of movement (e.g. upstream or downstream). Such movement 'decisions' can be involuntary, as occurs when an animal is passively transported by environmental forces (e.g. wind,

current, (Nagel et al., 2021)) or active such as when individuals follow cues (Zens et al., 2017). For example, in rivers, individuals that disperse upstream are likely to have heightened energy requirements compared to those that disperse downstream because they have to swim against the prevailing current (Enders et al., 2003; Hinch & Rand, 1998). Likewise, individuals that remain in their natal reach might incur energetic costs associated with maintaining their position in refuges from high flow velocity (Whiterod et al., 2018). Whether the benefits of these movements outweigh their respective costs is complex and depends on where individuals moved from and to, and the future environmental conditions (Barraquand & Benhamou, 2008; Kahler et al., 2001).

One particularly useful and important measurement of individual performance is an individual's growth, as it is strongly associated with an individual's size at age, fecundity and in some cases, survival (Barneche et al., 2018; Sogard, 1997). Growth of aquatic animals such as freshwater fish is sensitive to the environmental conditions experienced, particularly during juvenile life stages when individuals are more susceptible to extremes in environmental conditions (Davidson et al., 2010). Once individuals are sufficiently developed to actively disperse, they can move upstream or downstream within the confines of essentially linear riverine environment. The direction in which individuals move is likely to incur different energetic costs and risks of predation or capture, and the environments that they encounter all conflate to play a critical role in governing both short-term and lifetime changes in growth (Barrow et al., 2021; Diouf et al., 2009).

Golden perch (*Macquaria ambigua*) is a wide-ranging, potamodromous fish native to Australia's Murray-Darling Basin (MDB) that has a high propensity for movement at all life stages (Koehn, Raymond, et al., 2020). Adults spawn into the water column and the eggs and larvae drift on river currents into downstream nursery habitats (Stuart & Sharpe, 2020; Zampatti & Leigh, 2013). Once individuals become free-swimming (approx. 5 days old), they either remain, or actively disperse upstream or downstream from their nursery habitat (Koehn, Raymond, et al., 2020; Kopf et al., 2014). Long-distance juvenile dispersal away from natal reaches and among river reaches is most commonly observed in spring and summer when fish are

approximately 1 year old, triggered by flow-related cues (Mallen-Cooper, 1996; Zampatti, Leigh, et al., 2018). Seasonal, interannual and spatial variation in river flow in turn plays a key role in shaping local habitat quality and overall productivity (Humphries et al., 2014; Mallen-Cooper, 1999). Examining the costs and benefits of long-distance dispersal and residency is highly relevant to managers given an emphasis on movement of wide-ranging species, such as golden perch, in environmental water strategies (Murray–Darling Basin Authority, 2020) and mitigating barriers to movement (Barrett and Mallen-Cooper 2006) because growth relates to age-dependent size and thus survival and reproductive potential (Murchie et al., 2008).

Here, we examined how dispersal phenotypes combine with environmental conditions to influence juvenile growth of golden perch. Specifically, we addressed four related questions: (1) Does the direction in which an individual disperses impact their growth? (2) How does the spatial (across reaches) and temporal (across years) environmental context affect the relationship between dispersal and growth? (3) Are these spatiotemporal effects on growth mediated by river discharge? (4) Does the dispersal direction impact an individual's longevity? We identified three potential juvenile dispersal phenotypes in wild golden perch: individuals remaining resident in their natal reach; fish that disperse upstream from their natal reach; and fish that disperse downstream from their natal reach. We compared these three wild dispersal types to the second-year growth of stocked fish from across the MDB to assess whether there were any differences in growth responses between wild and hatchery-bred fish.

2 | METHODS

2.1 | Study region and sample collection

The MDB covers 1,073,000 km² of land in eastern Australia and comprises 22 major catchments that drain into the continent's two largest rivers: the Murray River (2508 km in length) and the Darling River (2740 km in length, including its longest tributary). A large proportion of the MDB is naturally semi-arid and hydrologically variable (Leblanc et al., 2012). Golden perch occur naturally throughout the MDB, with populations augmented by the stocking of hatchery-bred fish. Our study focussed on fish in 13 river reaches in the MDB (Figure 1): the lower Murray, mid Murray, upper Murray, lower Darling, mid Darling, Condamine–Balonne, Macquarie, Murrumbidgee, Edward–Wakool, Campaspe, Loddon, Broken and Goulburn rivers. Fish were collected by boat electrofishing, using either a 5 kW or 7.5 kW Smith Root electrofishing unit (Smith Root, Vancouver, WA, United States). Study reaches were defined using a water-chemistry based isoscape (Zampatti et al., 2019). This isoscape, developed using water samples collected between 2011 and 2018 ($n=726$), was temporally stable across most reaches and allowed us to recreate the natal reach and dispersal history of each wild-caught golden perch by correlating the chemical composition of water with that of each fish's otolith (Kennedy et al., 2002; Sturrock et al., 2012). Wild-captured individuals raised in hatcheries on the Murrumbidgee River were included in the analyses. Hatchery-raised fish stocked into the Murrumbidgee River were chemically indistinguishable from

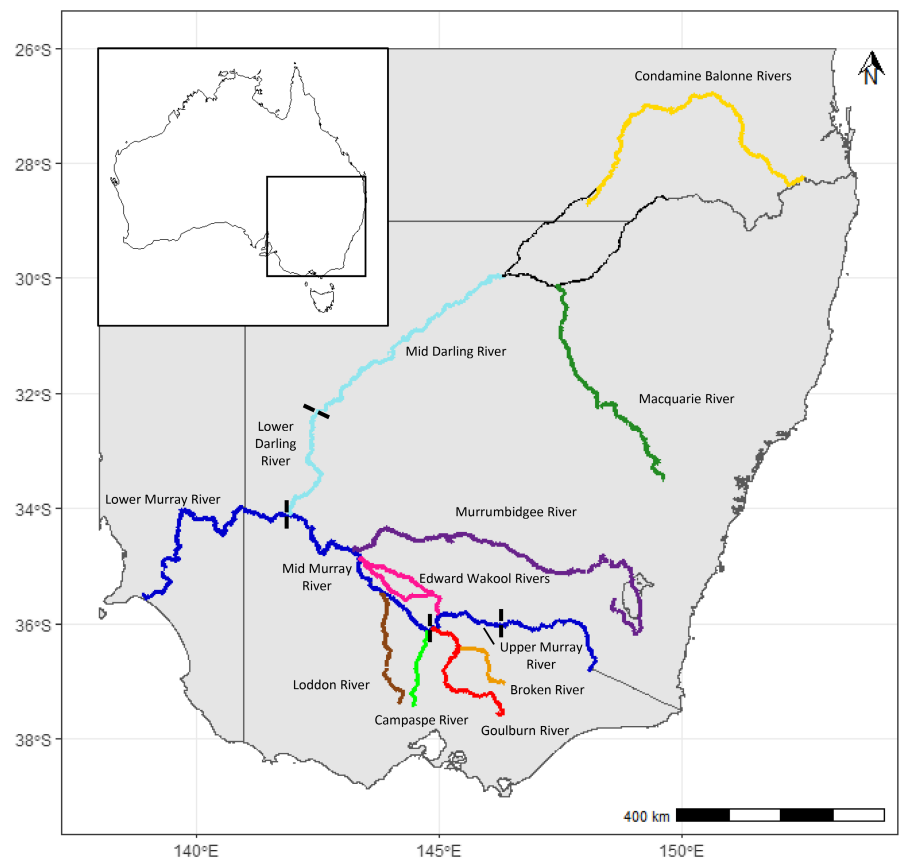


FIGURE 1 Map of the Murray-Darling Basin in south-eastern Australia. Colours denote river reaches with different Sr compositions. Multiple reaches with different Sr compositions within the Murray River (dark blue) and Darling River (light blue) are denoted by thick black lines.

wild-spawned Murrumbidgee fish as they shared the same water and so were combined into a separate Murrumbidgee/Hatchery group ($n=19$). We sourced 559 sectioned golden perch otoliths collected for previous studies (Zampatti et al., 2015, 2019; Zampatti, Strawbridge, et al., 2018) from the study reaches (Table 1) and used these to recreate individual movement and growth histories.

2.2 | Natal reach, dispersal and growth

A single 400- to 600- μm thick section was prepared from each otolith for strontium isotope ratio and annual growth increment analyses. Each otolith was imaged using a CCD digital camera (The Imagine Source, Charlotte, NC, USA) mounted onto a Leica M80 (Leica, Wetzlar, Germany) dissecting microscope at 16 \times magnification. We counted the opaque zones on the dorsal side of the sulcus to estimate age and measured the distance between the outer edge of the first zone to the outer edge of the second zone to estimate second-year growth (Anderson et al., 1992). This second-year growth measurement was subsequently used as a proxy for second-year somatic growth (Campana & Jones, 1992; Martino et al., 2019). We did not include the first annual increment as the width of this can vary due to differences in spawning date and in sectioning of otoliths.

Our otoliths had previously been analysed for strontium isotope ratios ($^{87}\text{Sr}/^{86}\text{Sr}$) using laser ablation-inductively coupled mass spectrometry (LA-ICP-MS). Dissolved $^{87}\text{Sr}/^{86}\text{Sr}$ in water is primarily derived from the underlying geology of the local and upstream catchment and can provide a geographically unique marker in otoliths (Brennan et al., 2015; Kennedy et al., 2002). Otoliths were ablated along a transect from the primordium to the outer edge. However, here we focussed on the $^{87}\text{Sr}/^{86}\text{Sr}$ profile from only the first and second growth increments as these captured movement history in a fish's juvenile life phase.

We used an assignment algorithm described in Zampatti et al. (2019), Thiem et al. (2022) and Zampatti et al. (2022) to identify an individual's natal reach, and any subsequent among-reach movements across their first 2 years of life. The assignment algorithm used a regression tree approach, beginning at the location of capture to assign a probability that a given region of the otolith was from each possible river reach. Details on the assignment algorithm approach are outlined in the Appendix S2.

We classified individuals as *resident* if they stayed within a single reach for the first 2 years of life, *downstream disperser* if they moved downstream to another reach in the first 2 years of life and *upstream disperser* if they moved upstream at least once in the first 2 years of life. The *upstream disperser* classification included individuals that moved in both a downstream and upstream direction within the first 2 years of life, because we assumed that these individuals have similar energetic demands as those that only moved upstream. Finally, *hatchery* individuals, generally stocked between one to 2 months of age, were included as an out-group comparison with wild-spawned individuals.

2.3 | Statistical analysis

We used a Bayesian mixed effects model to investigate the influence of dispersal on the second-year growth of golden perch. The response variable was otolith growth measurements from an individual's second year of life, which we log transformed to satisfy model assumptions. We included a fixed effect for the four dispersal types (*dispersal*) and a random effects structure that quantified spatial and temporal variation in how dispersal could affect growth (Table 2). We used this base model to assess differences in growth among dispersal pathways and partition variation among random effects components.

The base model structure was:

$$\begin{aligned} \text{growth} \sim & \text{dispersal} + \\ & (-1 + \text{dispersal} \mid \text{natal reach}) + \\ & (-1 + \text{dispersal} \mid \text{year 2 location}) + \\ & (-1 + \text{dispersal} \mid \text{year}) + \\ & (-1 + \text{dispersal} \mid \text{natal reach: year}) + \\ & (-1 + \text{dispersal} \mid \text{year 2 location: year}). \end{aligned}$$

Here, the notation $(-1 + x \mid z)$ and $(-1 + x \mid w: z)$ represents random effects for each level of x at each level within the grouping variable z or each combination of grouping variables w and z , respectively. Random effects of dispersal introduced separate intercepts for each dispersal type and level within a grouping variable (Table 2); stand-alone random intercepts were removed from the model (denoted by -1 in the equation above) to avoid identifiability issues (Bates et al., 2015).

We added hydrological terms to our base model to assess whether temporally variable local discharge moderated the effects of dispersal on growth (i.e. dispersal-discharge interactions). We spatiotemporally matched each reach's seasonal discharge estimates to otolith-derived locations from the natal-year and second year of an individual's life. We represented discharge with six different variables, each representing a distinct hypothesis (Table S1). The six discharge variables relied on daily flows in the first two water years (July 1–June 30) following spawning. Variables focussed on two important temporal periods throughout the year for fish movement and growth: austral spring (September to November) and austral summer (December to March). The variables were: (1) natal-year spring discharge, (2) second-year spring discharge, (3) change in spring discharge between first and second years, (4) natal-year summer discharge, (5) second-year summer discharge and (6) change in summer discharge between first and second years (Table S1). Positive values of discharge change meant that the later year had higher discharge than the preceding year. We log-transformed discharge variables 1, 2, 4 and 5 (Table S1) to ensure that large observations did not dominate parameter estimates. Specific details about how the discharge variables were calculated are outlined in the in Table S1. Hatchery fish were excluded from this analysis as the discharge variables required data from an individual's natal-year/location.

We compared the base growth model to models containing different combinations of interactions between each of the six discharge variants and dispersal using the WAIC metric (Vehtari et al., 2017),

TABLE 1 The natal reach (identified using Sr. isotope ratios), total number, age, natal-year and size range of fish used in this study.

Natal reach ^a	Number of fish	Age range (years)	Natal-year range	Size range (mm)	Discharge range (median, min and max mL/day)
Lower Murray River	78	2-25	1991-2014	134-515	8408 (0-140,483)
Mid Murray River	73	2-22	1996-2015	313-549	5922 (1365-59,905)
Upper Murray River	9	3-15	2003-2013	287-487	9863 (1488-189,427)
Lower Darling River	141	2-21	1997-2014	95-494	253 (0-21,668)
Mid Darling River	31	3-11	2007-2015	298-479	398 (0-43,438)
Loddon River	8	6-12	2006-2010	405-515	17 (0-46,062)
Goulburn River	31	3-24	1994-2015	295-520	825 (190-145,683)
Macquarie River	6	3-8	2010-2015	319-397	20 (0-10,323)
Condamine-Balonne Rivers	20	2-10	2008-2016	214-462	0 (0-236,044)
Murrumbidgee River/Hatchery	19	3-19	1997-2015	240-522	4958 (235-205,250)
Hatchery	143	2-20	1998-2016	171-540	-

^aSome individuals moved into the Broken and Edward-Wakool systems, but no individuals had a natal origin in these rivers, so they are excluded from this table.

TABLE 2 The random effects terms and their biological description included in the Bayesian mixed effects model. Random effects terms were all included in the model structure.

Random effect	Description
(-1 + dispersal natal reach)	Spatial variation in growth, and in the effect of dispersal on growth, due to where a fish starts its life.
(-1 + dispersal year 2 location)	Spatial variation in growth, and in the effect of dispersal on growth, due to where a fish resides in year 2
(-1 + dispersal natal-year)	Temporal variation in growth, and in the effect of dispersal on growth, due to the year a fish hatched
(-1 + dispersal natal reach: natal-year)	Spatiotemporal variation in growth, and in the effect of dispersal on growth, due to where and when a fish starts its life
(-1 + dispersal year 2 location: natal-year)	Spatiotemporal variation in growth, and in the effect of dispersal on growth, due to where a fish resides in year 2 and when a fish starts its life

calculated with the loo package in R (Vehtari et al., 2020). We used the variance in model predictions to calculate Bayesian R^2 values (a measure of absolute model fit) and the relative amount of variation explained by each random effect (Gelman et al., 2019). Further details on the Bayesian modelling methods are outlined in the Appendix S2.

Finally, we tested whether different dispersal types influenced individual longevity using a linear mixed effects model. The response variable was the age at capture, and we included a fixed effect of dispersal type and a random effects structure mirroring that used in our growth analysis outlined above.

3 | RESULTS

Of the 559 otolith samples, 47.4% ($n=265$) were resident individuals that remained in their nursery area, 25.2% ($n=141$) were hatchery origin fish, 17.2% ($n=96$) dispersed downstream and 10.2% ($n=57$) dispersed upstream at one point in their first 2 years of life. Individuals ranged from 2 to 25 years of age at capture and measurements of second-year growth were available across 26 years (1992-2017).

3.1 | Base model

Model diagnostics indicated that all models had converged and effectively sampled the parameter space (Figures S3 and S4). Average second-year growth was greatest for individuals that dispersed compared to those that remained resident. Growth of downstream dispersers was on average 10% greater than residents, growth of upstream dispersers was 6% greater than residents, and growth of hatchery fish was 13% greater than residents (Figure 2). The spatiotemporal effects of natal-year location and year interacting with dispersal type, and second-year location and year interacting with dispersal type explained the most growth variation, compared with other variables in the model (Figure S2).

3.2 | Discharge model

Several models that included discharge variables were more parsimonious than the base model, but all models explained similar amounts of variation (37%-38%; Table S2), noting that random

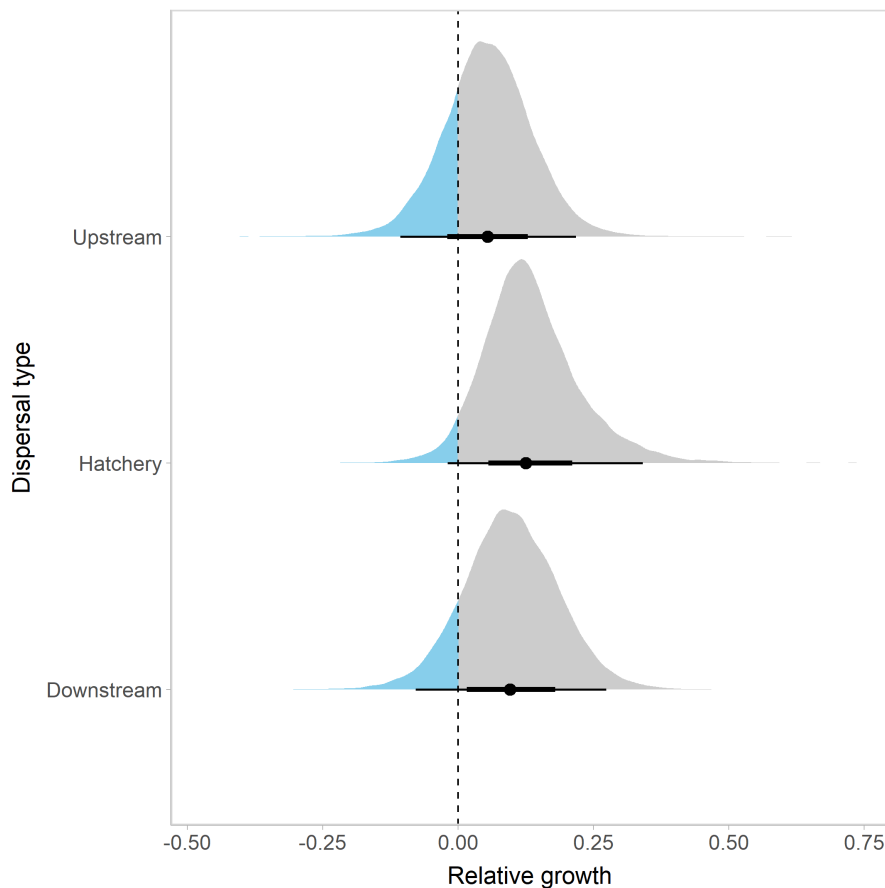


FIGURE 2 Predicted second-year otolith growth (mm) of golden perch expressing different dispersal types (black dots) relative to resident individuals, represented by the vertical dotted line. Error bars show 66% and 95% credible intervals, and the shaded grey is the density of growth measurements.

effect structures may account for considerable amounts of variation even in models with few or no discharge variables.

The model that included natal-year summer discharge performed the best (based on WAIC), followed by the model that included the natal-year spring discharge (Δ WAIC <2, Table S2). Natal-year summer discharge was associated with diminished growth of all dispersal types (Figure 3). In contrast, natal-year spring discharge was associated with increased growth of downstream and upstream dispersers but decreased growth in residents (Figure 3).

3.3 | Longevity model

Age at capture of resident fish was higher (on average) compared to other dispersal types (Table S3; Figure S5). Residents were 8% older than downstream dispersers, 4% older than upstream dispersers and 1% older than hatchery fish (Table S3; Figure S5).

4 | DISCUSSION

Second-year growth was strongly associated with dispersal direction in juvenile golden perch. Proportions of individuals moving and remaining resident were similar to previous studies on dispersal patterns of mobile fish (Radinger & Wolter, 2014). Downstream dispersers, upstream dispersers and hatchery fish all grew faster compared

to individuals that remained resident at or near their natal location. The differences in growth attributable to dispersal type were, however, dependent on the local environmental context. Increased natal-year summer discharge was linked with reduced growth for all types of fish, whereas increased natal-year spring discharge was linked with faster growth of dispersers and slow growth of resident fish. Our observed dispersal-dependent differences in growth persisted despite our inability to consider fine-scale spatial microhabitat variability or short-term movements, which suggests these growth patterns are robust. Here, we propose several mechanisms relating to how environmentally mediated differences in food resources and energetic costs could explain the link between dispersal type and growth.

Our observed differences in growth among dispersal types may indicate that each group of fish experienced different environmental conditions. In landscapes where environmental conditions are spatiotemporally variable, such as semi-arid lowland rivers, individuals that move (downstream and upstream dispersers) may benefit by actively tracking areas of higher productivity and favourable habitat (Barrow et al., 2021; Crook et al., 2020; Roberts et al., 2019). In contrast, individuals that remain resident in their natal habitat may benefit when conditions are favourable, but can be disadvantaged if conditions deteriorate (Acker et al., 2021). Alternatively, individuals may express phenotypic traits, such as boldness, competitiveness and dispersal tendency (Myles-Gonzalez et al., 2015), that may result in differences in access to food resources and ultimately, changes in

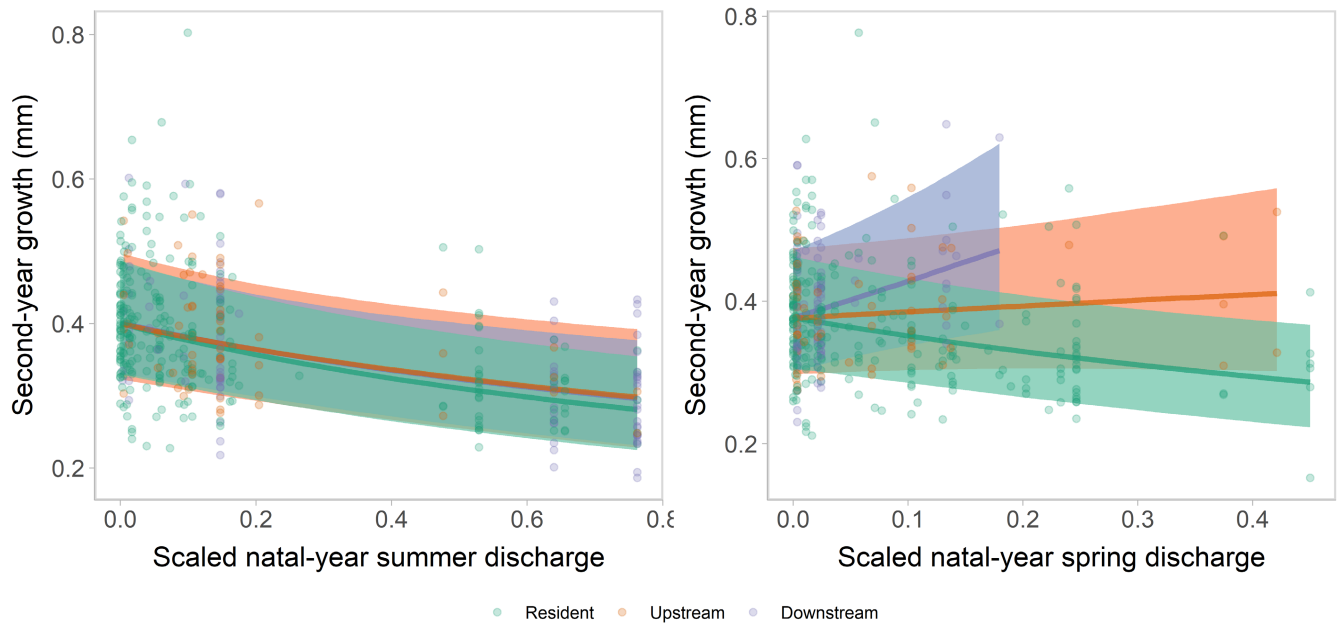


FIGURE 3 Predicted second-year otolith growth (mm) of golden perch expressing different dispersal types under increasing river discharge. The left panel is natal-year summer discharge as a proportion of the long-term median of annual maximum discharge and the right panel is natal-year summer discharge. Points represent partial residuals, and the shading represents 80% credible intervals.

growth. Dispersal can, however, be highly risky and dispersing individuals are more likely to encounter predators throughout their lives than residents, particularly as bolder individuals can also be naive to predators (Furey et al., 2016).

While the dispersers that survive may benefit from reduced competition and thus faster growth in new habitats, residents may experience lower mortality rates that offset the costs of reduced growth (Hartson & Kennedy, 2015; van Moorter et al., 2021). The presence of such a cost-benefit trade-offs may be one explanation for why resident golden perch persist despite growth being higher for dispersers, which was supported by our longevity results where evidence suggested that age at capture could be higher for resident fish than those that dispersed. The increased growth of stocked fish may be because they experienced optimal conditions in early life and are generally released to bolster low wild populations (especially for threatened species or populations subject to recreational harvest) and thus may experience lower intraspecific competition (Hunt et al., 2010). Therefore, stocked individuals that survive may express phenotypes that are the most beneficial for survival in a post-release environment (in this case, fast growth) resulting in these phenotypes being over-represented in the surviving fish samples (Barrow et al., 2020; Fleming et al., 2002). However, following release, stocked fish may also suffer higher mortality or reduced future reproductive output due to selectivity within the hatchery, poor condition, small size, injury during transportation or behavioural deficiencies including a lack of predator awareness and inability to forage for food in wild environments (Brown & Day, 2002; Sales et al., 2023; Sorrentino et al., 2020).

Labile traits, such as juvenile growth, are sensitive to both spatio-temporal environmental variation and persistent carryover effects

from early-life experience (Brett et al., 1969; O'Connor et al., 2014). We found that the spatiotemporal interactions between time and location of spawning, and between time and location of a fish's second year of life, explained the most variation in second-year growth. This finding may suggest that the impact of the environment in an individual's natal-year could carry over to second-year growth. That is, individuals that begin their life in a productive (or unproductive) location would have fast (or slow) growth and may retain this growth trajectory later in life (Burton et al., 2013; Jonsson & Jonsson, 2014; Post, 2003). A (perhaps less plausible) explanation is that productivity pulses (associated with favourable environmental conditions) take time to manifest at higher trophic levels (Tonkin et al., 2017), with changes in the growth of golden perch only becoming evident in the year following favourable conditions (Balcombe et al., 2012). Although possible, this is unlikely given that young golden perch feed close to the bottom of the food-chain (Rowland, 1996) with prey that respond quickly to environmental change (*sensu* van der Sleen et al., 2022). Further, resident individuals, who would most likely experience a lagged environmental effect because they remain in the same location, did not benefit from increased natal-year spring discharge as dispersers did.

Our analysis partially attributed the observed spatiotemporal variation in golden perch growth to natal-year summer and spring discharges. Such discharges can vary widely among sites due to differences in rainfall and river regulation (Mallen-Cooper & Zampatti, 2018). Most samples (89.8%) were from southern MDB, which likely weights our results to be more relevant to these reaches. In the rivers of the MDB, and particularly in the south, summer discharge is often naturally low which leads to increased water temperature and a greater prevalence of low-velocity, within-channel

'slackwater' habitats (Humphries et al., 1999). This natural flow regime is favourable for key juvenile golden perch prey such as micro- and macro-invertebrates and the larval and juvenile stages of summer-spawned fish (Humphries et al., 2006) and could explain our observed increase in golden perch growth under these conditions. High within-channel summer discharges that now occur due to irrigation releases in regulated river reaches of the southern MDB, may reduce these habitats, food availability and, subsequently, growth (Tonkin et al., 2021). Unnaturally high discharges may also inhibit the foraging ability and increase energy expenditure of juvenile fish (*sensu* Post, 2003; Tetzlaff et al., 2005; Whiterod et al., 2018), causing slower growth which may carry over from an individual's natal-year to their second year, where the same slow growth trajectory continues (Del Rio et al., 2021; O'Connor et al., 2014).

High natal-year spring discharge, which coincides with the spawning season for golden perch across most of the southern MDB (Koehn, Raymond, et al., 2020), had both positive and negative impacts on juvenile growth, depending on the dispersal strategy. High spring discharge is known to drive large golden perch recruitment events (Stuart & Sharpe, 2020). Locally high abundances of juvenile fish may mean increased competition for resources and differentially impact on the growth of resident fish (Rose et al., 2001). In contrast, individuals that successfully disperse away from natal areas in high spring flow years to less densely occupied habitats may experience a competitive release and gain a growth advantage (Marco-Rius et al., 2013). Conversely, in years of low spring flow with limited recruitment, competition among individuals in the second year for food resources is lower, resulting in no apparent benefit for dispersal (Morrongiello et al., 2014). In contrast, the northern MDB is often subject to high summer, rather than just spring discharges and with higher water temperatures, providing an extended spawning period (Koehn, Raymond, et al., 2020). Inferences relevant to the southern MDB may therefore not apply to all systems across this large river basin.

We detected relatively few downstream dispersers that hatched in years with high spring discharge, despite the growth benefits experienced by this phenotype. That said, a lack of downstream movers in these years does not mean that it did not occur. Individual movements may have been on a smaller, within-reach scale and thus not captured in our analysis. Or, there may have been an increased prevalence of passively dispersing golden perch eggs and larvae on high discharge events (King et al., 2016) such that movement occurred at too young an age to be detected in our Sr. transects. Importantly though, the strong positive impact of high spring discharge for moving individuals outweighs the smaller positive effect of low summer discharge, which suggests that, comparatively, high overbank spring flows are likely to be a stronger driver of fast growth years.

Large increases in discharge can have contrasting impacts on the energetic requirements of dispersal. For example, dispersing upstream against river discharge incurs considerable energetic costs that in turn can impact on growth (Whiterod et al., 2018). Upstream movements of age-1 golden perch can be rapid or staged, but nonetheless are strongly associated with increases in discharge (Koehn,

Raymond, et al., 2020). Only those individuals that had a good start in life may have had the energy reserves to move upstream (Barrow et al., 2021; Roberts et al., 2019). These energetic costs are especially pronounced when compared to downstream dispersal where individuals may undertake essentially passive and thus largely energy neutral movements (Enders et al., 2003; Lopes et al., 2019). Both upstream and downstream dispersers are likely to receive a growth benefit from moving towards locations with more abundant food resources. However, the growth benefit for upstream dispersers may be tempered by the heightened energy costs of moving against the current. Such a phenomena conforms with our observations of larger growth benefits in downstream compared to upstream dispersers. Compared to downstream dispersers and upstream dispersers, resident individuals could therefore have reduced encounters with prey and decreased capacity to chase prey or move to more preferable locations (Tetzlaff et al., 2005).

Together, our results provide valuable insight into the effects of directional movement on juvenile fish growth. We show that all dispersal phenotypes can benefit, depending on the spatiotemporal environmental context. However, dispersers incurred growth advantages in a wider range of environmental conditions. We demonstrated other benefits associated with residency, such as longevity, but were unable to determine other processes like reproductive output. The growth benefits detected in our study are likely to be conservative given that we were not able to assess the value of fine scale habitat and productivity drivers. Overall, our findings emphasise the importance of connected river systems to enable individuals to undertake movements in all directions and potentially benefit from access to spatially incongruent sources of productivity driven by variability in river discharge (Koehn, Balcombe, et al., 2020; Murchie et al., 2008).

AUTHOR CONTRIBUTIONS

Conceptualisation: JSB, JRM, JDK, JDLY; developing methods: JSB, JRM, JDK, JDLY; data analysis: JSB, JRM, JDK, BF, JDLY; preparation figures and tables: JSB, JDLY; conducting the research, data interpretation, writing: all authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data from the analysis in this manuscript are provided via figshare at <https://doi.org/10.26188/22774001.v1>. Data used in this study are provided specifically for purposes of reproducibility.

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