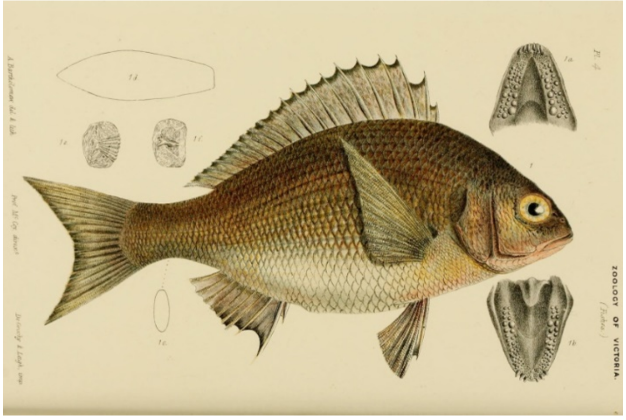
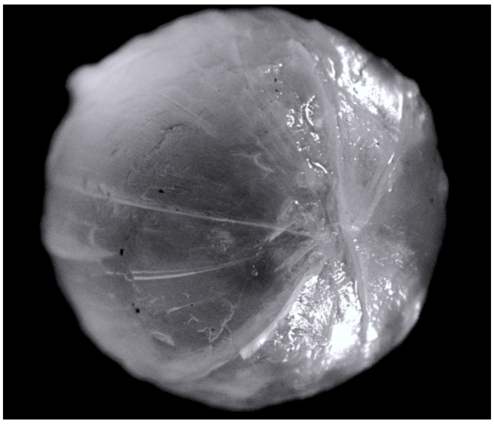
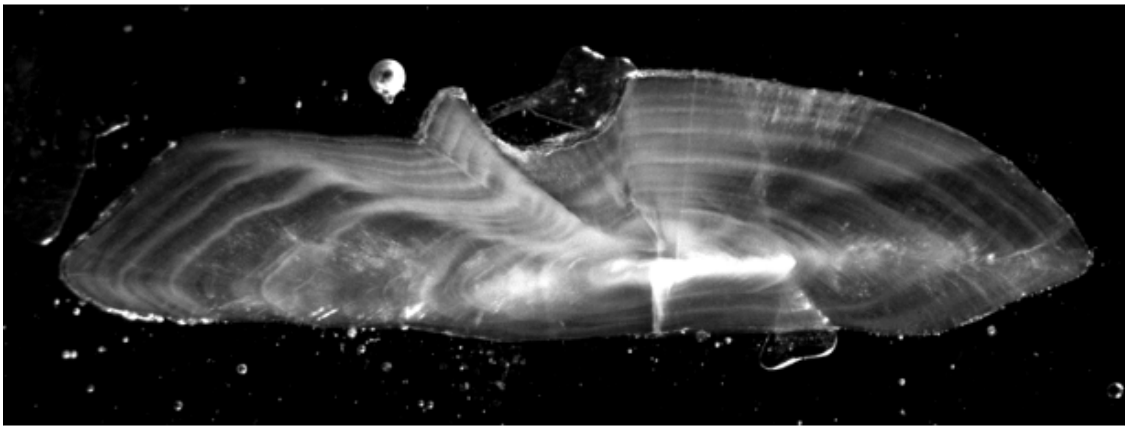
UNMASKING THE IMPACTS AND CONSEQUENCES OF ENVIRONMENTAL CHANGE ON PARTIALLY MIGRATING FISH POPULATIONS

a combined approach using otoliths and eye lenses







Thirun Gawarammana (A1834482)

Supervised by Dr Patrick Reis-Santos & Prof. Bronwyn Gillanders

Submitted in partial fulfilment of the requirements for the degree of Bachelor of Science (Honours), Discipline of Ecology and Evolutionary Biology, School of Biological Sciences.

The University of Adelaide
May 2025

THE UNIVERSITY
of ADELAIDE

Table of Contents

Cover page: Illustration of a black bream (*Acanthopagrus butcheri*) by Arthur Bartholomew in McCoy, F (1899) 'Prodromus of the Zoology of Victoria ' (Government of Victoria: Victoria, Australia), License: Public domain. Photos by author (T. Gawarammana).

Declaration

I certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name, in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name, for any other degree or diploma in any university or other tertiary institution without the prior approval of the University of Adelaide and where applicable, any partner institution responsible for the joint award of this degree.

I acknowledge that copyright of published works contained within this thesis resides with the copyright holder(s) of those works.

I also give permission for the digital version of my thesis to be made available on the web, via the University's digital research repository, the Library Search and also through web search engines, unless permission has been granted by the University to restrict access for a period of time.

Thirun Gawarammana

May 2025

Acknowledgements

First and foremost, I would like to express my immense gratitude to my brilliant supervisors, Patrick Reis-Santos and Bronwyn Gillanders for giving me the opportunity to work on this project. You have both been outstanding role models, and your constant and unwavering support throughout this process has been invaluable. I would like to acknowledge the South Australian Research and Development Institute (SARDI) for donating all the samples used in this project. This research was supported by the Australian Research Council's Discovery Projects funding scheme (DP220103846). I would like to extend my gratitude to the Goyder Institute for Water Research Coorong, Lower Lakes and Murray Mouth (CLLMM) Research Centre for their part in funding this project, and for offering further support and resources whenever I needed them. Thank you to the staff at Adelaide Microscopy for helping analyse otolith samples, and a special thank you to Tony Hall at Mawson Analytical Spectrometry Services for your help with developing and optimising the eye lens analysis.

I would like to extend a very special thank you to the amazing Rhiannon Van Eck, for teaching me absolutely everything I know in the otolith lab. I would not have made it past the processing stage without you. I am grateful to Koster Sarakinis for his guidance on bream dissections, and to all the brilliant volunteers who helped me process my many samples. I would also like to thank Joe Widdrington for always being a friendly face I could go to with my endless coding and modelling questions. A massive thank you to all my friends in the honours room and beyond, for helping me hold onto my sanity by always keeping things light and fun. I am extremely grateful to have been a part of the Gillanders Aquatic Ecology Laboratory, whose support and encouragement kept me motivated throughout the year, making my first step into the world of research a rewarding and memorable experience.

Finally, thank you to my wonderful parents, my Amma and Thaththa, for always believing in me and seeing the value in my dreams from an ocean away. You have been the foundation of everything I have achieved since day one.

Abstract

Partial migration, characterised by the coexistence of diverse migratory life histories (i.e., contingents) within a single population, is widespread among migratory fish taxa. The relative proportions of contingents are fundamental in shaping population dynamics including the resilience, productivity and stability of a population against environmental variability. This study leveraged life history data archived in fish otoliths and eye lenses to determine the effects of broad-scale environmental change on migrant proportions and assess the ecological outcomes of contrasting life history strategies in a partially migrating population of black bream (*Acanthopagrus butcheri*) in the Coorong Lagoon, South Australia. Analysis of lifetime otolith Ba:Ca profiles identified the presence of two distinct life history contingents representing estuarine resident and freshwater migrant *A. butcheri.* Generalised linear modelling demonstrated that the number of freshwater migrations per year was negatively associated with annual mean monthly rainfall and positively associated with annual mean monthly salinity. Although marginally non-significant, migrants had better mean body condition (Fulton's *K* condition factor) compared to residents. Eye lens stable isotope ratio analysis revealed divergent lifetime trends in dietary history, with $\delta^{13}C$ enriched in residents and depleted in migrants. Contrary to expectations of age-related ascensions in trophic level, $\delta^{15}N$ declined with age in both resident and migrant *A. butcheri.* Overall, identifying the environmental drivers and ecological outcomes of diverse migratory life histories has important implications for managing partially migrating fish populations under an era of accelerated anthropogenic and climatic changes to aquatic habitats.

1. Introduction

1.1 Partial migration

The ocean is a dynamic network of life, which relies on the connectivity between populations, communities and ecosystems to fuel marine productivity and resilience (Carr *et al.* 2017). Population connectivity describes the exchange of individuals among geographically isolated subpopulations within a metapopulation (Cowen *et al.* 2007), and is maintained by larval dispersal and the displacement or movement of individuals (Nathan *et al.* 2008; Leis *et al.* 2011). For species with mobile adults, such as fish, adult movement is a key paradigm of population connectivity (Frisk *et al.* 2014). In particular, adult migration is a powerful form of persistent and directional movement between habitats (Brönmark *et al.* 2014; Alò *et al.* 2021), with numerous fish species migrating to track spatially and temporally variable resources such as food, shelter and mates (Chapman *et al.* 2014). However, it is increasingly documented in many migratory fish species, that rather than the whole population migrating, only a proportion of the population migrates (Gillanders *et al.* 2015; Bryan *et al.* 2019; Steffen *et al.* 2023; Almeida *et al.* 2024). This within-population variation in migratory propensity is termed "partial migration" (Chapman *et al.* 2011b).

Partially migrating fish populations consist of groups of individuals (known as contingents), that are residents or migrants (Chapman *et al.* 2011b), with each population potentially having multiple contingents that differ in migration route or destination (Gahagan *et al.* 2015; Morissette *et al.* 2016). Partial migration has been identified across a diverse range of freshwater, estuarine and marine migratory fish taxa, including carps, salmons, eels, breams, or temperate basses, and even elasmobranchs (reviewed by Chapman *et al.* 2012b). Migrating contingents are instrumental in maintaining population connectivity, as they drive nutrient and genetic exchange by feeding and breeding between the resident and overwintering habitats (Chapman *et al.* 2011a). However, the global abundance of migratory fish populations has declined by 81% between 1970 and 2020 (Deinet *et al.* 2024), with ~21% of the assessed species classified as threatened by the International Union for Conservation of Nature (Deinet *et al.* 2020).

Migratory life histories are vulnerable to declining structural connectivity between aquatic ecosystems, caused by climate-related changes to flow regimes and sea levels (Franklin *et al.* 2024), as well as the accelerated anthropogenic fragmentation of the seascape (Lennox *et al.* 2025). It is therefore crucial to characterise the factors that drive variation in contingent proportions over time, to inform the management of partially migrating fish populations in a manner that conserves plasticity in migratory behaviour.

1.2 Migration propensity and the environment

While the fundamental driver of variation in migration propensity remains unknown, the most widely acknowledged theoretical mechanism for the migrant-resident dichotomy is the threshold model (Pulido *et al.* 1996). This model proposes that populations exhibit a normally distributed "liability" trait that underpins migration, and a "threshold" within that trait, determines the behavioural phenotype. If an individual's liability surpasses the threshold, the migratory phenotype is expressed, while individuals with liabilities below the threshold remain residents. The propensity to migrate has been linked to various genetically determined liability traits which often dictate migration success, notably, metabolic rate, swimming endurance, boldness, and body size (Chapman *et al.* 2011c; Kitano *et al.* 2012; Kelson *et al.* 2019; Eldøy *et al.* 2021).

However, liability traits are also extrinsic, as environmental variables (e.g., water flow or level fluctuations, temperature, salinity, food availability) can influence contingent proportions (Archer *et al.* 2020; Massie *et al.* 2022; Roberts *et al.* 2024). Environmental liability traits are particularly prominent in highly dynamic habitats such as estuaries and coastal watersheds, where stream flow dynamics are key determinants of migration propensity. For example, low rainfall, elevated freshwater discharge or unstable flow increase the proportion of migrants in partially migrating estuarine and coastal fish populations (Bunch *et al.* 2022; Lisi *et al.* 2022; Roberts *et al.* 2024). While the propensity to migrate is likely a result of genotype-by-environment interaction, the environment appears to hold greater significance in determining realised migratory life history (Ferguson *et al.* 2019; Prentice *et al.* 2023).

Overall, while migration propensity has a genetic basis, its phenotypic expression is shaped by environmental conditions (e.g., key liability traits such as larval growth rate are strongly influenced by freshwater flow and tidal currents) (Pulido 2011; Kelson *et al.* 2020; Arai *et al.* 2024). The phenomenon of 'contingent switching', whereby fish may switch between migratory and resident life histories (Gahagan *et al.* 2015), further highlights the environmental influence on contingent proportions. If environmental conditions in the resident habitat change, such that the cost of migration outweighs the benefits, migrants may revert to residency (Bond *et al.* 2015), and vice versa; residents may become migrants if the benefits outweigh the cost (Quinn *et al.* 2017). Furthermore, the liability threshold itself may shift towards either extreme in response to changing environmental conditions across the habitats, which could potentially modify contingent proportions (Pulido 2011). Extreme environmental changes, such as migratory barriers, place strong directional selection on partially migrating populations, which may elicit rapid evolution towards obligate residency (Phillis *et al.* 2016). Given the strong environmental influence on the migration-resident dichotomy, understanding how migrant proportions may respond to broad-scale environmental change has important implications for conserving the numerous ecological services conferred by migrants.

1.3 Implications of partial migration

In partially migrating fish populations, the temporary partitioning of individuals reduces the likelihood that all members of a cohort will encounter adverse environmental conditions (Morita *et al.* 2014). As the two contingents endure different mortality and reproductive fitness, their joint outcome dampens total population variability. This is known as an ecological “portfolio effect”, whereby even weak asynchronicity in life histories buffers the collective population against environmental variability and promotes long-term stability and sustainability of a species (Schindler *et al.* 2010; Schindler *et al.* 2015). Contingent structure also influences population dynamics in partially migrating estuarine fish. When individual life histories become more synchronous, such as when the proportion of migrants decreases, population productivity and resilience declines (Kerr *et al.* 2010).

In addition to trophic implications for the aggregate population, migratory decisions may also have important implications for the migrating individual itself. While freshwater migrants of partially migrating estuarine fishes have shown higher growth rates (Roberts *et al.* 2019) and improved body condition compared to residents (Gillanders *et al.* 2015), the potential dietary shifts or trophic advantages associated with migration is understudied, largely due to the difficulty of accessing and comparing dietary life history data between contingents. However, novel archival tissues capable of tracking dietary divergence through time show promise for identifying how migratory life history may shape the trophic ecologies of migrants compared to residents.

1.4 Archival tissues as natural tags

Microchemical analysis of archival tissues such as otoliths (fish ear bones), eye lenses, opercula, fin rays and scales provide high resolution chronologies of fish life history (Tzadik *et al.* 2017). These tissues grow in layers by assimilating elements from the surrounding water and/or diet, forming metabolically inert increments that are deposited annually and reflect a fish's entire life. Elemental analysis of otoliths has been used extensively to characterise partial migration (Morissette *et al.* 2016; Rohtla *et al.* 2020; Russell *et al.* 2022). Since concentrations of major (e.g., Sr) and trace (e.g., Ba, Mn) elements in annual otolith increments are determined by the surrounding environment, including by physicochemical parameters such as temperature and salinity (Reis-Santos *et al.* 2013), they serve as a chronological record of the environments visited by a fish over its lifetime. For instance, Sr and Ba are enriched in marine and freshwater, respectively (Elsdon *et al.* 2008), such that otolith Ba:Ca and Sr:Ca profiles are widely used to reconstruct movement of fish across salinity gradients (Walther and Limburg 2012; Fowler *et al.* 2016; Arai *et al.* 2025). Peaks in otolith Ba:Ca profiles are particularly useful for identifying freshwater migrants in partially migrating estuarine fish (Gillanders *et al.* 2015).

Fish diet reconstruction using otoliths is challenging, given that proteins constitute only ~0.45% of otolith weight (Hüssy *et al.* 2004). Fish eye lenses, however, primarily consist of carbon and nitrogen-rich structural proteins deposited in concentric segmented layers, or laminae (Dahm *et al.* 2007). Moreover, the lens diameter is strongly proportional to body length, with new laminae added during periods of somatic growth, however, unlike otoliths, each layer does not reflect an annual increment (Kurth *et al.* 2019; Bell-Tilcock *et al.* 2021). The isotopic ratio of ^{13}C:^{12}C (expressed as $\delta^{13}C$) in lamina proteins reflect dietary carbon sources, while ^{15}N:^{14}N (expressed as $\delta^{15}N$) also relate to diet and reflect trophic position, as consumer $\delta^{15}N$ signatures are 3 – 4‰ enriched relative to their diets (Post 2002; Reis-Santos *et al.* 2023). Compared to conventional tissues used for diet reconstruction, which only reflect recent diet due to continuous metabolic turnover (e.g., muscle tissue), laminae undergo little to no remodelling, thus providing a sequential, lifelong record of dietary inputs (Wallace *et al.* 2014). Therefore, if isotopic baselines of ecosystems are known, isotopic signatures of eye lenses allow the tracking of ontogenetic diet shifts (Young *et al.* 2022), habitat transitions (Bell-Tilcock *et al.* 2021), nursery origins (Bastos *et al.* 2024) and potentially dietary divergence between residents and migrants in partially migrating fish. Given that contingents spend significant durations in separate environments, they likely encounter different nutritional sources and qualities, potentially resulting in contrasting ecological outcomes. Ultimately, combining chemical information from otoliths and eye lenses allows the evaluation of potential trophic or dietary shifts achieved by migration compared to resident life histories. Understanding how trophic outcomes differ between migratory life histories is crucial, as differences in diet may translate to differences in individual fitness, which has important implications for the persistence of partially migrating fish populations.

1.5 Aims and objectives

The overall aim of this study was to evaluate whether lifetime chemical and isotopic information archived in fish otoliths and eye lenses could be harnessed to reconstruct changes in habitat use and diet shifts related to migratory life history, and to use this information to understand the impacts of environmental change on contingent proportions in partially migrating fish populations. Specifically, by leveraging lifetime chemical and isotopic information recorded in fish otoliths and eye lenses, I aimed to 1) identify how broad-scale changes to freshwater discharge, rainfall, water temperature, and salinity influence the proportion of migrants in a partially migrating estuarine fish population, and 2) investigate potential differences in dietary or trophic outcomes related to migrant life history compared to resident behaviour.

2. Materials and Methods

2.1 Study site and species

Located at the terminus of the Murray River, the Coorong is a narrow micro-tidal lagoon system, extending parallel to the South Australian coastline as a part of the larger Coorong Lower Lakes and Murray Mouth system (Figure 1) (Mosley *et al.* 2020). Conditions in the Coorong vary along a salinity gradient, alternating from generally fresh to marine near the mouth, to estuarine in the North Lagoon and hypersaline in the South Lagoon (Brookes *et al.* 2009). Freshwater influence in the Coorong is constantly fluctuating due to varying barrage flow, rainfall, tidal influence and sea levels (Webster 2011; Brookes *et al.* 2021). Furthermore, the Coorong has experienced severe environmental changes induced by climate-related events including the Millennium Drought (Leterme *et al.* 2015) and the recent 2022-2023 River Murray floods (Mosley *et al.* 2024). Thus, the Coorong serves as an excellent natural scenario to model the effects of environmental change on partially migrating fish populations.

The black bream (*Acanthopagrus butcheri)* is a temperate sparid species distributed throughout southern Australia, extending from New South Wales to Western Australia (Norriss *et al.* 2002). *A. butcheri* is estuarine-dependent as their egg and larval development require high salinities associated with salt wedges (Nicholson *et al.* 2008; Williams *et al.* 2013). However, its tolerance to a wide range of salinities enables movement into freshwater rivers and lakes (Hindell *et al.* 2008). *A. butcheri* was chosen as the focal species, as their populations are known to exhibit partial migration within the Murray River Estuary adjacent to the Coorong Lagoon (Gillanders *et al.* 2015). Additionally, the feeding habits and ontogenetic diet shifts of this species are well-described in the literature. Briefly, black bream are benthic omnivores with diverse diets (including bivalves, polychaetes, macrophytes) that undergo ontogenetic shifts with body size, which vary with the prey taxa available in the estuary (Sarre *et al.* 2000; Chuwen *et al.* 2007; Sakabe 2009; Potter *et al.* 2022).

2.2 Sample collection

All samples were collected by the South Australian Research and Development Institute (SARDI) as part of routine stock assessments. *A. butcheri* was sampled from the ‘Seven Mile’ SARDI monitoring site located in the Coorong North Lagoon (Figure 1) in October 2024, using multi-panel and commercial gill nets. Total length (mm), fork length (mm), total weight (g) and gonad weight (g) were recorded and sagittal otoliths and whole eyes were extracted. Otoliths were rinsed clean with demineralized water, air-dried and stored in microtubes, while whole eyes were stored frozen at -20^{0}C until further processing (n = 123).

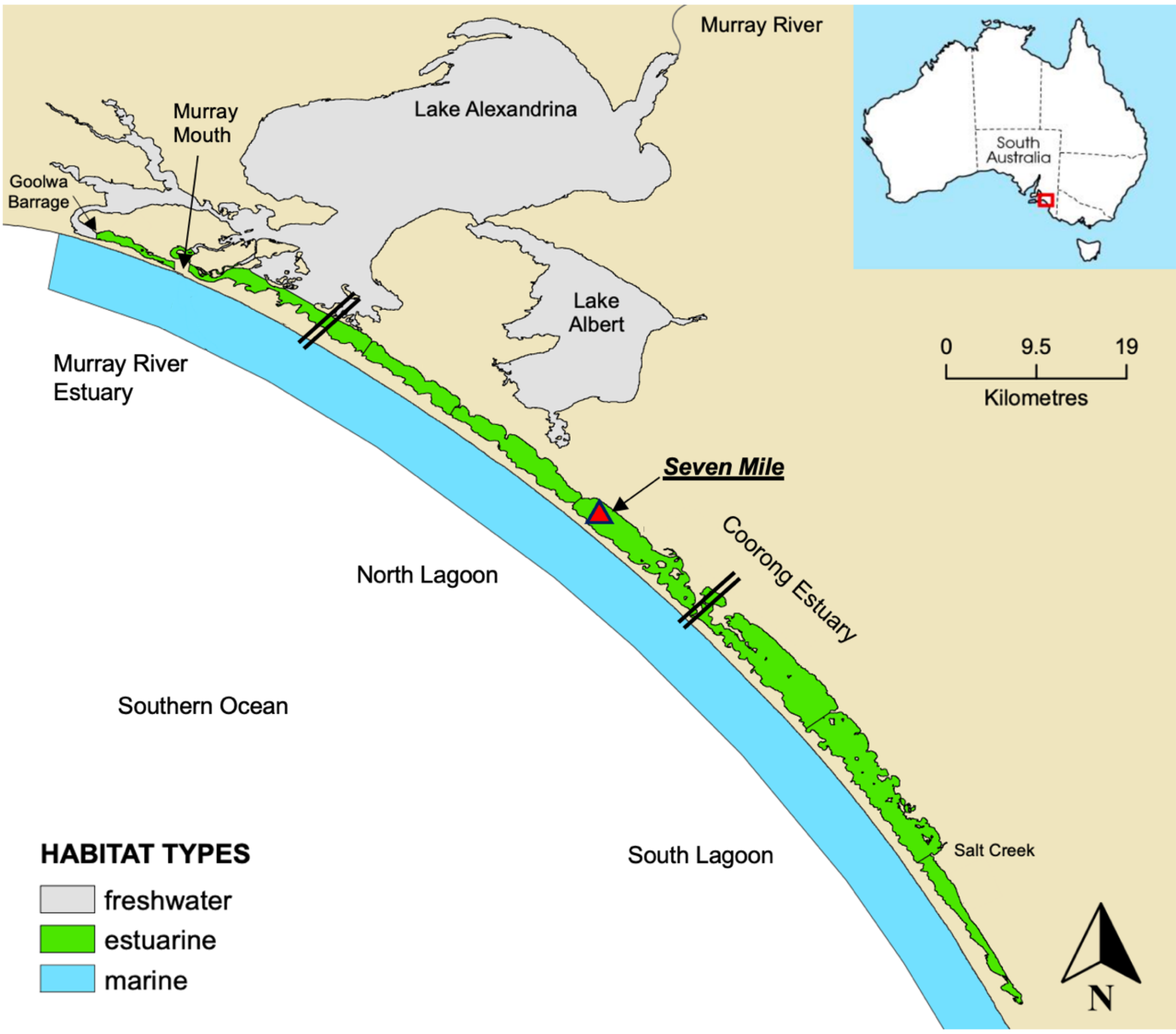


Figure 1. Map depicting Coorong Lagoon and Murray River Estuary, with *A. butcheri* sampling location “Seven Mile” highlighted by red triangle. Double lines indicate boundaries separating the Murray River Estuary, and North and South Lagoons. Adapted from Lester *et al.* (2009); Ye *et al.* (2018); Earl (2020).

2.3 Sample preparation

2.3.1 Otolith preparation

Otoliths were embedded in indium-spiked (30 ppm) epoxy resin and hardened in an oven at ~50-60^{0}C. Indium (^{115}In) was used as a marker for distinguishing otolith material from the resin (Reis-Santos *et al.* 2012). An Isomet low-speed saw fitted with twin spaced diamond blades was used to section otoliths transversely through the core, to produce thin sections of ~300-350 µm thickness. The sections were then wet polished on both sides using lapping films with successively finer grit sizes (30, 9, 3 µm). Polished sections were randomly mounted on glass slides (26mm x 76mm) using indium-spiked thermoplastic glue and sonicated with ultra-pure (Milli-Q) water prior to chemical analysis (Figure 2A).

2.3.2 Eye lens delamination

Eye lenses were dissected from whole eyes and rinsed sparingly, with droplets of ultra-pure (Milli-Q) water. Each lens was placed in a Petri dish under a dissecting stereomicroscope for delamination. Following protocols outlined by Bell-Tilcock *et al.* (2021), first the lens suture (the point where a lamina fuses together) was located (Figure 2B). Using fine-tip forceps, a singular lamina was removed by peeling naturally defined sections that fuse at the suture. Sequential laminae were peeled from one pole to the other, always beginning at the same pole, until the lens nucleus (hard core) was reached. Throughout the delamination process, ultra-pure water was used sparingly and only when needed to moisten the lens when it became brittle, as some lens crystallin proteins are water-soluble (Wallace *et al.* 2014). Laminae were desiccated in an oven at 25^{0}C for ~45 minutes, and individual lamina were homogenised by crushing. A ~0.6 mg subsample per lamina was weighed using an analytical balance and wrapped in an 8 x 5mm pressed tin capsule for isotopic analysis.

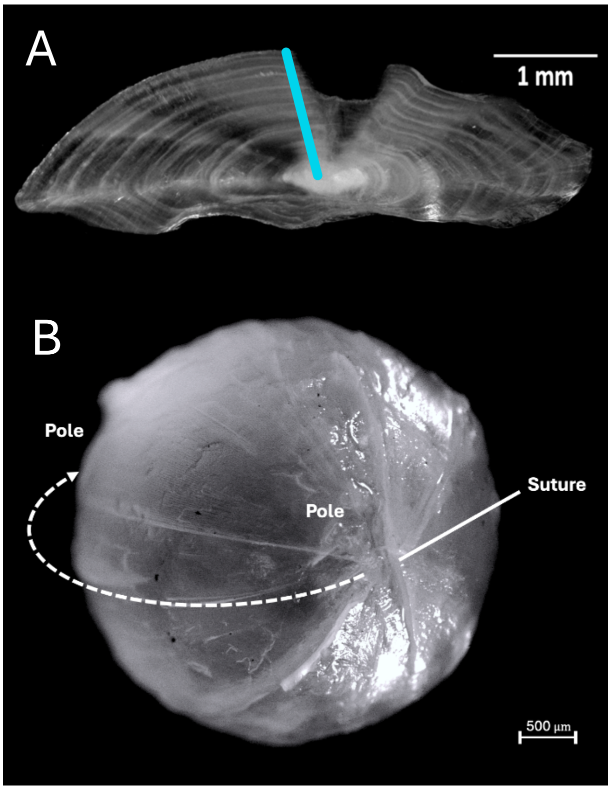


Figure 2. Sectioned *A. butcheri* otolith (**A**) illustrating the orientation and trajectory of the ablation transect (blue line). Microscope image of *A. butcheri* eye lens (**B**) depicting suture position and peeling motion from one pole to the other (dashed line). (Otolith image courtesy of Koster Sarakinis).

2.4 Otolith sample processing

2.4.1 Laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS)

Lifetime otolith elemental composition (n = 123) was analysed using Laser Ablation Inductively Coupled Plasma Mass Spectrometry (LA-ICP-MS), with an Agilent 7900x ICP-MS paired with a RESOlution-LR 193nm Excimer laser system. A selection of 11 elements were quantified, namely, lithium (^{7}Li), sodium (^{23}Na), magnesium (^{24}Mg), phosphorus (^{31}P), calcium (^{44}Ca), manganese (^{55}Mn), copper (^{63}Cu), zinc (^{66}Zn), strontium (^{88}Sr), barium (^{137}Ba) and lead (^{208}Pb). Indium (^{115}In) was also quantified to detect contamination by epoxy or thermoplastic glue caused by cracks in the otoliths, while calcium (^{43}Ca) was measured as an internal standard to monitor signal drift (Yoshinaga *et al.* 2000).

Aligned with expected increment size for *A. butcheri*, a beam size of 30 µm was applied (Sarakinis *et al.* 2024). A transect covering each fish's entire life history was ablated adjacent to the sulcal groove, from the primordium to the otolith edge (Figure 2A), using a speed of 3 µms^{-1}, frequency of 10 Hz, and fluence of 3.5 J/cm^{2}. NIST 612, a certified glass reference material, was ablated every ~5-10 samples throughout analysis, for sample calibration and monitoring instrument drift (National Institute of Standards and Technology 2024). Two carbonate standards, MACS-3 and KCSp-1NP were ablated at the start and end of each analysis to evaluate external precision (Jochum *et al.* 2012). The mean recovery of all elements ranged from 100.00% to 100.44% for NIST 612. The coefficient of variation per element ranged from 0.17% to 1.14% (NIST 612), 1.29% to 11.34% (MACS-3) and 0.94% to 12.24% (KCSp-1NP), and were considered within acceptable limits of precision and accuracy.

2.4.2 Data reduction and treatment

Raw LA-ICP-MS outputs were converted from counts per second (cps) to parts per million (ppm) in *Iolite* software (Paton *et al.* 2011), by subtracting background signals and applying calibration curves generated from NIST 612 counts. Elemental concentrations (ppm) were ratioed to calcium (element:Ca) (µmol/mol) (Yoshinaga *et al.* 2000).

2.4.3 Otolith ageing

Otolith sections were imaged under a dissecting microscope using the software *ImageJ* (Schneider *et al.* 2012). Once the otolith core and edge were defined, annual growth increments were counted by identifying the opaque bands along the ablation scar, following the *A. butcheri* ageing protocol outlined by Morison *et al.* (1998). Increment widths were measured and assigned a year and age by back-calculating from the year of capture. For each fish, the distance measurements along the ablated transect, representing a time series of element:Ca ratios, were aligned with the increment widths measured in *ImageJ*, allowing elemental concentrations to be matched to otolith growth and a corresponding year.

2.5 Eye lens isotope ratio mass spectrometry (IRMS)

Forty *A. butcheri* were selected for dietary stable isotope ratio analysis (n=40). Laminae were analysed for $\delta^{13}C$ and $\delta^{15}N$ by Mawson Analytical Spectrometry Services, using a continuous flow isotope ratio mass spectrometer (Nu Horizon, Wrexham, UK) paired to an elemental analyser (EA3000, EuroVector, Pavia, Italy). Stable isotope ratios were expressed in δ notation (parts per mil, ‰) relative to standards (Vienna Pee Dee Belemnite for $\delta^{13}C$ and atmospheric abundance for $\delta^{15}N$):

$$\delta^{13}C = [(R_{\text{sample}}/R_{\text{standard}})-1] \text{ x } 1000.$$

$$\delta^{15}N = [(R_{\text{sample}}/R_{\text{standard}})-1] \text{ x } 1000.$$

Where R_{sample} is the abundance ratio of ^{13}C /^{12}C or ^{15}N /^{14}N in the sample, and R_{standard} is this ratio in the standard. Samples were corrected for instrument drift and normalized based on reference values using the USGS88 Marine Collagen Certified Reference material (n=3) ($\delta^{13}C$ = USGS88 -16.06 *‰*, $\delta^{15}N$ = USGS88 14.96*‰*) and in-house standards (n=14), glycine ($\delta^{13}C$ = glycine -31.2*‰,* $\delta^{15}N$ = glycine 1.32*‰*) and glutamic acid ($\delta^{13}C$ = glutamic acid – 16.72*‰,* $\delta^{15}N$ = glutamic acid – 6.17*‰)* calibrated against USGS and IAEA certified reference materials (USGS40, USGS 41, IAEA-2).

2.6 Data analysis

2.6.1 Otolith chemistry

Element:Ca profiles were smoothed using a rolling mean (window size = 7 values) to minimize noise and enhance signal fluctuations that may be indicative of migration (*R* package *zoo*, Zeileis and Grothendieck 2005). Lifetime profiles of smoothed Ba:Ca were plotted against calendar year to visually identify potential migrations to freshwater. Considering freshwater resident *A. butcheri* exhibit approximately double the Ba:Ca signals as estuarine residents, a threshold of 20 µmol/mol was used to infer freshwater migration, based on an approximate Ba:Ca baseline of 10 µmol/mol observed across all individuals (Elsdon and Gillanders 2005).

Element:Ca time series features, specifically, mean, variance, linearity, curvature, trend, spike, entropy and autocorrelation of lags and residuals were extracted and scaled for K-means clustering analyses to group fish with similar profile trends (*R* package *tsfeatures*, Hyndman *et al.* 2023). Clustering algorithms using feature data from Ba:Ca alone, Sr:Ca alone, Ba:Ca and Sr:Ca combined, and all element:Ca ratios combined, were run, with number of clusters specified (K) ranging from 2 to 5 (*R* package *stats*, R Core Team 2024). For each predicted K, a silhouette score was calculated to evaluate the similarity of each profile to its assigned cluster centroid relative to the nearest neighbouring centroid (*R* package *factoextra*, Kassambara and Mundt 2020). A greater score suggests better cluster separation, thus a more appropriate number of clusters. Cluster assignment by the algorithm with the highest silhouette score and least cluster overlap (determined by visualization of clusters in scatterplots) was selected for subsequent analysis. An F1 score was also calculated to estimate the agreement between the grouping of fish by K-means clustering and ground truth assignment through visual inspection of Ba:Ca profiles (Landuyt *et al.* 2020).

2.6.2 Body condition estimation

Fulton's K condition factor was calculated for each fish, where a higher K value indicates better body condition (Caldarone *et al.* 2012).

$$K = \frac{\text{Total weight (g)} - \text{gonad weight (g)}}{\text{Fork length}^3\ \text{(cm)}} \times 100$$

Gonad weight was deducted from total weight as it showed high variability within 50g weight classes, and fork length was used as some fish lacked total length estimates due to fin damage. Fish were divided into groups per cluster assignment by the most appropriate K-means clustering, and an ANOVA (analysis of variance) was used to test for significant differences in Fulton's K values between groups. Assumptions for ANOVA were met, as estimated using Shapiro Wilk's test for normality and Levene's test for homogeneity of variance.

2.6.3 Modelling environmental influence on migration

The mean monthly water temperature (°C), salinity (electrical conductivity, µS/cm at 25°C), rainfall (mm) and discharge (mm) per year, spanning from 2010 to 2024 (the lifespan of the oldest fish in the sample) were calculated from monitoring stations across the Coorong North Lagoon (Department for Environment and Water 2021). In line with cluster analysis outcomes and expected influence of freshwater on otolith Ba, mean annual Ba:Ca was initially modelled against water temperature, salinity, rainfall and discharge data using generalized linear models (Gamma and Log-normal distributions) to assess the influence of environmental conditions on chemical signatures related to migration. However, model diagnostics (*DHARMa* residuals) indicated poor fits, with significant deviations from expected quantiles (*R* package *DHARMa*, Hartig 2024) (Appendix 1, Figures S1-2).

Therefore, to improve model robustness, the continuous response variable was transformed into count data, by summing the total migration events per year across all fish. Individual Ba:Ca profiles were inspected, and peaks above the 20 µmol/mol threshold were counted as migration events for the corresponding years. The number of migration events per year were then modelled against environmental variables using generalized linear models (GLM) fitted using a Poisson distribution with a log link function. Rainfall and discharge were found to be positively correlated (*R* package *GGally*, Schloerke *et al.* 2021) (Appendix 2, Figure S3), and were therefore modelled separately by constructing two global models: one excluding rainfall data and another excluding discharge data (Table 1). The dredge function (*R* package *MuMIn*, Bartoń 2025) was applied separately to the global models, to identify the most parsimonious model based on the corrected Akaike Information Criterion weight (AICc). Finally, the most parsimonious model was tested with a random effect for year, to assess whether variation among years independently influenced the number of migrations beyond the effects of environmental conditions (*R* package *MuMIn*, Bartoń 2025). For each model, residual Q-Q plots and residual deviations from expected quantiles were assessed to select the model that best fit the data (*R* package *DHARMa*, Hartig 2024).

Table 1. Global Poisson GLMs constructed to model rainfall and discharge data separately, to eliminate multicollinearity

Model including	Global model
Rainfall	glm(Migration.events ~ mean_salinity + mean_water_Tr + mean_rainfall, family = poisson(link = "log"))
Discharge	glm(Migration.events ~ mean_salinity + mean_water_Tr + mean_discharge, family = poisson(link = "log"))

2.6.4 Eye lens chemistry

To ensure representation of all migratory life histories in the sample, lifetime otolith Ba:Ca profiles were visually inspected to select 15 potential migrants to freshwater and 15 potential residents for eye lens stable isotope ratio analysis, along with 10 randomly sampled individuals (n=40). Group assignment and confirmation of membership were later confirmed by K-means clustering. The mean $\delta^{13}C$ and $\delta^{15}N$ values per lamina were calculated for each group to produce a biplot of $\delta^{13}C$ against $\delta^{15}N$, to visualise lifetime trends within each group. The biplot was facet wrapped by cohort to inspect potential variation over time. Due to the non-independence of data resulting from repeated measurements per fish, mixed-effects models with a random effect of Fish_ID were used to examine potential differences in lifetime $\delta^{13}C$, $\delta^{15}N$ and C:N ratios between groups and assess trends in $\delta^{13}C$, $\delta^{15}N$ and C:N ratios across laminae within each group (*R* package *lme4*, Bates *et al.* 2015). All statistical analyses were conducted in R (R Core Team 2024), with the additional package ggplot2 (Wickham 2016) used for plotting.

3. Results

A total of 123 *A. butcheri* were analysed for lifetime otolith elemental profiles (LA-ICP-MS), while 40 of those individuals were selected for eye lens stable isotope ratio analysis (IRMS). Individuals ranged between 291 and 405 mm (fork length) in size. Based on otolith aging, cohorts represented the 2010 to 2019 age classes, and age at capture ranged from 5 to 14 years, with the majority of fish (64.2%) 5 years old (2019 cohort).

3.1 Determining life history contingents

Among all the tested combinations of elements, K-means clustering using Ba:Ca data consistently produced the highest silhouette scores, indicating it was the most effective for distinguishing between lifetime trends in otolith profiles (Table 2) (Appendix 3, Figure S4). The highest silhouette score was obtained when K = 2 clusters were specified, suggesting that there were most likely two profile types and life history groups in the sample. Furthermore, the lack of overlap between clusters indicates strong differences between the two profile patterns (Figure 3). Therefore, cluster assignment by Ba:Ca data (K = 2) was implemented for further inference and analyses. The majority of fish (108) were included in cluster 1, while fewer individuals (15) were assigned to cluster 2. Ba:Ca profiles against calendar year were plotted separately for each cluster to visualise differences in lifetime trends (Figure 4). All individuals in cluster 2 had large fluctuations in Ba:Ca, with at least one peak in Ba:Ca across the life history exceeding the threshold of 20 µmol/mol used to define freshwater migration in *A. butcheri* (Figure 4B). Contrastingly, in cluster 1, Ba:Ca profiles showed reduced range variation, smaller oscillations, and never exceeded the 20 µmol/mol threshold, apart from one individual at the start of their life history (Figure 4A).

Table 2. Summary of K-means clustering analyses based on various otolith element:Ca feature data and K value combinations, with best clustering algorithm highlighted in yellow.

Element:Ca ratio(s) analysed	Number of clusters	Silhouette score	Silhouette score rank
Ba:Ca	K = 2	0.382	1
	K = 3	0.212	4
	K = 4	0.218	2
	K = 5	0.218	3
Sr:Ca	K = 2	0.184	5
	K = 3	0.157	8
	K = 4	0.166	7
	K = 5	0.182	6

Ba:Ca + Sr:Ca	K = 2	0.121	10
	K = 3	0.127	9
	K = 4	0.113	11
	K = 5	0.113	12
All Element:Ca (Li, Na, Mg, P, Mn, Cu, Zn, Sr, Ba, Pb)	K = 2	0.064	13
	K = 3	0.062	14
	K = 4	0.050	15
	K = 5	0.048	16

The F1 score (83.87%) indicated good agreement between quantitative (K-means clustering) and qualitative (visual inspection) classification of fish as migrants. Therefore, fish assigned to cluster 1 and cluster 2 are henceforth defined as residents and migrants respectively, for further analyses and interpretations.

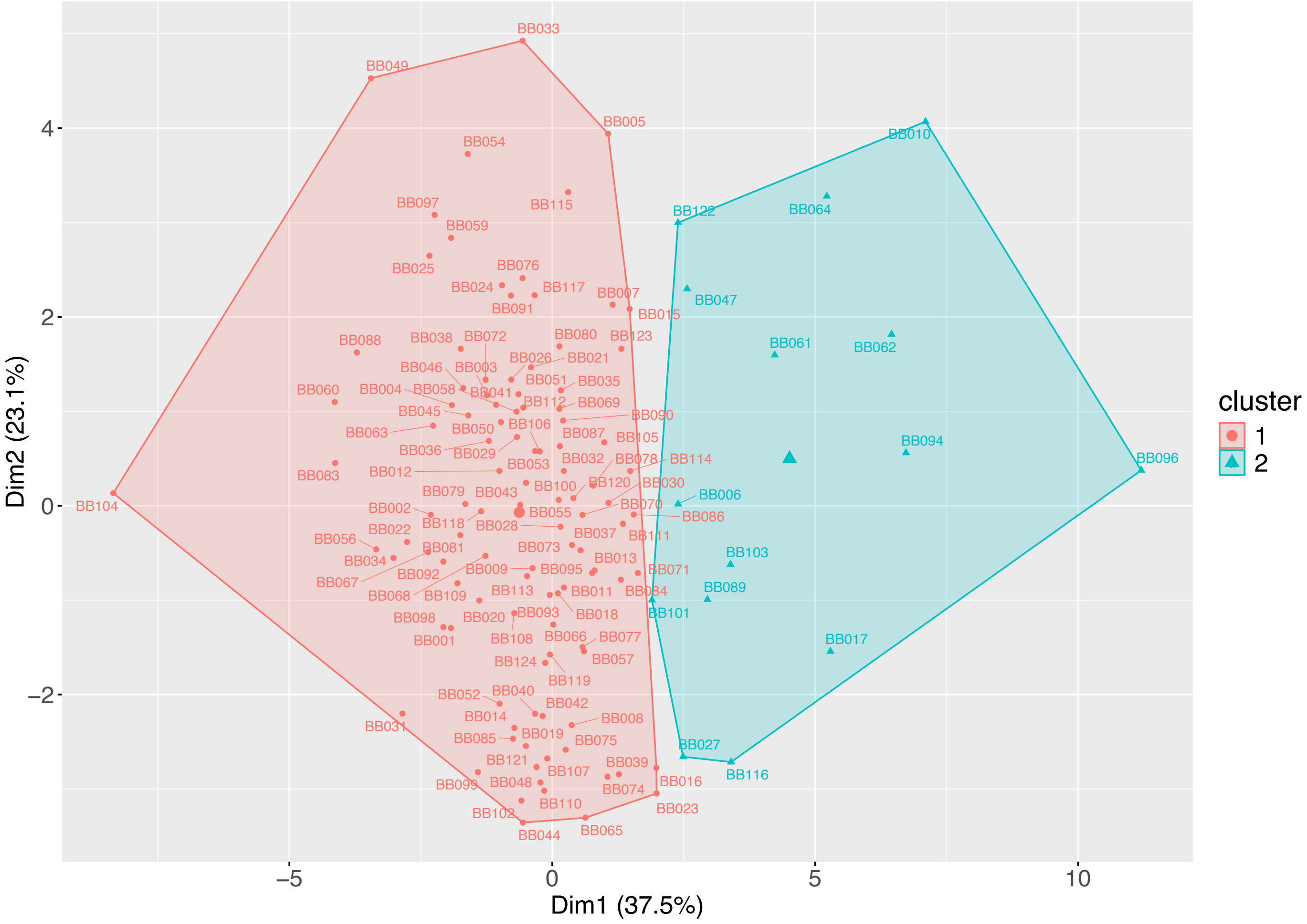


Figure 3. Scatterplot depicting K-means clustering results based on otolith Ba:Ca feature data with K = 2 clusters specified (n = 123). Colours and symbols reflect the different clusters. Numbers are sample ID.

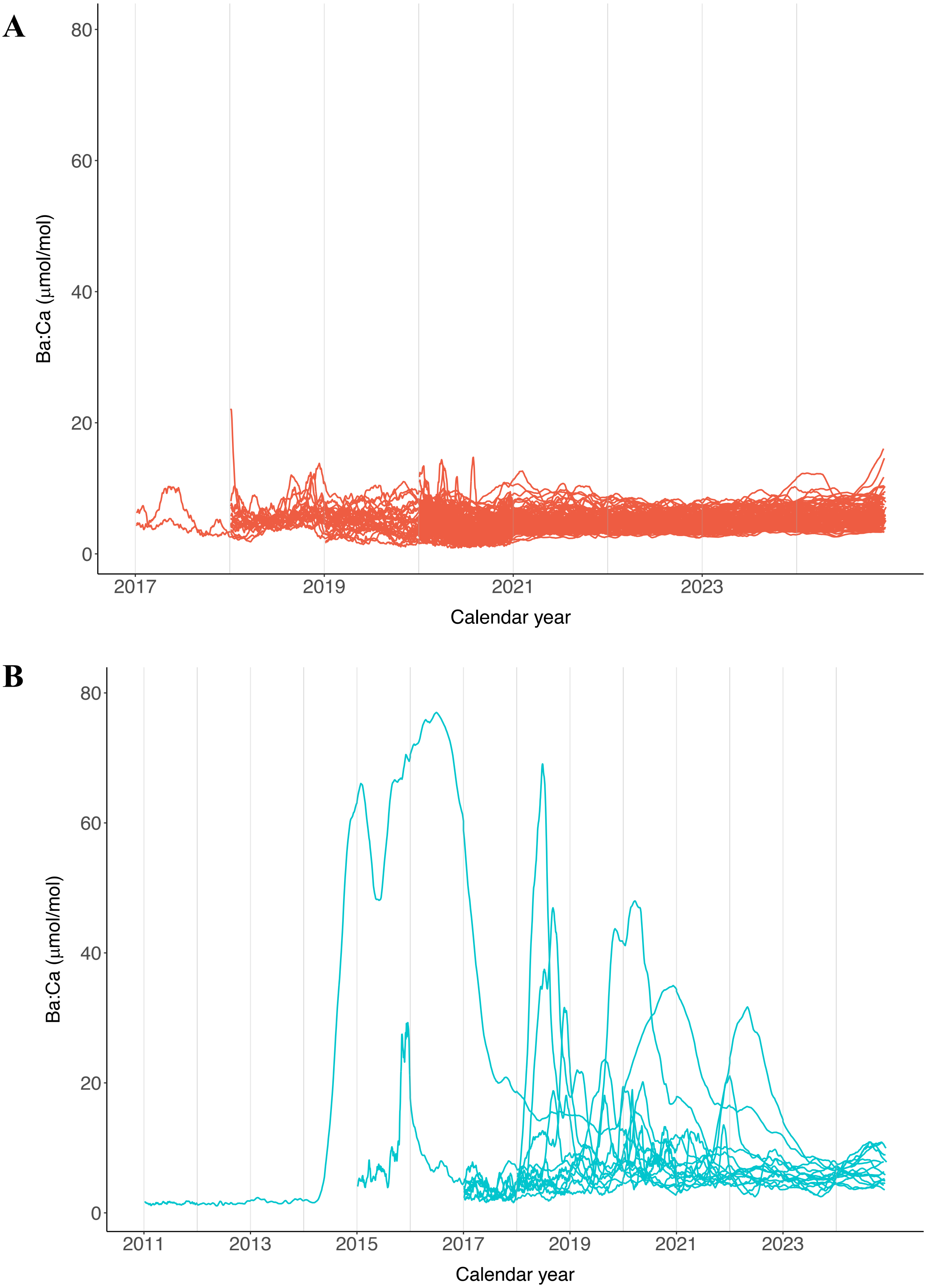


Figure 4. Otolith Ba:Ca profiles against calendar year for fish assigned to cluster 1 (**A**) and cluster 2 (**B**) by K-means clustering using Ba:Ca data with K = 2 clusters specified (n = 123). Ba:Ca exceeding 20 µmol/mol were considered indicative of freshwater migrations. Note x-axis varies between plots.

3.2 Fulton's *K* condition factor

The migrating contingent had better body condition compared to residents, as indicated by a marginally higher average Fulton's *K* value (Table 3), although this difference was not significant ($F_{(1, 121)} = 3.802$, $p = 0.054$).

Table 3. Fish body condition estimated by Fulton's *K* factor, with mean and standard error per contingent.

Contingent	Mean	SE
Resident	2.29	0.0145
Migrant	2.37	0.0374

3.3 Correlating migration events per year with environmental data

Resident *A. butcheri* were excluded from modelling as only migrant profiles had migration events. The best model from the global model including rainfall had the higher AICc weight (Table 4a) and was considered the best-performing GLM. This model was tested for overdispersion by comparing *DHARMa* simulated and observed residual standard deviations, and no significant overdispersion was detected (dispersion = 0.836, $p = 0.736$). Additionally, there was no substantial support for including a year random effect as a GLMM approach. (See Appendix 4: Table S1-S2 for full model comparisons). Both rainfall and salinity had significant effects on the number of migration events per year (Table 4b). Mean monthly rainfall per year showed a negative association, while mean monthly salinity per year showed a positive association with the number of migrations per year (Figure 5).

Table 4. AICc weights for the best ranked GLM and GLMM within two global models including either rainfall or discharge (a) and summary statistics for the best-performing GLM (b). Significance under a given *p* value is represented by asterisks, where ** <0.01 and *** <0.001.

(a) Global model	Best model	logLik	AICc weight
Rainfall	Migration.events ~ mean_rainfall + mean_salinity	-23.840	0.774
Discharge	Migration.events ~ mean_salinity	-28.040	0.604
Rainfall	Migration.events ~ mean_rainfall + mean_salinity + (1|Year)	-23.840	0.690

(b) Coefficient	Estimate	SE	*z*	*p*
Intercept	0.753	0.209	3.610	<0.001***
mean_rainfall	-0.498	0.181	-2.745	<0.010**
mean_salinity	0.713	0.185	3.844	<0.001***

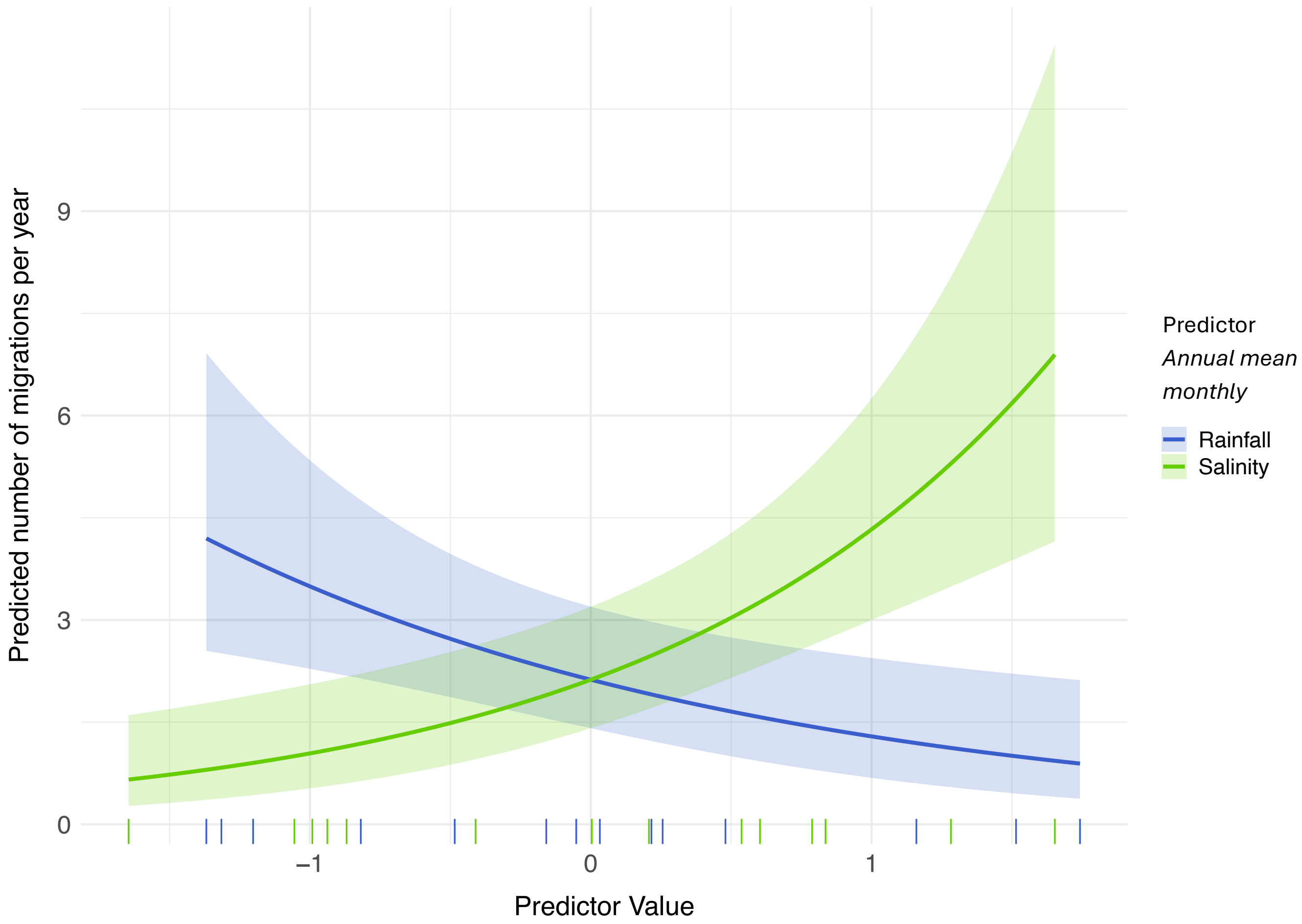


Figure 5. Model predicted trends in *A. butcheri* migrations per year as a function of annual mean monthly rainfall (blue) and salinity (green), with 95% confidence intervals indicated by shaded ribbons (n = 15 fish). Predictions were derived from the best fit Poisson model, by varying one predictor while holding the other constant at its mean. Rug ticks along the x axis represent the distribution of observed data for rainfall and salinity.

3.4 Determining lifetime dietary divergence between life histories

Lifetime trends in $\delta^{13}C$ and $\delta^{15}N$ in eye lens laminae differed between migrants and residents, with mean $\delta^{13}C$ generally becoming less depleted with age in residents and more depleted in migrants (Figure 6A). For both residents and migrants, mean $\delta^{15}N$ generally declined with age. However, the overall range of values was low, with variation across all residents and migrants below 0.8‰ and 0.5‰, respectively. Trends in $\delta^{13}C$ and $\delta^{15}N$ varied by cohort for both migrants and residents (Figure 6B). For migrants from certain cohorts (2014, 2017, 2019) lifetime $\delta^{13}C$ became less depleted, while resident $\delta^{13}C$ became more depleted in the 2018 cohort. Notably, only the oldest migrant (aged 14 years at capture), from the 2010 cohort showed a slight increase in $\delta^{15}N$ with age.

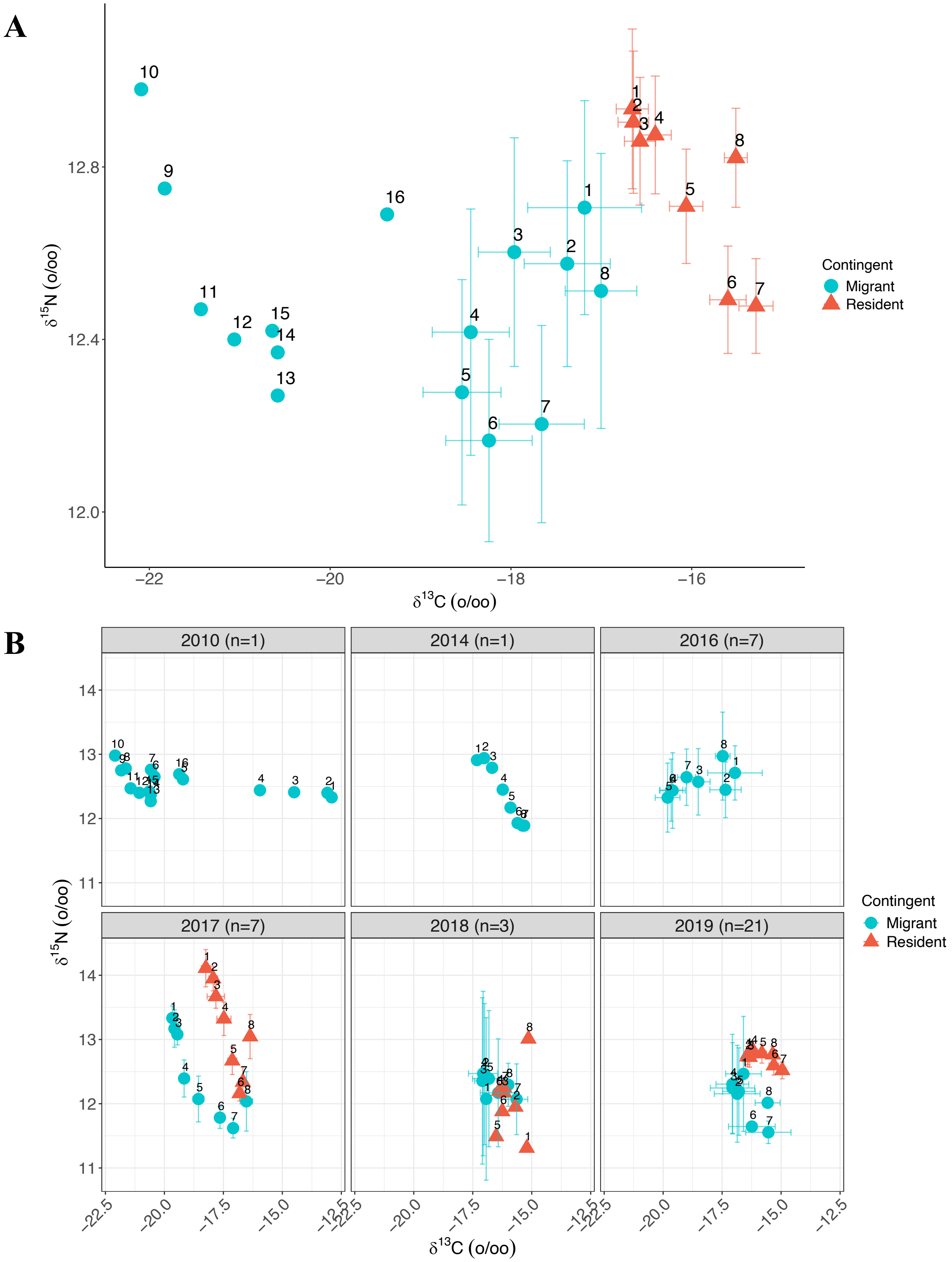


Figure 6. Biplots of mean δ^{13}C and δ^{15}N per lamina with standard error bars, showing lifetime trends in diet within each contingent (**A**) and by cohort (**B**) (n = 40 fish). Laminae are numbered from 1 (innermost lamina) to 16 (outermost lamina), reflecting increase in fish size and age. Sample sizes (n) per cohort are indicated at the top of each grid in **(B)**. Note number of laminae does not necessarily correlate to age.

Mixed-effects modelling revealed that resident δ^{13}C was enriched by 1.83 ± 0.30 ‰ compared to migrants, while δ^{15}N and C:N did not differ significantly between contingents (Table 5a). Mixed-effects modelling of δ^{13}C, δ^{15}N and C:N across laminae showed that in migrants, δ^{13}C became significantly more depleted with age at a rate of -0.123 ± 0.054 ‰ per lamina, while in residents, δ^{13}C became significantly less depleted at a greater rate of 0.215 ± 0.016 ‰ per lamina (Table 5b) (Figure 7A). Residents showed a gradual decline in δ^{15}N with age (-0.050 ± 0.016 ‰), and although not significant, a similar depletion trend was observed in migrants (Figure 7B). Lifetime C:N increased slightly with age in both residents and migrants, although this trend was only significant in residents (Table 5b).

Table 5. Summary of mixed-effects models to compare δ^{13}C, δ^{15}N and C:N between contingents (**a**) and trends across laminae per contingent (**b**). All models included a random effect for individual fish (1|Fish_ID). Model estimates (**a**) are given for the resident contingent. Effect significance under a *p* value of 0.05 is indicated by *.

(a) Model	Estimate	SE	Residual variance	Residual Std.Dev	*p*
δ^{13}C ~ Contingent	1.833	0.302	1.570	1.250	$4.51e^{-07*}$
δ^{15}N ~ Contingent	0.326	0.222	0.297	0.545	0.151
C:N ~ Contingent	-0.006	0.011	0.005	0.011	0.608

(b) Contingent	Model	Estimate	SE	*p*	Trend
Resident	δ^{13}C ~ Lamina	0.215	0.016	$<2e-16^{*}$	Increase
	δ^{15}N ~ Lamina	-0.050	0.014	$3.79e^{-4*}$	Decline
	C:N ~ Lamina	$3.42e^{-4}$	$1.63e^{-4}$	0.037^{*}	Increase
Migrant	δ^{13}C ~ Lamina	-0.123	0.054	0.024^{*}	Decline
	δ^{15}N ~ Lamina	-0.040	0.021	0.056	Decline
	C:N ~ Lamina	0.004	$2.5e^{-4}$	0.091	Increase

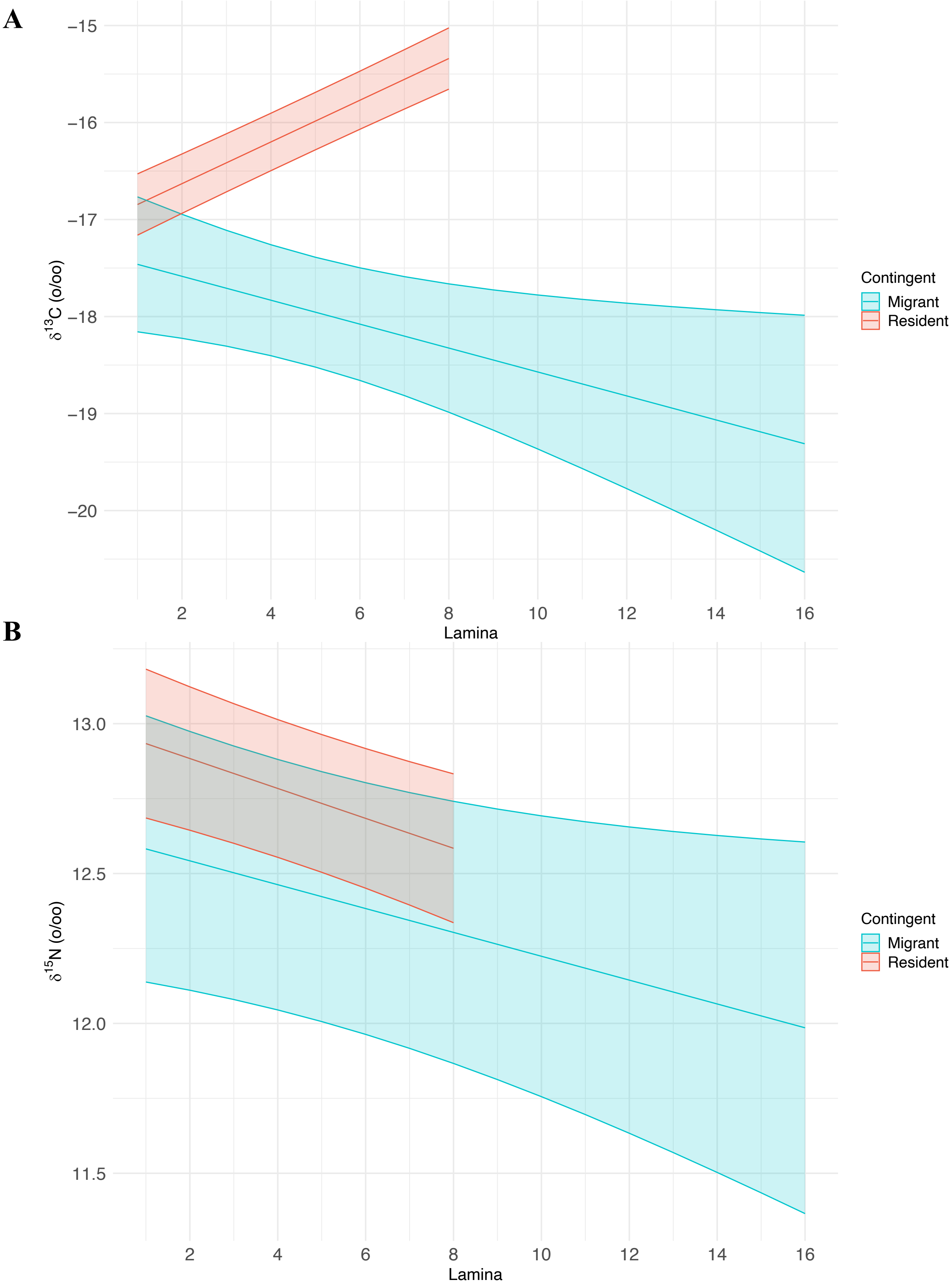


Figure 7. Mixed-effects model trends in δ^{13}C (**A**) and δ^{15}N (**B**) across laminae per contingent, with shaded ribbons representing 95% confidence intervals (n = 40 fish). Laminae are numbered in order of increasing fish age, from 1 (innermost lamina) to 16 (outermost lamina) although they may not equate to age.

4. Discussion

This study leveraged lifetime chemical information archived in fish otoliths and eye lenses, to identify how broad-scale environmental changes influence migrant proportions, and how migratory life history relates to dietary and ecological outcomes in a partially migrating population of *A. butcheri* in the Coorong Lagoon. Analysis of lifetime otolith Ba:Ca profiles revealed two distinct life history contingents, consistent with previous observations of partial migration for this species in the Coorong Lagoon (Gillanders *et al.* 2015). Resident otolith Ba:Ca profiles had concentrations approximately around 10 µmol/mol whereas migrant Ba:Ca profiles exhibited peaks exceeding well above the 20 µmol/mol threshold, indicating migration from the resident estuary habitat towards freshwater. Cluster assignment by the most appropriate K-means analysis showed good agreement with visual contingent assignment based on inspection of otolith Ba:Ca profiles, with the K-means algorithm used to distinguish clusters consistent with the suggested 20 µmol/mol threshold used to qualitatively assign contingent status based on visual inspection of Ba:Ca profiles.

Generalised linear modelling revealed significant influences of broad-scale environmental change on within-year contingent proportions. Years with low mean monthly rainfall and high mean monthly salinity were associated with increased freshwater migration events per year. Consistent with observations by Gillanders *et al.* (2015), *A. butcheri* migrants had better body condition (Fulton's *K* condition factor) than residents, although this difference was marginally non-significant ($p = 0.054$). This difference in body condition suggests a trade-off where the energetic costs of migration are offset by the access to improved foraging opportunities, supporting growth despite movement demands (Altenritter *et al.* 2018). Eye lens stable isotope ratio analysis revealed that migrant $\delta^{13}C$ became more depleted with age, while resident $\delta^{13}C$ became less depleted. The depletion in migrant $\delta^{13}C$ aligns with exploitation of freshwater food webs, as baseline $\delta^{13}C$ becomes more depleted along a gradient from marine to freshwater food webs (Dias *et al.* 2023). Contrary to the anticipated ontogenetic increase in trophic position, $\delta^{15}N$ declined with age in both residents and migrants. Overall, combining life history data recorded in otoliths and eye lenses facilitated a comprehensive reconstruction of how the environment shapes migratory decision, and how this decision subsequently influences ecological outcomes in partially migrating fish populations.

4.1 The influence of broad-scale environmental change on contingent structure

Understanding how contingent proportions in partially migrating fish species respond to environmental variability is crucial for predicting the persistence of intra-population life history diversity under an era of accelerated climatic and anthropogenic changes to aquatic habitats. Migration propensity in partially migrating fish has been associated with environmental cues such as temperature, salinity, food availability, monsoonal rainfall and flow stability (Wysujack *et al.* 2009; Archer *et al.* 2020; Lisi *et al.* 2022; Massie *et al.* 2022; Roberts *et al.* 2024). The number of *A. butcheri* migrations per year increased during years with lower mean monthly rainfall and high mean monthly salinity in the Coorong North Lagoon. Given the strong salinity gradient in the Coorong Lagoon, the peaks in otolith Ba:Ca likely indicate northward migration towards the less saline Murray Mouth and lower reaches of the freshwater lakes and Murray River (Mosley *et al.* 2023). These findings align with the influence of environmental liability traits on migration propensity in estuarine fishes, whereby declines in rainfall and increasing salinity promotes freshwater migration (Massie *et al.* 2022; Roberts *et al.* 2024).

The increased freshwater migrations exhibited by *A. butcheri* during years with high mean monthly salinity likely reflect suboptimal physiological conditions induced by increased salinity. Freshwater input from river discharge and rainfall are key determinants of salinity gradients in estuaries, which shape habitat suitability and availability for estuarine fishes (Brookes *et al.* 2022). Although estuarine fish are well adapted to cope with a wide range of salinities (Marshall 2012; Kültz 2015; Su *et al.* 2022), exposure to salinity levels exceeding their upper tolerance limits can trigger oxidative stress and increased energy requirements for osmoregulation (Hossain *et al.* 2016). This manifests as several physiological, metabolic and behavioural changes, including reduced feeding and body condition, abnormal swimming behaviour and increased mortality related to salinity stress (Hossain *et al.* 2016; Komoroske *et al.* 2016). During the period captured by this study, mean monthly salinity exceeded the upper salinity limit of *A. butcheri* in the Coorong Lagoon (~60 parts per thousand (ppt) / ~90,000 µS/cm at 25°C) (Noell *et al.* 2009), reaching up to 109,000 µS/cm at 25°C. Therefore, while *A. butcheri* are dependent on estuarine salinities for breeding success and larval survival (Hassell *et al.* 2008; Nicholson *et al.* 2008; Williams *et al.* 2013), it is likely that higher salinity conditions prompted freshwater migration.

The increased migrations to freshwater during years with low mean monthly rainfall are likely due to the indirect effects of rainfall on salinity, as well as its direct impacts on *A. butcheri* growth and condition. Regional rainfall, which influences estuarine salinity, is a strong determinant of *A. butcheri* recruitment variability (Jenkins *et al.* 2010). Rainfall is positively correlated to inter-annual growth in *A. butcheri* (Doubleday *et al.* 2015), and declines in annual rainfall induces reduced body condition and delayed maturation, likely a result of hypoxia and diminished food availability (Cottingham *et al.* 2018). Ultimately, it is likely that *A. butcheri* exhibited more freshwater migrations during years with low rainfall and high salinity in the Coorong Lagoon to track habitats more suited to their physiological requirements. This is further exemplified by Gillanders *et al.* (2015), who observed that during the Millennium Drought, when these conditions were amplified (i.e., extreme low rainfall and high salinity due to evaporation and barrage closure (Brookes *et al.* 2009)), the proportion of *A. butcheri* migrants was much greater (38%) compared to the findings of this study (12%) when fish were sampled following 2023 flood conditions in the Coorong Lagoon (Mosley *et al.* 2024). These trends pose concern for the persistence of *A. butcheri* in an ever-changing system threatened by climate change.

Large regions of the Coorong Lagoon are currently experiencing persistent hypersalinity coinciding with reduced freshwater inflow and evapo-concentration (Mosley *et al.* 2023). Without appropriate freshwater influence from river discharge and rainfall, *A. butcheri* habitat suitability in the Coorong Lagoon is expected to contract by up to ~38% (Brookes *et al.* 2022). Climate change is likely to exacerbate the environmental conditions that promote freshwater migration in *A. butcheri*. Estuaries in Mediterranean type climates, such as the Coorong, are predicted to experience dramatic declines in freshwater flow and increased frequency and extent of hypersalinity, due to diminished and unpredictable rainfall, rising sea levels and increased evapo-concentration under warming conditions (Hallett *et al.* 2018). Therefore, it is likely that the number of *A. butcheri* migrations to freshwater per year will increase under future environmental conditions predicted for the Coorong Lagoon.

A greater proportion of migrants weakens the portfolio effects conferred by the coexistence of diverse life histories in partially migrating fish populations (Schindler *et al.* 2010; Schindler *et al.* 2015). Population dynamics in partially migrating fish populations are highly sensitive to contingent proportions, where an increased representation of migrants diminishes long-term population stability (Kerr *et al.* 2010). It is possible that under worsening conditions in the resident North Lagoon habitat, an increased number of migrations by *A. butcheri* may have detrimental consequences for resident stock stability (Chapman *et al.* 2012a).

4.2 Ecological outcomes of contrasting life history strategies

To my knowledge, this is the first study to apply eye lens stable isotope ratio analysis to identify divergent lifetime dietary trends between two contrasting life history strategies in a partially migrating fish population. Similar to findings by Toledo *et al.* (2020), who used stable isotope hind-casting models to reconstruct lifetime diet history in partially migrating *Merluccius australis*, migrant and resident *A. butcheri* had shifts in dietary composition, reflective of habitat utilization. For both migrants and residents, an ontogenetic increase in δ^{15}N was expected as predatory fish often occupy higher trophic positions with age by overcoming gape limitation (Choi *et al.* 2020; Vecchio *et al.* 2021; Ruiz-Cooley and Ordiano-Flores 2025). However, the opposite trend was observed, with both migrant and resident mean δ^{15}N declining with age, even if only very slightly. This may be due to an age-related increased reliance on primary producers as *A. butcheri* can become increasingly omnivorous in eutrophic estuaries (Chuwen *et al.* 2007). Although *A. butcheri* diets in the Coorong Lagoon primarily consist of invertebrates and smaller fish (Lamontagne *et al.* 2016), their highly opportunistic feeding habits and frequent hypereutrophic conditions in the lagoon suggest adults may supplement their diet with macrophytes (Sarre *et al.* 2000; Chuwen *et al.* 2007; Mosley *et al.* 2023). However, without fully characterising estuarine and freshwater food webs in this system, temporal variations in the isotopic baselines of δ^{15}N across the lagoon cannot be ruled out.

Furthermore, estuarine residents were expected to have lower δ^{15}N compared to freshwater migrants, as *A. butcheri* fall lower in trophic position with increasing salinity, potentially due to the consumption of less preferred (smaller) food sources (Brookes *et al.* 2009). However, δ^{15}N did not significantly differ between contingents, suggesting that migrants and residents occupy the same trophic position irrespective of the habitat utilized. Contrastingly, δ^{13}C in migrant and resident diets showed initial overlap, possibly due to residual maternal nutrients in the yolk sac or the consumption of similar estuarine diets during early growth, but subsequently diverged as life history strategies emerged. The general depletion in migrant δ^{13}C aligns with freshwater migration, as freshwater food webs typically exhibit lower baseline $\delta^{13}C$ compared to estuaries, owing to the depleted $\delta^{13}C$ in the terrestrial organic matter available to freshwater primary producers (Lamb *et al.* 2006; Dias *et al.* 2023). The lifetime trends in $\delta^{13}C$ and $\delta^{15}N$ were inconsistent among cohorts, likely due to the fluctuation of baseline $\delta^{13}C$ and $\delta^{15}N$ in the Coorong Lagoon, owing to variable freshwater influence, lagoon-channel connectivity and evaporation rates (Tulipani *et al.* 2014; Mosley *et al.* 2020).

Migrants exhibited better mean body condition compared to residents, although this finding was marginally non-significant. Body condition, as determined by Fulton's *K* factor, is positively correlated to individual lipid content, energy reserves and gonadal development (Mozsár *et al.* 2015; Schloesser and Fabrizio 2017), hence the trend for higher condition in migrant *A. butcheri* indicates they are likely to have better individual fitness compared to residents. As fish body condition is density dependent (Haberle *et al.* 2023), the improved body condition may be related to reduced competition, allowing greater individual access to food resources in freshwater food webs (Caldarone *et al.* 2012; Altenritter *et al.* 2018). Furthermore, in the Coorong Lagoon, the energy density (energy per unit area), protein and lipid content of benthic *A. butcheri* food sources increase further northwards towards the Murray Mouth (Dittmann *et al.* 2022), indicating that food sources available to migrants are energetically superior. Overall, while migration is an energetically costly strategy, there are trade-offs such as improved resources or environmental conditions likely driving the persistence of partial migration. Moreover, migration decisions are influenced by physiological condition, as fish in poorer condition with lower energy reserves are less likely to migrate due to the high energetic demands. For example, Brodersen *et al.* (2008) found that common roach (*Rutilus rutilus*) in low body condition were less likely to migrate from shallow lakes to connecting streams during winter. These distinctions in ecological outcomes, combined with the strong environmental influence on migrant proportions, have important implications for managing partially migrating *A. butcheri* populations in the Coorong Lagoon.

4.3 Implications for management

Globally, the physicochemical conditions of estuaries are rapidly deteriorating due to compound effects from human use, over-fishing and climate change, including modifications to environmental flow, sea surface level, salinity, water temperature, and connectivity (Whitfield *et al.* 2023). Large regions of southern Australia are projected to experience declines in wet season rainfall and prolonged drought conditions (Steffen *et al.* 2018). Within the Coorong Lagoon in particular, climate change is predicted to reduce flow and increase evaporation rates, resulting in further extreme salinities and declines in water level and connectivity (Lester *et al.* 2009). Maintaining diverse life history strategies, particularly under climate change, is crucial for sustaining the stability, productivity and resilience of estuarine fish populations relying on partial migration (Arai *et al.* 2025). Understanding the species-specific environmental drivers of migration, as identified by this study, will aid habitat restoration efforts to support migratory and resident populations.

A considerable portion of climate change-related degradation in the Coorong Lagoon can be averted by reducing upstream freshwater extraction (Lester *et al.* 2013). For partially migrating *A. butcheri,* effective strategies for management may include compensatory barrage releases during months with low regional precipitation, to counter potential surges in salinity. Given the projected sea level rise under climate change, fortification of the natural sandbars separating the lagoon from the Southern Ocean may be necessary to reduce marine incursion and maintain *A. butcheri* habitat suitability in the North Lagoon. While preserving *A. butcheri* stock biomass in the resident estuary is important for sustaining genetic diversity, under increasingly deteriorating conditions, it becomes crucial to ensure structural connectivity to allow the expression of migration. *A. butcheri* populations trapped in estuaries exceeding their upper salinity limits have experienced mass mortalities when there were barriers to freshwater migration (Hoeksema *et al.* 2006). Therefore, it is imperative to maintain structural connectivity between the Coorong Lagoon system and the lower reaches of the Murray River, to facilitate key migration pathways along the salinity gradient under extreme conditions.

4.4 Limitations

All *A. butcheri* used in this study were sampled from a single site within a narrow sampling period during a fishery survey. If fish were caught from multiple sites across the salinity gradient, otolith Ba:Ca edge chemistry (i.e., representative of location of capture) could have been used to further support salinity thresholds rather than using pre-existing thresholds based on other studies.

A common caveat of otolith science is the uncertainty in interpreting patterns in chemical profiles as fish movement when they could also reflect fluctuations in the environment (Elsdon *et al.* 2008). However, the interpretation of peaks in Ba:Ca profiles as freshwater migration is supported by additional observations. First, the peaks in Ba:Ca were not exclusive to specific years and instead varied between individuals, likely indicating individual movement as opposed to physicochemical changes to the resident habitat. Second, the declining $\delta^{13}C$ observed in the lamina of fish designated as freshwater migrants reflect feeding in freshwater food webs. Finally, while elevated Ba can also be indicative of hypersaline conditions in the Coorong South Lagoon (Brookes *et al.* 2009), it is highly unlikely that *A. butcheri* migrated southwards as the extremely high salinity is well beyond its upper tolerance limits. Furthermore, increases in otolith Ba:Ca under hypersalinity do not exceed 10 µmol/mol (Gillanders and Munro 2012), therefore the Ba:Ca peaks exceeding 20 µmol/mol in *A. butcheri* migrants were more consistent with freshwater migration. However, supporting migration studies with tagging techniques such as acoustic or passive integrated transponder telemetry would help to further resolve movement pathways and unequivocally demonstrate timings and periodicity of freshwater migration (Kagley *et al.* 2017; Massie *et al.* 2022; Dzul *et al.* 2024).

Since otolith Ba:Ca data were transformed to migration events per year by aggregating the number of migrations across all migrants, I was unable to account for individual Fish_ID as an indirect random effect when constructing GLMs to model the influence of environmental variables on *A. butcheri* migration. Genetic liability is an inherent feature of migration propensity and is likely to influence the number of migrations undertaken by each individual. Dynamic time warp analysis could further assist in detecting and isolating complex temporal patterns in individual migration, in relation to environmental cues, especially where responses are asynchronous (Hegg and Kennedy 2021).

4.5 Future directions

Future research could consider replication of this study across different years, estuaries and particularly for freshwater populations of *A. butcheri*, to determine if the observed effects of environmental change on migration are consistent across *A. butcheri* populations. While an increased proportion of migrants poses concern for population stability, it simultaneously affords individual fitness advantages, especially under adverse environmental conditions. Therefore, to effectively inform management decisions for *A. butcheri* populations in the Coorong Lagoon, further demographic analyses are necessary to identify the appropriate relative proportions of migrants and residents required for maintaining a viable and stable population. It is also worth estimating within-year growth rates from otolith increments to demonstrate if freshwater migration confers growth advantages under differing conditions (Gillanders *et al.* 2015). Within-year growth data, in combination with body condition estimates and lifetime dietary history from eye lenses would further elucidate the complex ecological outcomes of diverse life history strategies in partially migrating fish populations.

Unlike otoliths, which contain time-resolved life history information, eye lenses incorporate new laminae during periods of somatic growth (Kurth *et al.* 2019; Bell-Tilcock *et al.* 2021), which complicates the alignment of diet shifts with migration events. To further resolve life history patterns in isotopic composition, it is important to sample individuals across the entire size range to establish relationships between eye lens diameter, otolith diameter and age. These calibration curves are likely to be species-specific, as otolith and eye lens morphology vary significantly among species (Bantseev *et al.* 2004; Haimovici *et al.* 2023). To further assist in linking diet shifts with movement, it is worth characterising C and N ratios along the Coorong salinity gradient, including dissolved, particulate and primary producers, to identify the boundaries of food webs likely encountered by migrants. Since the life history trends in diets were not consistent across cohorts, the distribution of these nutrients should be quantified by year or season, to account for the dynamic nature of nutrient cycling in the Coorong lagoon.

5. Conclusion

This study demonstrated that the integration of lifetime chemical data stored in fish otoliths and eye lenses offers a promising avenue of research into understudied aspects of fish partial migration. The effects of broad-scale environmental change on migrant proportions highlights the vulnerability of fish species with environmental liability traits in an era of rapid climate change. Given that partial migration may have evolved to sustain population stability in migratory species (De Leenheer *et al.* 2017), alterations to contingent proportions under changing environments will likely have detrimental consequences for the resilience and persistence of species relying on this behavioural diversity. This study capitalised on laminae within eye lenses, to characterise the often-overlooked ecological outcomes of diverse life history strategies in partially migrating fish populations. The dietary divergence between contingents highlights migrant dependence on multiple food webs, which emphasizes the importance of maintaining structural connectivity among aquatic habitats. Ultimately, by characterising how partially migrating fish populations may respond to environmental change, we can inform the management of these populations in a manner that conserves the diverse life history strategies that will jointly contribute to species persistence under climate change.

6. References

Almeida, R, Tanner, SE, Mateus, CS, Ribeiro, F, Quintella, BR (2024) Not so much a sea bass: divergent European sea bass (*Dicentrarchus labrax* L.) freshwater incursions. *Journal of Fish Biology* **104**, 1241-1246.

Alò, D, Lacy, SN, Castillo, A, Samaniego, HA, Marquet, PA (2021) The macroecology of fish migration. *Global Ecology and Biogeography* **30**, 99-116.

Altenritter, ME, Zydlewski, GB, Kinnison, MT, Zydlewski, JD, Wippelhauser, GS (2018) Understanding the basis of shortnose sturgeon (*Acipenser brevirostrum*) partial migration in the Gulf of Maine. *Canadian Journal of Fisheries and Aquatic Sciences* **75**, 464-473.

Arai, K, Best, JE, Craig, CA, Lyubchich, V, Miller, NR, Secor, DH (2024) Early growth and environmental conditions control partial migration of an estuarine-dependent fish. *Marine Ecology Progress Series* **732**, 149-166.

Arai, K, Best, JE, Lyubchich, V, Miller, NR, Secor, DH (2025) Lifetime carryover of early partial migration behaviors in an estuarine-dependent fish under climate change. *Canadian Journal of Fisheries and Aquatic Sciences* **82**, 1-17.

Archer, LC, Hutton, SA, Harman, L, McCormick, SD, O'Grady, MN, Kerry, JP, Poole, WR, Gargan, P, McGinnity, P, Reed, TE (2020) Food and temperature stressors have opposing effects in determining flexible migration decisions in brown trout (*Salmo trutta*). *Global Change Biology* **26**, 2878-2896.

Bantseev, V, Moran, KL, Dixon, DG, Trevithick, JR, Sivak, JG (2004) Optical properties, mitochondria, and sutures of lenses of fishes: a comparative study of nine species. *Canadian Journal of Zoology* **82**, 86-93.

Bartoń, K (2025) MuMIn: Multi-Model Inference. R package version 1.48.4.

Bastos, RF, Condini, MV, Barbosa, EF, Oliveira, RL, Almeida, LL, Garcia, AM, Hostim-Silva, M (2024) Seeing further into the early steps of the endangered Atlantic goliath grouper (*Epinephelus itajara*): Eye lenses high resolution isotopic profiles reveal ontogenetic trophic and habitat shifts. *Marine Environmental Research* **198**, 106517.

Bates, D, Mächler, M, Bolker, B, Walker, S (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67**, 1-48.

Bell-Tilcock, M, Jeffres, CA, Rypel, AL, Sommer, TR, Katz, JVE, Whitman, G, Johnson, RC, Trueman, C (2021) Advancing diet reconstruction in fish eye lenses. *Methods in Ecology and Evolution* **12**, 449-457.

Bond, MH, Miller, JA, Quinn, TP (2015) Beyond dichotomous life histories in partially migrating populations: cessation of anadromy in a long-lived fish. *Ecology* **96**, 1899-1910.

Brodersen, J, Nilsson, PA, Hansson, L-A, Skov, C, Brönmark, C (2008) Condition-dependent individual decision-making determines cyprinid partial migration. *Ecology* **89**, 1195-1200.

Brönmark, C, Hulthén, K, Nilsson, PA, Skov, C, Hansson, L-A, Brodersen, J, Chapman, BB (2014) There and back again: migration in freshwater fishes. *Canadian Journal of Zoology* **92**, 467-479.

Brookes, J, Aldridge, K, Hipsey, M, Busch, B, Ye, Q, Gibbs, M, Paton, D (2021) Ecological condition of the Lower Lakes and Coorong. In 'Ecohydrology from catchment to coast: Murray-Darling Basin, Australia: its future management.' (Eds BT Hart, NR Bond, N Byron, CA Pollino, MJ Stewardson.) Vol. 1 pp. 95-108. (Elsevier: Amsterdam, Netherlands)

Brookes, J, Lamontagne, S, Aldridge, K, Benger, S, Bissett, A, Bucater, L, Cheshire, A, Cook, P, Deegan, B, Dittmann, S, Fairweather, P, Fernandes, M, Ford, P, Geddes, M, Gillanders, B, Grigg, N, Haese, R, Krull, E, Langley, R, Ye, Q (2009) An ecosystem assessment framework to guide management of the Coorong: final report of the CLLAMMecology Research Cluster. CSIRO: Water for a Healthy Country National Research Flagship, Canberra.

Brookes, JD, Huang, P, Zhai, SY, Gibbs, MS, Ye, Q, Aldridge, KT, Busch, B, Hipsey, MR (2022) Environmental flows to estuaries and coastal lagoons shape the salinity gradient and generate suitable fish habitat: predictions from the Coorong, Australia. *Frontiers in Environmental Science* **10**, 796623.

Bryan, DR, Feeley, MW, Nemeth, RS, Pollock, C, Ault, JS (2019) Home range and spawning migration patterns of queen triggerfish *Balistes vetula* in St. Croix, US Virgin Islands. *Marine Ecology Progress Series* **616**, 123-139.

Bunch, AJ, Hershey, H, Reger, GR, Hoogakker, FJ, Donovan, BS, Farmer, TM (2022) A Bayesian multistate approach to evaluate movements of an invasive freshwater estuarine-opportunist. *Canadian Journal of Fisheries and Aquatic Sciences* **79**, 213-222.

Caldarone, EM, MacLean, SA, Sharack, B (2012) Evaluation of bioelectrical impedance analysis and Fulton's condition factor as nonlethal techniques for estimating short-term responses in postsmolt Atlantic salmon to food availability. *Fishery Bulletin* **110**, 257-270.

Carr, MH, Robinson, SP, Wahle, C, Davis, G, Kroll, S, Murray, S, Schumacker, EJ, Williams, M (2017) The central importance of ecological spatial connectivity to effective coastal marine protected areas and to meeting the challenges of climate change in the marine environment. *Aquatic Conservation: Marine and Freshwater Ecosystems* **27**, 6-29.

Chapman, BB, Brönmark, C, Nilsson, JÅ, Hansson, LA (2011a) The ecology and evolution of partial migration. *Oikos* **120**, 1764-1775.

Chapman, BB, Brönmark, C, Nilsson, JÅ, Hansson, LA (2011b) Partial migration: an introduction. *Oikos* **120**, 1761-1763.

Chapman, BB, Hulthén, K, Blomqvist, DR, Hansson, L-A, Nilsson, JA, Brodersen, J, Anders Nilsson, P, Skov, C, Brönmark, C (2011c) To boldly go: individual differences in boldness influence migratory tendency. *Ecology Letters* **14**, 871-876.

Chapman, BB, Hulthén, K, Brodersen, J, Nilsson, PA, Skov, C, Hansson, L-A, Brönmark, C (2012a) Partial migration in fishes: causes and consequences. *Journal of Fish Biology* **81**, 456-478.

Chapman, BB, Hulthén, K, Wellenreuther, M, Hansson, L-A, Nilsson, J-Å, Brönmark, C (2014) Patterns of animal migration. In 'Animal Movement Across Scales.' (Eds L-A Hansson., S Åkesson.) pp. 11-35. (Oxford University Press: Oxford)

Chapman, BB, Skov, C, Hulthén, K, Brodersen, J, Nilsson, PA, Hansson, L-A, Brönmark, C (2012b) Partial migration in fishes: definitions, methodologies and taxonomic distribution. *Journal of Fish Biology* **81**, 479-499.

Choi, J-Y, Kim, S-K, Kim, J-C, Yoon, J-D (2020) Trophic position and diet shift based on the body size of *Coreoperca kawamebari* (Temminck & Schlegel, 1843). *Journal of ecology and environment* **44**, 1-7.

Chuwen, BM, Platell, ME, Potter, IC (2007) Dietary compositions of the sparid *Acanthopagrus butcheri* in three normally closed and variably hypersaline estuaries differ markedly. *Environmental Biology of Fishes* **80**, 363-376.

Cottingham, A, Huang, P, Hipsey, MR, Hall, NG, Ashworth, E, Williams, J, Potter, IC (2018) Growth, condition, and maturity schedules of an estuarine fish species change in estuaries following increased hypoxia due to climate change. *Ecology and Evolution* **8**, 7111-7130.

Cowen, RK, Gawarkiewicz, G, Pineda, J, Thorrold, SR, Werner, FE (2007) Population connectivity in marine systems: an overview. *Oceanography* **20**, 14-21.

Dahm, R, Schonthaler, HB, Soehn, AS, van Marle, J, Vrensen, GFJM (2007) Development and adult morphology of the eye lens in the zebrafish. *Experimental Eye Research* **85**, 74-89.

De Leenheer, P, Mohapatra, A, Ohms, HA, Lytle, DA, Cushing, JM (2017) The puzzle of partial migration: adaptive dynamics and evolutionary game theory perspectives. *Journal of Theoretical Biology* **412**, 172-185.

Deinet, S, Flint, R, Puleston, H, Baratech, A, Royte, J, Thieme, ML, Nagy, S, Hogan, ZS, Januchowski-Hartley, S, Wanningen, H (2024) The Living Planet Index (LPI) for migratory freshwater fishes 2024 update: technical report. World Fish Migration Foundation, The Netherlands. Available at http://icsfarchives.net/20318/.

Deinet, S, Scott-Gatty, K, Rotton, H, Twardek, WM, Marconi, V, McRae, L, Baumgartner, LJ, Brink, K, Claussen, JE, Cooke, SJ, Darwall, W, Eriksson, BK, Garcia de Leaniz, C, Hogan, Z, Royte, J, Silva, LGM, Thieme, ML, Tickner, D, Waldman, J, Wanningen, H, Weyl, OLF, Berkhuysen, A (2020) The Living Planet Index (LPI) for migratory freshwater fish: technical report. World Fish Migration Foundation, The Netherlands. Available at https://worldfishmigrationfoundation.com/wp-content/uploads/2020/07/LPI_report_2020.pdf.

Department for Environment and Water, GoSA (2021) 'Water Data SA.' Available at https://water.data.sa.gov.au/ [Accessed 13 March 2025].

Dias, E, Morais, P, Antunes, C, Hoffman, JC (2023) The benthic food web connects the estuarine habitat mosaic to adjacent ecosystems. *Food Webs* **35**, e00282.

Dittmann, S, Ye, Q, Furst, D, Newbery, A, Nitschke, J, Bucater, L, Pyke, W, Kent, J, Schroder, L, Henkens, J, Baring, R, Lam-Gordillo, O, Brookes, J, Short, D (2022) Food resource availability, energy content and nutritional value of major food sources for key fish and waterbird species under varying environmental conditions in the Coorong. Goyder Institute for Water Research No. 22/12, Adelaide, SA. Available at https://goyderinstitute.org/wp-content/uploads/2023/06/goyder_trs_22-12_major_food_sources_key_fish_bird_species_coorong.pdf.

Doubleday, ZA, Izzo, C, Haddy, JA, Lyle, JM, Ye, Q, Gillanders, BM (2015) Long-term patterns in estuarine fish growth across two climatically divergent regions. *Oecologia* **179**, 1079-1090.

Dzul, MC, Kendall, WL, Yackulic, CB, Van Haverbeke, DR, Mackinnon, P, Young, K, Pillow, MJ, Thomas, J (2024) Estimating migration timing and abundance in partial migratory systems by integrating continuous antenna detections with physical captures. *Journal of Animal Ecology* **93**, 796-811.

Earl, J (2020) Assessment of the South Australian Lakes and Coorong Fishery in 2018/19. South Australian Research and Development Institute, SARDI Research Report Series No. 1059, South Australia. Available at https://pir.sa.gov.au/__data/assets/pdf_file/0017/373130/Attachment_D_LCF_assessment_report_2018-19_FINAL_FINAL_20200528.pdf.

Eldøy, SH, Bordeleau, X, Lawrence, MJ, Thorstad, EB, Finstad, AG, Whoriskey, FG, Crossin, GT, Cooke, SJ, Aarestrup, K, Rønning, L, Sjursen, AD, Davidsen, JG (2021) The effects of nutritional state, sex and body size on the marine migration behaviour of sea trout. *Marine Ecology Progress Series* **665**, 185-200.

Elsdon, TS, Gillanders, BM (2005) Alternative life-history patterns of estuarine fish: barium in otoliths elucidates freshwater residency. *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 1143-1152.

Elsdon, TS, Wells, BK, Campana, SE, Gillanders, BM, Jones, CM, Limburg, KE, Secor, DH, Thorrold, SR, Walther, BD (2008) Otolith chemistry to describe movements and life-history parameters of fishes: hypotheses, assumptions, limitations and inferences. In 'Oceanography and Marine Biology: An Annual Review.' (Eds RN Gibson, RJA Atkinson, JDM Gordon.) pp. 303-336. (CRC Press: United Kingdom)

Ferguson, A, Reed, TE, Cross, TF, McGinnity, P, Prodöhl, PA (2019) Anadromy, potamodromy and residency in brown trout *Salmo trutta*: the role of genes and the environment. *Journal of Fish Biology* **95**, 692-718.

Fowler, AM, Smith, SM, Booth, DJ, Stewart, J (2016) Partial migration of grey mullet (*Mugil cephalus*) on Australia's east coast revealed by otolith chemistry. *Marine Environmental Research* **119**, 238-244.

Franklin, PA, Bašić, T, Davison, PI, Dunkley, K, Ellis, J, Gangal, M, González-Ferreras, AM, Gutmann Roberts, C, Hunt, G, Joyce, D, Klöcker, CA, Mawer, R, Rittweg, T, Stoilova, V, Gutowsky, LFG (2024) Aquatic connectivity: challenges and solutions in a changing climate. *Journal of Fish Biology* **105**, 392-411.

Frisk, MG, Jordaan, A, Miller, TJ (2014) Moving beyond the current paradigm in marine population connectivity: are adults the missing link? *Fish and Fisheries* **15**, 242-254.

Gahagan, BI, Fox, DA, Secor, DH (2015) Partial migration of striped bass: revisiting the contingent hypothesis. *Marine Ecology Progress Series* **525**, 185-197.

Gillanders, BM, Izzo, C, Doubleday, ZA, Ye, Q (2015) Partial migration: growth varies between resident and migratory fish. *Biology Letters* **11**, 20140850.

Gillanders, BM, Munro, AR (2012) Hypersaline waters pose new challenges for reconstructing environmental histories of fish based on otolith chemistry. *Limnology and Oceanography* **57**, 1136-1148.

Haberle, I, Bavčević, L, Klanjscek, T (2023) Fish condition as an indicator of stock status: Insights from condition index in a food-limiting environment. *Fish and Fisheries* **24**, 567-581.

Haimovici, M, Dos S. Rodrigues, L, Lucato, SHB, De A. Freire, M, Fischer, LG, Cardoso, LG (2023) Otolith atlas for marine fishes of the southwestern Atlantic occurring along southern Brazil (28° S-34° S). *Marine and Fishery Sciences* **37**, 53-207.

Hallett, CS, Hobday, AJ, Tweedley, JR, Thompson, PA, McMahon, K, Valesini, FJ (2018) Observed and predicted impacts of climate change on the estuaries of south-western Australia, a Mediterranean climate region. *Regional Environmental Change* **18**, 1357-1373.

Hartig, F (2024) DHARMa: Residual diagnostics for hierarchical (multi-level / mixed) regression models. R package version 0.4.7.

Hassell, KL, Coutin, PC, Nugegoda, D (2008) Hypoxia, low salinity and lowered temperature reduce embryo survival and hatch rates in black bream *Acanthopagrus butcheri* (Munro, 1949). *Journal of Fish Biology* **72**, 1623-1636.

Hegg, JC, Kennedy, BP (2021) Let's do the time warp again: non-linear time series matching as a tool for sequentially structured data in ecology. *Ecosphere* **12**, e03742.

Hindell, JS, Jenkins, GP, Womersley, B (2008) Habitat utilisation and movement of black bream *Acanthopagrus butcheri* (Sparidae) in an Australian estuary. *Marine Ecology Progress Series* **366**, 219-229.

Hoeksema, SD, Chuwen, BM, Potter, IC (2006) Massive mortalities of the black bream *Acanthopagrus butcheri* (Sparidae) in two normally-closed estuaries, following extreme increases in salinity. *Journal of the Marine Biological Association of the United Kingdom* **86**, 893-897.

Hossain, MA, Aktar, S, Qin, JG (2016) Salinity stress response in estuarine fishes from the Murray Estuary and Coorong, South Australia. *Fish Physiology and Biochemistry* **42**, 1571-1580.

Hüssy, K, Mosegaard, H, Jessen, F (2004) Effect of age and temperature on amino acid composition and the content of different protein types of juvenile Atlantic cod (*Gadus morhua*) otoliths. *Canadian Journal of Fisheries and Aquatic Sciences* **61**, 1012-1020.

Hyndman, R, Kang, Y, Montero-Manso, P, O'Hara-Wild, M, Talagala, T, Wang, E, Yang, Y (2023) '*tsfeatures*: Time series feature extraction.' Available at https://pkg.robjhyndman.com/tsfeatures/,https;//github.com/robjhyndman/tsfeatures.

Jenkins, GP, Conron, SD, Morison, AK (2010) Highly variable recruitment in an estuarine fish is determined by salinity stratification and freshwater flow: implications of a changing climate. *Marine Ecology Progress Series* **417**, 249-261.

Jochum, KP, Scholz, D, Stoll, B, Weis, U, Wilson, SA, Yang, Q, Schwalb, A, Börner, N, Jacob, DE, Andreae, MO (2012) Accurate trace element analysis of speleothems and biogenic calcium carbonates by LA-ICP-MS. *Chemical Geology* **318-319**, 31-44.

Kagley, AN, Smith, JM, Fresh, KL, Frick, KE, Quinn, TP (2017) Residency, partial migration, and late egress of subadult Chinook salmon (*Oncorhynchus tshawytscha*) and coho salmon (*O. kisutch*) in Puget Sound, Washington. *Fishery Bulletin* **115**, 544-555.

Kassambara, A, Mundt, F (2020) Factoextra: extract and visualize the results of multivariate data analyses. R package version 1.0.7 2020.

Kelson, SJ, Miller, MR, Thompson, TQ, O'Rourke, SM, Carlson, SM (2019) Do genomics and sex predict migration in a partially migratory salmonid fish, *Oncorhynchus mykiss*? *Canadian Journal of Fisheries and Aquatic Sciences* **76**, 2080-2088.

Kelson, SJ, Miller, MR, Thompson, TQ, O'Rourke, SM, Carlson, SM (2020) Temporal dynamics of migration-linked genetic variation are driven by streamflows and riverscape permeability. *Molecular Ecology* **29**, 870-885.

Kerr, LA, Cadrin, SX, Secor, DH (2010) The role of spatial dynamics in the stability, resilience, and productivity of an estuarine fish population. *Ecological Applications* **20**, 497-507.

Kitano, J, Ishikawa, A, Kume, M, Mori, S (2012) Physiological and genetic basis for variation in migratory behavior in the three-spined stickleback, *Gasterosteus aculeatus*. *Ichthyological Research* **59**, 293-303.

Komoroske, LM, Jeffries, KM, Connon, RE, Dexter, J, Hasenbein, M, Verhille, C, Fangue, NA (2016) Sublethal salinity stress contributes to habitat limitation in an endangered estuarine fish. *Evolutionary Applications* **9**, 963-981.

Kültz, D (2015) Physiological mechanisms used by fish to cope with salinity stress. *Journal of Experimental Biology* **218**, 1907-1914.

Kurth, BN, Peebles, EB, Stallings, CD (2019) Atlantic tarpon (*Megalops atlanticus*) exhibit upper estuarine habitat dependence followed by foraging system fidelity after ontogenetic habitat shifts. *Estuarine, Coastal and Shelf Science* **225**, 106248.

Lamb, AL, Wilson, GP, Leng, MJ, Leng, MJ (2006) A review of coastal palaeoclimate and relative sea-level reconstructions using delta (super 13) C and C/N ratios in organic material. *Earth-Science Reviews* **75**, 29-57.

Lamontagne, S, Deegan, BM, Aldridge, KT, Brookes, JD, Geddes, MC (2016) Fish diets in a freshwater-deprived semiarid estuary (The Coorong, Australia) as inferred by stable isotope analysis. *Estuarine, Coastal and Shelf Science* **178**, 1-11.

Landuyt, L, Verhoest, NEC, Van Coillie, FMB (2020) Flood mapping in vegetated areas using an unsupervised clustering approach on Sentinel-1 and -2 imagery. *Remote Sensing* **12**, 3611.

Leis, JM, van Herwerden, L, Patterson, HM (2011) Estimating connectivity in marine fish populations: What works best? In 'Oceanography and Marine Biology: An Annual Review.' (Eds RN Gibson, RJA Atkinson, JDM Gordon.) Vol. 49 pp. 193-234. (Taylor & Francis Group: United Kingdom)

Lennox, RJ, Birnie-Gauvin, K, Bate, C, Cooke, SJ, Haraldstad, T, Berhe, S, Penney, HD, Bangley, CW, Vollset, KW, Piczak, ML (2025) Marine fish passage - underappreciated threats to connectivity within the marine environment. *Marine Ecology* **46**, e12859.

Lester, RE, Fairweather, PG, Webster, IT, Quin, RA, Wilcox, BP (2013) Scenarios involving future climate and water extraction: ecosystem states in the estuary of Australia's largest river. *Ecological Applications* **23**, 984-998.

Lester, RE, Webster, IT, Fairweather, PG, Langley, RA (2009) Predicting the future ecological condition of the Coorong. The effect of management actions and climate change scenarios. Water for a Healthy Country National Research Flagship Series. CSIRO, Australia.

Leterme, SC, Allais, L, Jendyk, J, Hemraj, DA, Newton, K, Mitchell, J, Shanafield, M (2015) Drought conditions and recovery in the Coorong Wetland, South Australia in 1997-2013. *Estuarine, Coastal and Shelf Science* **163**, 175-184.

Lisi, PJ, Hogan, JD, Holt, G, Moody, KN, Wren, JLK, Kobayashi, DR, Blum, MJ, McIntyre, PB (2022) Stream and ocean hydrodynamics mediate partial migration strategies in an amphidromous Hawaiian goby. *Ecology* **103**, e3800.

Marshall, WS (2012) Osmoregulation in Estuarine and Intertidal Fishes. In 'Fish Physiology.' (Eds SD McCormick, AP Farrell, CJ Brauner.) Vol. 32 pp. 395-434. (Academic Press: Oxford, UK)

Massie, JA, Santos, RO, Rezek, RJ, James, WR, Viadero, NM, Boucek, RE, Blewett, DA, Trotter, AA, Stevens, PW, Rehage, JS (2022) Primed and cued: long-term acoustic telemetry links interannual and seasonal variations in freshwater flows to the spawning migrations of common snook in the Florida Everglades. *Movement Ecology* **10**, 48.

McCoy, F (1899) 'Prodromus of the Zoology of Victoria ' (Government of Victoria: Victoria, Australia)

Morison, AK, Coutin, PC, Robertson, SG (1998) Age determination of black bream, *Acanthopagrus butcheri* (Sparidae), from the Gippsland Lakes of south-eastern Australia indicates slow growth and episodic recruitment. *Marine and Freshwater Research* **49**, 491-498.

Morissette, O, Lecomte, F, Verreault, G, Legault, M, Sirois, P (2016) Fully equipped to succeed: migratory contingents seen as an intrinsic potential for striped bass to exploit a heterogeneous environment early in life. *Estuaries and Coasts* **39**, 571-582.

Morita, K, Tamate, T, Kuroki, M, Nagasawa, T (2014) Temperature-dependent variation in alternative migratory tactics and its implications for fitness and population dynamics in a salmonid fish. *Journal of Animal Ecology* **83**, 1268-1278.

Mosley, L, Dittmann, S, Ye, Q, Leyden, E, Newbery, A, Bucater, L, Howson, T, Giatas, G, Ahmed, D, Reardon, S, Teigeler, J, Tiller, G, Nitschke, J, Schroder, L, Sepe, C, Hay, A, Morris, N, Urgl, C, Nicol, J, Waycott, M (2024) South Australian Murray-Darling Basin 2022-2023 Flood Environmental Response in the Coorong. Goyder Institute for Water Research No. 2024/02, South Australia.

Mosley, L, Priestley, S, Brookes, J, Dittmann, S, Farkas, J, Farrell, M, Ferguson, A, Gibbs, M, Hipsey, M, Huang, J, Lam-Gordillo, O, Simpson, S, Teasdale, P, Tyler, J, Waycott, M, Welsh, D (2020) Coorong water quality synthesis with a focus on the drivers of eutrophication. Goyder Institute for Water Research No. 20/10, South Australia. Available at https://goyderinstitute.org/wp-content/uploads/2023/03/goyder_trs-20-10_coorong_water_quality_synthesis.pdf.

Mosley, LM, Priestley, S, Brookes, J, Dittmann, S, Farkaš, J, Farrell, M, Ferguson, AJ, Gibbs, M, Hipsey, M, Huang, J, Lam-Gordillo, O, Simpson, SL, Tyler, JJ, Waycott, M, Welsh, DT (2023) Extreme eutrophication and salinisation in the Coorong estuarine-lagoon ecosystem of Australia's largest river basin (Murray-Darling). *Marine Pollution Bulletin* **188**, 114648.

Mozsár, A, Boros, G, Sály, P, Antal, L, Nagy, SA (2015) Relationship between Fulton's condition factor and proximate body composition in three freshwater fish species. *Journal of Applied Ichthyology* **31**, 315-320.

Nathan, R, Getz, WM, Revilla, E, Holyoak, M, Kadmon, R, Saltz, D, Smouse, PE (2008) A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences* **105**, 19052-19059.

National Institute of Standards and Technology (2024) Standard Reference Material 612: Trace Elements in Glass - Certificate of Analysis. National Institute of Standards and Technology, USA.

Nicholson, G, Jenkins, GP, Sherwood, J, Longmore, A (2008) Physical environmental conditions, spawning and early-life stages of an estuarine fish: climate change implications for recruitment in intermittently open estuaries. *Marine and Freshwater Research* **59**, 735-749.

Noell, C, Ye, Q, Short, D, Bucater, L, Wellman, N (2009) Fish assemblages of the Murray Mouth and Coorong region, South Australia, during an extended drought period. Water for a Healthy Country National Research Flagship Series. CSIRO, Canberra, ACT. Available at http://pir.sa.gov.au/__data/assets/pdf_file/0004/231925/No_339_Fish_assemblages_of_the_Murray_Mouth_Published_alias.pdf.

Norriss, JV, Tregonning, JE, Lenanton, RCJ, Sarre, GA (2002) Biological synopsis of the black bream, *Acanthopagrus butcheri* (Munro) (Teleostei: Sparidae) in Western Australia with reference to information from other southern states. Department of Fisheries, Western Australia No. 93, Perth. Available at https://library.dpird.wa.gov.au/fr_rr/163/.

Paton, C, Hellstrom, J, Paul, B, Woodhead, J, Hergt, J (2011) Iolite: Freeware for the visualisation and processing of mass spectrometric data. *Journal of Analytical Atomic Spectrometry* **26**, 2508.

Phillis, CC, Moore, JW, Buoro, M, Hayes, SA, Garza, JC, Pearse, DE (2016) Shifting thresholds: rapid evolution of migratory life histories in steelhead/rainbow trout, *Oncorhynchus mykiss*. *Journal of Heredity* **107**, 51-60.

Post, DM (2002) Using stable isotopes to estimate trophic position: models, methods and assumptions. *Ecology* **83**, 703-718.

Potter, IC, Kanandjembo, A-R, Cottingham, A, Rose, TH, Linke, TE, Platell, ME (2022) A long-lived, estuarine-resident fish species selects its macroinvertebrate food source based on certain prey and predator traits. *Estuarine, Coastal and Shelf Science* **264**, 107691.

Prentice, PM, Thornton, A, Kolm, N, Wilson, AJ (2023) Genetic and context-specific effects on individual inhibitory control performance in the guppy (*Poecilia reticulata*). *Journal of Evolutionary Biology* **36**, 1796-1810.

Pulido, F (2011) Evolutionary genetics of partial migration – the threshold model of migration revis(it)ed. *Oikos* **120**, 1776-1783.

Pulido, F, Berthold, P, Van Noordwijk, AJ (1996) Frequency of migrants and migratory activity are genetically correlated in a bird population: evolutionary implications. *Proceedings of the National Academy of Sciences* **93**, 14642-14647.

Quinn, TP, Bond, MH, Brenkman, SJ, Paradis, R, Peters, RJ (2017) Re-awakening dormant life history variation: stable isotopes indicate anadromy in bull trout following dam removal on the Elwha River, Washington. *Environmental Biology of Fishes* **100**, 1659-1671.

R Core Team (2024) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reis-Santos, P, Gillanders, BM, Sturrock, AM, Izzo, C, Oxman, DS, Lueders-Dumont, JA, Hüssy, K, Tanner, SE, Rogers, T, Doubleday, ZA, Andrews, AH, Trueman, C, Brophy, D, Thiem, JD, Baumgartner, LJ, Willmes, M, Chung, M-T, Charapata, P, Johnson, RC, Trumble, S, Heimbrand, Y, Limburg, KE, Walther, BD (2023) Reading the biomineralized book of life: expanding otolith biogeochemical research and applications for fisheries and ecosystem-based management. *Reviews in Fish Biology and Fisheries* **33**, 411-449.

Reis-Santos, P, Gillanders, BM, Tanner, SE, Vasconcelos, RP, Elsdon, TS, Cabral, HN (2012) Temporal variability in estuarine fish otolith elemental fingerprints: implications for connectivity assessments. *Estuarine, Coastal and Shelf Science* **112**, 216-224.

Reis-Santos, P, Tanner, SE, Elsdon, TS, Cabral, HN, Gillanders, BM (2013) Effects of temperature, salinity and water composition on otolith elemental incorporation of *Dicentrarchus labrax*. *Journal of Experimental Marine Biology and Ecology* **446**, 245-252.

Roberts, BH, Morrongiello, JR, King, AJ, Morgan, DL, Saunders, TM, Woodhead, J, Crook, DA (2019) Migration to freshwater increases growth rates in a facultatively catadromous tropical fish. *Oecologia* **191**, 253-260.

Roberts, BH, Morrongiello, JR, Morgan, DL, King, AJ, Saunders, TM, Banks, SC, Crook, DA (2024) Monsoonal wet season influences the migration tendency of a catadromous fish (barramundi *Lates calcarifer*). *Journal of Animal Ecology* **93**, 83-94.

Rohtla, M, Matetski, L, Taal, I, Svirgsden, R, Kesler, M, Paiste, P, Vetemaa, M (2020) Quantifying an overlooked aspect of partial migration using otolith microchemistry. *Journal of Fish Biology* **97**, 1582-1585.

Ruiz-Cooley, RI, Ordiano-Flores, A (2025) Amino acid δ15N in eye lens laminae reveals life-time ontogenetic trophic shifts of a highly migratory species. *Journal of Fish Biology* 1-10.

Russell, A, Taylor, MD, Barnes, TC, Johnson, DD, Gillanders, BM (2022) Habitat transitions by a large coastal sciaenid across life history stages, resolved using otolith chemistry. *Marine Environmental Research* **176**, 105614.

Sakabe, R (2009) Ecology and life history characteristics of black bream, *Acanthopagrus butcheri*, in Tasmanian estuarine ecosystems. PhD thesis, University of Tasmania.

Sarakinis, KG, Reis-Santos, P, Ye, Q, Earl, J, Gillanders, BM (2024) Combining natural markers to investigate fish population structure and connectivity. *Estuarine, Coastal and Shelf Science* **308**, 108920.

Sarre, GA, Platell, ME, Potter, IC (2000) Do the dietary compositions of *Acanthopagrus butcheri* in four estuaries and a coastal lake vary with body size and season and within and amongst these water bodies? *Journal of Fish Biology* **56**, 103-122.

Schindler, DE, Armstrong, JB, Reed, TE (2015) The portfolio concept in ecology and evolution. *Frontiers in Ecology and the Environment* **13**, 257-263.

Schindler, DE, Hilborn, R, Chasco, B, Boatright, CP, Quinn, TP, Rogers, LA, Webster, MS (2010) Population diversity and the portfolio effect in an exploited species. *Nature* **465**, 609-612.

Schloerke, B, Cook, D, Larmarange, J, Briatte, F, Marbach, M, Thoen, E, Elberg, A, Toomet, O, Crowley, J, Hofmann, H, Wickham, H, 2021. GGally: Extension to 'ggplot2'. R package version 2.2.1 2024.

Schloesser, RW, Fabrizio, MC (2017) Condition indices as surrogates of energy density and lipid content in juveniles of three fish species. *Transactions of the American Fisheries Society* **146**, 1058-1069.

Schneider, CA, Rasband, WS, Eliceiri, KW (2012) NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* **9**, 671-675.

Steffen, C, Stephens, S, Dance, MA, Lippi, DL, Jensen, CC, Wells, RJD, Rooker, JR (2023) Estuarine-coastal connectivity and partial migration of southern flounder in the Gulf of Mexico. *Estuarine, Coastal and Shelf Science* **294**, 108545.

Steffen, W, Vertessy, R, Dean, A, Hughes, L, Bambrick, H, Gergis, J, Rice, M (2018) 'Deluge and drought: Australia's water security in a changing climate.' (Climate Council of Australia: Australia)

Su, M, Liu, N, Zhang, Z, Zhang, J (2022) Osmoregulatory strategies of estuarine fish *Scatophagus argus* in response to environmental salinity changes. *BMC Genomics* **23**, 545.

Toledo, P, Niklitschek, EJ, Darnaude, AM, Leiva, FP, Harrod, C, Lillo, S, Ojeda, V, Klarian, S, Molina-Burgos, BE, Gálvez, P, Canales-Aguirre, CB (2020) The trophic ecology of partial migration: insights from *Merluccius australis* off NW Patagonia. *ICES Journal of Marine Science* **77**, 1927-1940.

Tulipani, S, Grice, K, Krull, E, Greenwood, P, Revill, AT (2014) Salinity variations in the northern Coorong Lagoon, South Australia; significant changes in the ecosystem following human alteration to the natural water regime. *Organic Geochemistry* **75**, 74-86.

Tzadik, OE, Curtis, JS, Granneman, JE, Kurth, BN, Pusack, TJ, Wallace, AA, Hollander, DJ, Peebles, EB, Stallings, CD (2017) Chemical archives in fishes beyond otoliths: a review on the use of other body parts as chronological recorders of microchemical constituents for expanding interpretations of environmental, ecological, and life-history changes. *Limnology and Oceanography: Methods* **15**, 238-263.

Vecchio, JL, Ostroff, JL, Peebles, EB (2021) Isotopic characterization of lifetime movement by two demersal fishes from the northeastern Gulf of Mexico. *Marine Ecology Progress Series* **657**, 161-172.

Wallace, AA, Hollander, DJ, Peebles, EB (2014) Stable isotopes in fish eye lenses as potential recorders of trophic and geographic history. *PloS One* **9**, e108935.

Walther, BD, Limburg, KE (2012) The use of otolith chemistry to characterize diadromous migrations. *Journal of Fish Biology* **81**, 796-825.

Webster, IT (2011) Dynamic assessment of oceanic connectivity in a coastal lagoon - the Coorong, Australia. *Journal of Coastal Research* **27**, 131-139.

Whitfield, AK, Gillanders, BM, Able, KW (2023) Climate change effects on fish populations. In 'Climate change and estuaries.' (Eds M. J. Kennish, H. W. Paerl, JR Crosswell.) (CRC Press: Boca Raton)

Wickham, H (2016) ggplot2: Elegant graphics for data analysis. R package version 3.5.1

Williams, J, Jenkins, GP, Hindell, JS, Swearer, SE (2013) Linking environmental flows with the distribution of black bream *Acanthopagrus butcheri* eggs, larvae and prey in a drought affected estuary. *Marine Ecology Progress Series* **483**, 273-287.

Wysujack, K, Greenberg, LA, Bergman, E, Olsson, IC (2009) The role of the environment in partial migration: food availability affects the adoption of a migratory tactic in brown trout *Salmo trutta*. *Ecology of Freshwater Fish* **18**, 52-59.

Ye, Q, Giatas, G, Bucater, L, Short, D (2018) Coorong fish condition monitoring 2016/17: Black bream (*Acanthopagrus butcheri*), greenback flounder (*Rhombosolea tapirina*) and smallmouth hardyhead (*Atherinosoma microstoma*) populations. South Australian Research and Development Institute (Aquatic Sciences) No. 979, South Australia.

Yoshinaga, J, Nakama, A, Morita, M, Edmonds, JS (2000) Fish otolith reference material for quality assurance of chemical analyses. *Marine Chemistry* **69**, 91-97.

Young, MJ, Larwood, V, Clause, JK, Bell-Tilcock, M, Whitman, G, Johnson, R, Feyrer, F (2022) Eye lenses reveal ontogenetic trophic and habitat shifts in an imperiled fish, Clear Lake hitch (*Lavinia exilicauda chi*). *Canadian Journal of Fisheries and Aquatic Sciences* **79**, 21-30.

Zeileis, A, Grothendieck, G (2005) zoo : S3 infrastructure for regular and irregular time series. *Journal of Statistical Software* **14**, 1-27.

7. Appendices

Appendix 1: Assessing GLM fit across different families of probability distributions

Figure S1. *DHARMa* residual diagnostic plots for the best GLM (based on AICc weight) fitted using gamma (**A**) and log-normal (**B**) distributions, to model mean annual Ba:Ca against environmental variables. Significant quantile deviations between model predictions and *DHARMa* residuals (highlighted in red) indicate poor fit.

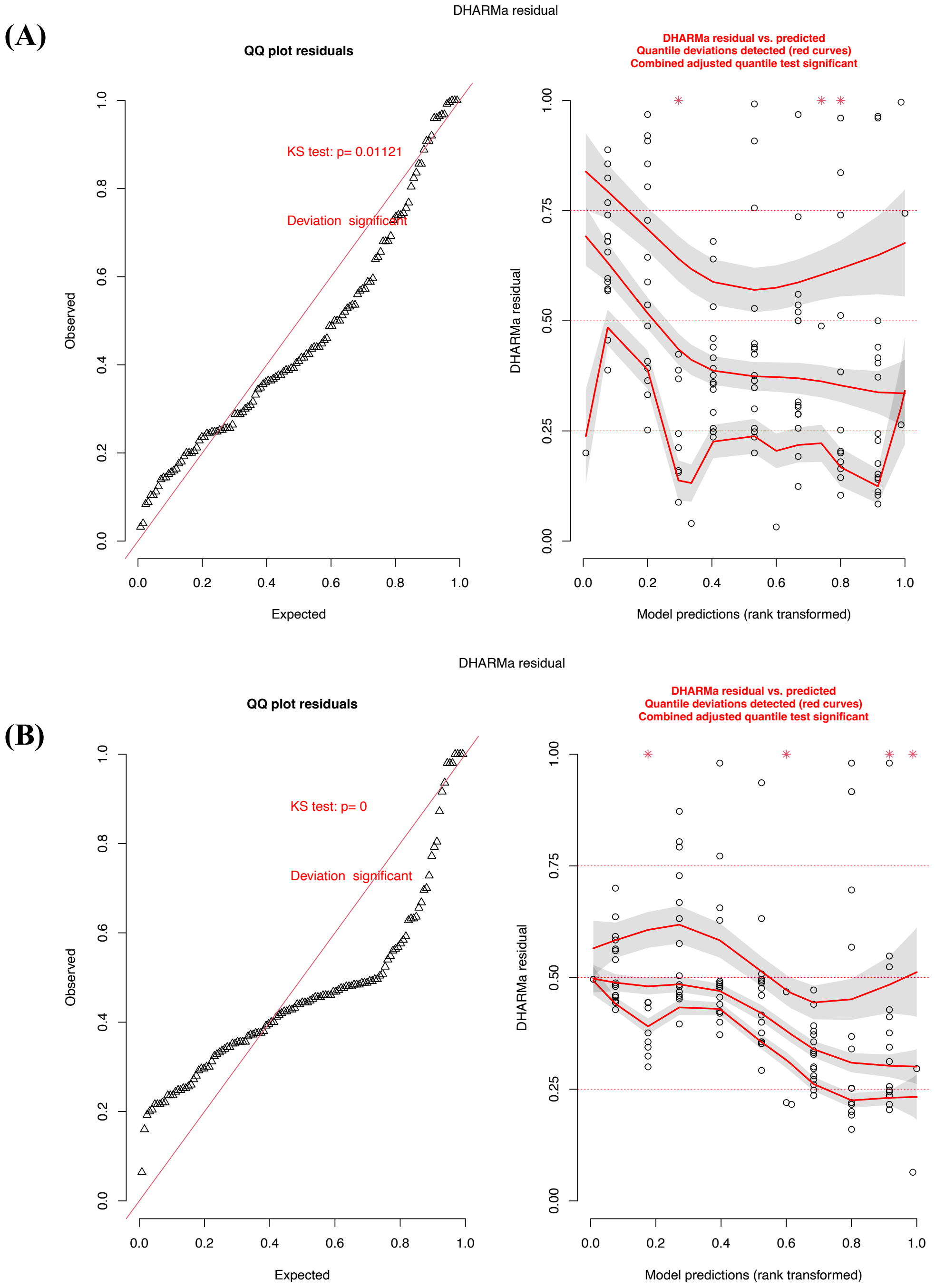
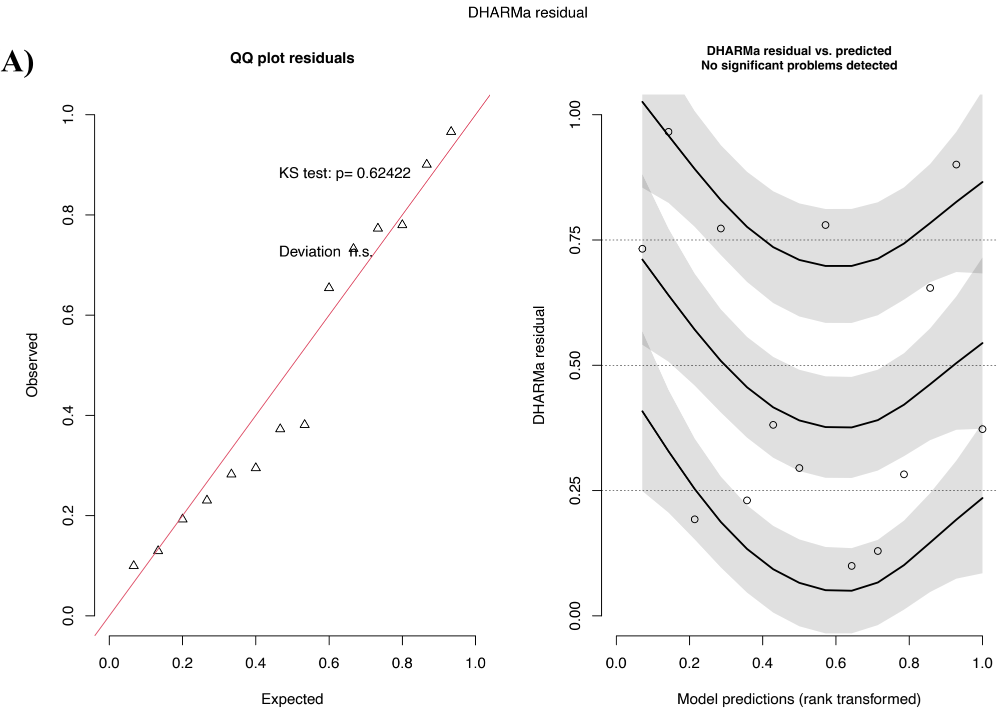
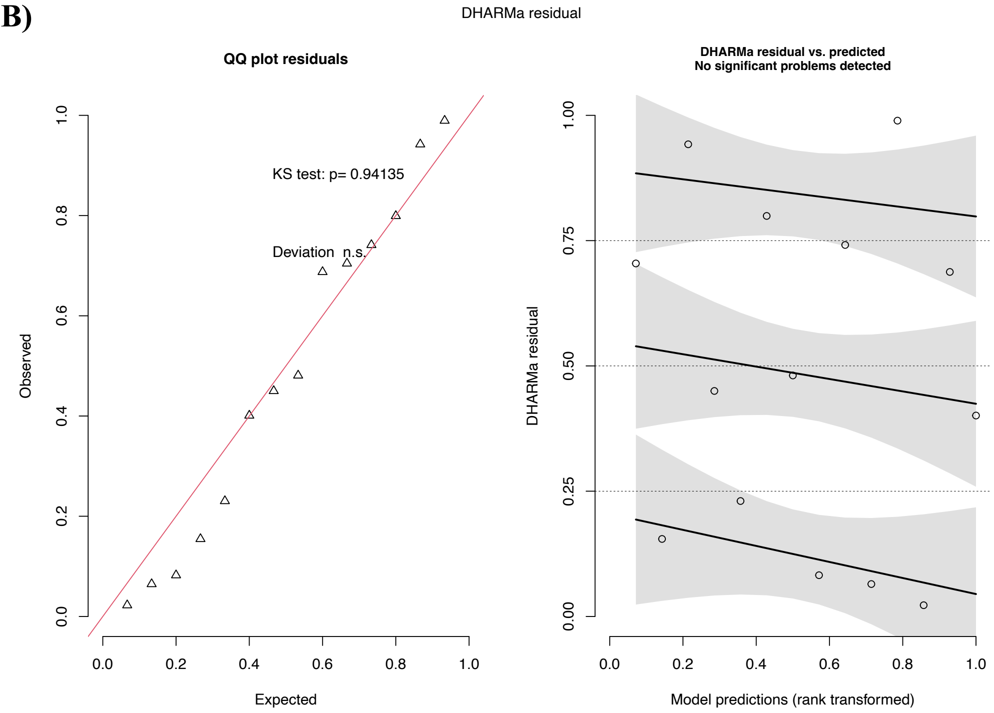


Figure S2. *DHARMa* residual diagnostic plots for the best GLM (based on AICc weight) fitted using a Poisson distribution, to model the number of migrations per year against environmental variables. Rainfall and discharge were modelled separately by constructing two global models: one including rainfall (and salinity and water temperature) (**A**) and the other including discharge (and salinity and water temperature) (**B**). Significant quantile deviations between model predictions and *DHARMa* residuals were not detected, indicating a better fit.

(A)

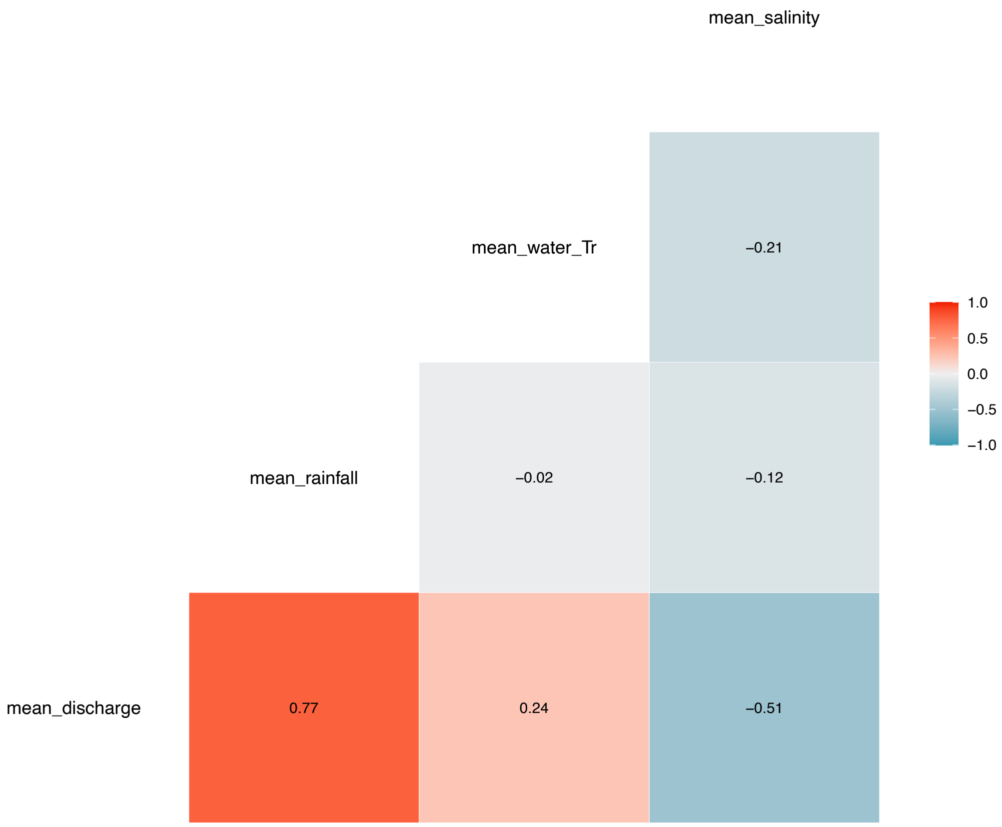


(B)



Appendix 2: Estimating multicollinearity between environmental variables

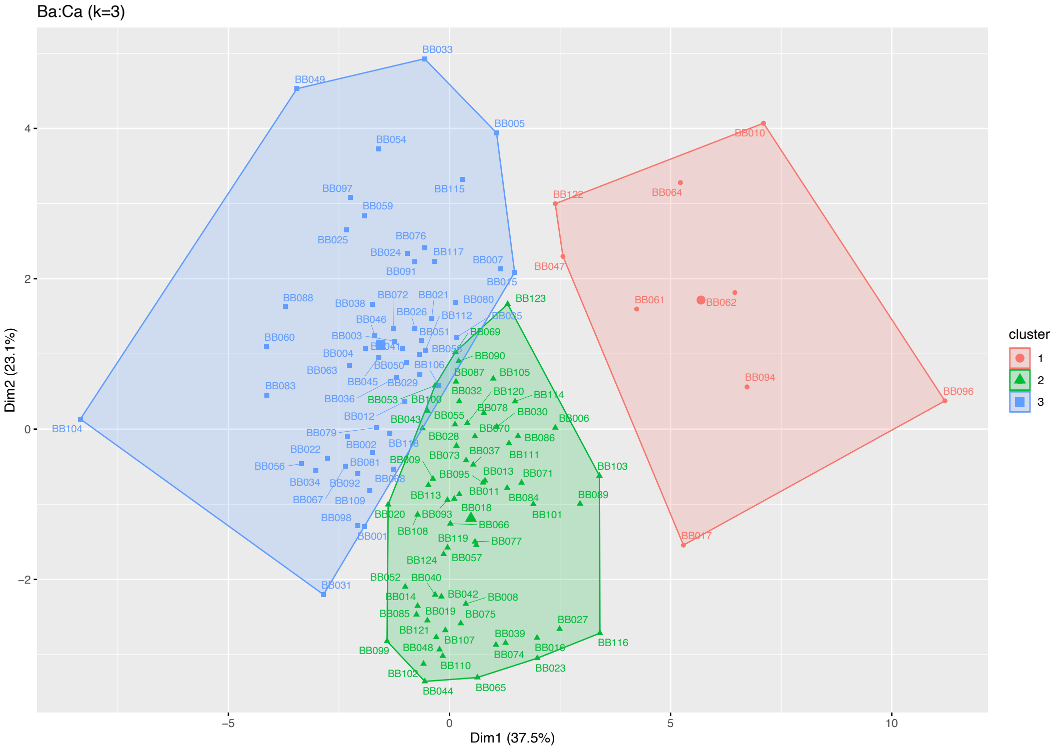
Figure S3. Pairwise correlation matrix to determine correlations between environmental variables prior to constructing GLMs. Annual mean monthly discharge and rainfall were found to be significantly positively correlated and were considered separately when building GLMs.



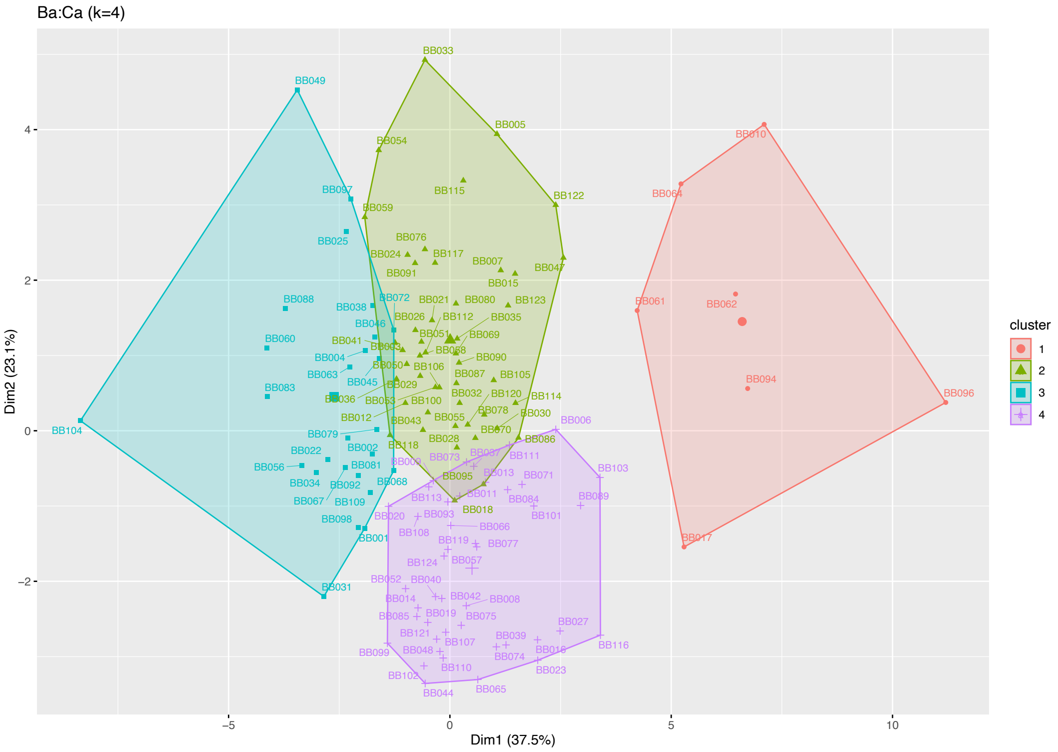
Appendix 3: Determining optimal K-means cluster separation based on otolith Ba:Ca data

Figure S4. K-means clustering results based on otolith Ba:Ca data when the number of clusters specified K= 3 (**A**), 4 (**B**) and 5 (**C**). Increasing K beyond K = 2, resulted in increasing overlap between clusters, indicating weaker separation.

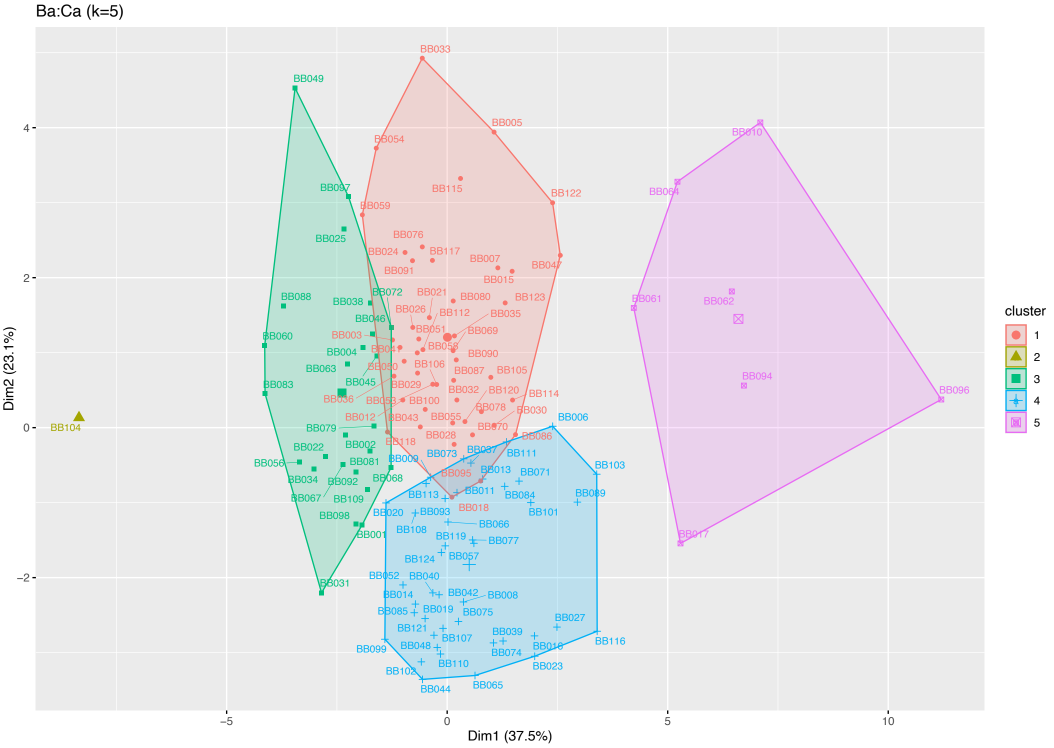
(A)



(B)



(C)


Ba:Ca (k=5)
Dim2 (23.1%)
Dim1 (37.5%)
4
2
0
−2
−5
0
5
10
cluster
1
2
3
4
5
BB033
BB049
BB005
BB054
BB010
BB097
BB115
BB122
BB064
BB059
BB025
BB076
BB024
BB117
BB007
BB091
BB047
BB015
BB088
BB038
BB072
BB021
BB080
BB123
BB061
BB062
BB026
BB112
BB035
BB046
BB051
BB060
BB003
BB069
BB004
BB041
BB058
BB090
BB063
BB050
BB106
BB087
BB105
BB094
BB083
BB045
BB029
BB032
BB120
BB114
BB096
BB036
BB053
BB100
BB078
BB030
BB012
BB043
BB055
BB006
BB079
BB070
BB104
BB028
BB086
BB118
BB002
BB022
BB037
BB073
BB111
BB009
BB081
BB056
BB103
BB013
BB071
BB095
BB034
BB092
BB068
BB011
BB084
BB089
BB113
BB067
BB109
BB018
BB020
BB093
BB101
BB098
BB066
BB108
BB017
BB001
BB119
BB077
BB124
BB057
BB052
BB040
BB031
BB014
BB042
BB008
BB085
BB019
BB075
BB027
BB121
BB039
BB107
BB099
BB048
BB016
BB074
BB116
BB110
BB023
BB102
BB065
BB044

Appendix 4: Model comparison using AICc

Table S1. Dredge results for the global model including rainfall **(A)**, global model including discharge **(B)** and the generalised linear mixed model including rainfall **(C)**, with the most parsimonious model per case study highlighted. M1 from table A was retained for further inference.

(A)

		Fixed effects						
Model	Intercept	mean_rainfall	mean_salinity	mean_temperature	df	AICc	Delta AICc	AICc weight
M1	**0.7529**	**-0.4978**	**0.7125**	**N/A**	**3**	**56.08**	**0.00**	**0.772**
M2	0.7301	-0.5308	0.7190	0.1870	4	59.30	3.22	0.154
M3	0.8641	N/A	0.7270	N/A	2	61.17	5.09	0.060
M4	0.8642	N/A	0.7272	-0.0032	3	64.48	8.40	0.011
M5	0.9773	-0.5263	N/A	N/A	2	69.86	13.78	$7.86e^{-04}$
M6	0.9728	-0.5284	N/A	0.1957	3	72.26	16.18	$2.36e^{-04}$
M7	1.0986	N/A	N/A	N/A	1	76.49	20.41	$2.86e^{-05}$
M8	1.0957	N/A	N/A	0.0788	2	78.99	22.91	$8.16e^{-04}$

(B)

		Fixed effects						
Model	Intercept	mean_discharge	mean_salinity	mean_temperature	df	AICc	Delta AICc	AICc weight
M1	**0.8640**	**N/A**	**0.7270**	**N/A**	**2**	**61.17**	**0.00**	**0.604**
M2	0.8482	-0.2071	0.6762	N/A	3	63.22	2.05	0.217
M3	0.8642	N/A	0.7272	-0.0031	3	64.48	3.31	0.115
M4	0.8025	-0.4465	0.6270	0.2972	4	65.74	4.57	0.061
M5	0.9808	-0.6381	N/A	0.4397	3	73.57	12.40	$1.23e^{-03}$
M6	1.0366	-0.3886	N/A	N/A	2	74.67	13.50	$7.07e^{-04}$
M7	1.0986	N/A	N/A	N/A	1	76.49	15.32	$2.85e^{-04}$
M8	1.0957	N/A	N/A	0.0787	2	78.99	17.82	$8.14e^{-05}$

(C)

		Fixed effects			Random effect				
Model	Intercept	mean_rainfall	mean_salinity	mean_temp	(1|Year)	df	AICc	Delta AICc	AICc weight
M1	**0.7529**	**-0.4978**	**0.7125**	**N/A**	**None**	**4**	**60.12**	**0.00**	**0.690**
M2	0.7716	N/A	0.7345	N/A	None	3	62.92	2.79	0.171
M3	0.7301	-0.5308	0.7190	0.1870	None	5	64.36	4.23	0.083
M4	0.7696	N/A	0.7328	0.0258	None	4	66.95	6.82	0.023
M5	0.7672	N/A	N/A	N/A	None	2	67.81	7.69	0.015
M6	0.7844	-0.4855	N/A	N/A	None	3	68.01	7.89	0.013
M7	0.7617	N/A	N/A	0.1439	None	3	70.92	10.80	0.003
M8	0.7768	-0.5170	N/A	0.2461	None	4	71.40	11.27	0.002

Table S2. AICc comparison of most parsimonious model as a GLM without a random effect for year (M1(A)), and when extended as a GLMM approach by including a random effect for year ((M1(C)). Model M1(A) was retained for further inference.

Model	Intercept	Fixed effects		Random effects	df	AICc	Delta AICc	AICc weight
M1(A)	**0.7529**	**Rainfall**	**Salinity**		**3**	**56.1**	**0.00**	**0.883**
M1(C)	0.7529	Rainfall	Salinity	(1|Year)	4	60.1	4.04	0.117