


REGULAR ARTICLE

Habitat-use strategies of young barramundi (*Lates calcarifer*) in a heavily modified landscape

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Abstract

Barramundi (*Lates calcarifer*) is a facultatively catadromous species that migrates between saltwater and fresh water to complete its life cycle. Modified riverine landscapes may limit these migratory paths and alter the environmental cues that migratory fish rely on to trigger migration. This study aims to determine the timing and prevalence of migration strategies of *L. calcarifer* in modified habitats and to identify the environmental parameters associated with these movements. Historical habitat use was interpreted from mean otolith Sr:Ca ratios as a proxy for ambient salinity. In this study, 27.9% (range: 16.1%–50.0% per year) of *L. calcarifer* exhibited catadromy, which is lower than what has been found for this species in other regions. Juvenile *L. calcarifer* adopted a catadromous strategy either early in life or not at all. Across the nine cohorts represented in the study, the fraction of catadromous individuals showed a moderately positive trend ($r = 0.34$ – 0.50), though not statistically significant, with wetter and cooler wet seasons. In the modified landscape of the Burdekin basin, North Queensland Australia, other factors may influence the likelihood of barramundi adopting a catadromous life strategy. Habitat connectivity is crucial for the viability of wild *L. calcarifer* populations and associated fisheries. Freshwater management should consider the timing required for juvenile *L. calcarifer* to access freshwater habitats and consider further interventions to improve habitat connectivity.

KEYWORDS

aging, Burdekin River basin, catadromous, changepoint analysis, migration, otolith microchemistry

1 | INTRODUCTION

In many species, migration behaviour is not obligatory but facultative (Secor, 2015; Shen et al., 2009; Thibault et al., 2007). Plasticity in migration is believed to be a long-term adaptive strategy as it increases resilience against unpredictable changing environmental conditions (Chapman et al., 2012; Secor et al., 2020). Variations in movement strategies can result from unique individual internal

capacity (e.g., age, life stage, growth rate, or maturity status) or environmental conditions (Nathan et al., 2008). For instance, as sea surface temperature increases, sockeye salmon populations can migrate earlier or later in the season (Hodgson et al., 2006; Kovach et al., 2015). Adding further complexity, some individuals may not have the opportunity to migrate as their migratory routes have been disconnected, therefore requiring a change in migration strategy. For example, a population of diadromous *Galaxias maculatus* has adapted

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to becoming landlocked by completing their life cycle within the lake (Chapman et al., 2006). Understanding how migratory species respond to their environments and adapt their migratory strategies can help us identify appropriate interventions to support these species amid changing environmental conditions.

Aquatic migratory species initiate their movements in response to natural cues such as changes in water temperature (Hodgson et al., 2006; Kovach et al., 2015; Legrand et al., 2021) and river flow rate (Robins et al., 2005; Williams et al., 2014). River flow significantly influences the life history of many migratory species by facilitating migration and creating optimal conditions for growth (Robins et al., 2005; Russell & Garrett, 1985). Natural fluctuations in river discharge volumes and precipitation are essential for maintaining healthy aquatic ecosystems. However, anthropogenic landscape modifications and barriers (e.g., dams, weirs, bund walls) disrupt these natural flow patterns, altering the timing and volume of river discharge. Such modifications can have profound impacts on migratory species by hindering the movement pathways necessary for completing their life cycles, as evidenced in species like the American eel (*Anguilla rostrata*, Lesueur 1817) (Walker et al., 2020) and the spotted grunter (*Posadas commersonii*, Lacépède, 1801) (Childs et al., 2008).

Several tools have been adopted to study movement patterns of migratory species. The live movement of fish can be tracked using traditional mark-recapture tags (Davis & Kirkwood, 1984; Moore & Reynold, 1982) and acoustic and radio telemetry tags (Crook et al., 2020; Honda et al., 2012). Historical movement can be traced from calcified body parts, particularly otoliths (Elsdon & Gillanders, 2003; Reis-Santos et al., 2022). The composition of chemical elements deposited in the otolith provides a historical record of changes in diet, physiological state and ambient environmental conditions (Hüssy et al., 2020). In combination with age-estimation from otolith annuli, these chemical signatures allow the environmental exposure history of individual fish to be identified by tracing changes in elemental signatures across their lives, including the timing of major changes in ambient conditions (McCulloch et al., 2005; Milton et al., 2000; Milton & Chenery, 2003).

The barramundi, *Lates calcarifer* (Bloch 1790), is a facultatively catadromous fish, with varying proportions of the population migrating to freshwater environments after hatching in marine waters (Crook et al., 2016; Milton & Chenery, 2005). During the wet season, some young-of-the-year migrate upstream to reside in rivers, billabongs and flooded wetlands that become connected during flood events (Davis, 1985). As the flooding recedes and habitat connectivity diminishes at the end of the wet season, these migrants can remain in freshwater habitats. Initially, freshwater occupancy was believed to last 3 to 4 years (Grey, 1987), but later studies found that it could extend to 6 to 10 years for some individuals (Crook et al., 2016). Conversely, other individuals complete their life cycle entirely in the marine environment without exhibiting migratory behaviour (Crook et al., 2016; McCulloch et al., 2005; Roberts et al., 2024).

Freshwater migrant *L. calcarifer* are known to grow faster (Leahy et al., 2022; Roberts et al., 2019) and transition to females sooner (Roberts et al., 2021) than their saltwater counterparts. Adopting a

catadromous strategy that includes freshwater migration appears to be beneficial for *L. calcarifer*. However, this strategy also entails risks, such as delayed opportunity for reproduction, or becoming stranded in a landlocked freshwater habitat (Dunstan, 1959; Roberts et al., 2019). The presence of both migratory and resident individuals within populations is therefore crucial for population resilience to environmental variability.

The proportions of each strategy may vary across *L. calcarifer* populations, reflecting the differing environmental conditions each population encounters. In its Australian range, the proportion of catadromous *L. calcarifer* that were sampled from estuarine and marine habitats ranges from 40% in the Fitzroy River in Central Queensland (Milton et al., 2008) to 76.1% in the Daly River in the Northern Territory (Roberts et al., 2024). As a result of faster growth and earlier sex change, catadromous juveniles can potentially become larger females and therefore exhibit disproportionately higher fecundity (Dunstan, 1959). Unless the costs or barriers to adopting catadromy are too great, we expect the freshwater migration strategy to be abundant, as it can promote greater reproductive success in *L. calcarifer* (Milton et al., 2008; Milton & Chenery, 2005).

The heavily modified landscape of the Burdekin River basin in the Dry Tropics region of Queensland presents an opportunity to test a model of different movement strategies in diadromous fish species such as *L. calcarifer*. High demand for water resources has led to complex changes in freshwater flows within this basin (Davis et al., 2014). Intense irrigation infrastructure such as dams and weirs has altered the natural river flow regime and hinders the upstream movement of fish. Additionally, earthen bund walls near the tidal interface have been installed to protect grazing lands and agricultural crops from salt-water intrusion. Consequently, these walls reduce connectivity by preventing seasonal flooding and the movement of diadromous species to nursery habitats during high tides (Hyland, 2002; Karim et al., 2021). Moreover, water quality has deteriorated due to aquatic weeds, sedimentation, eutrophication and pesticide contamination from agricultural run-off, further reducing the accessibility of tidal creeks and freshwater habitats for fish (Hyland, 2002; Karim et al., 2021; Perna & Burrows, 2005; Waltham, Pyott, et al., 2020). In short, anthropogenic activities in this area have extensively altered the river flow regime, potentially changing the environmental cues that migratory species rely on and reducing connectivity between estuarine and freshwater habitats.

Establishing fundamental knowledge about the life history of *L. calcarifer* populations requires understanding the proportion of each life strategy and how it is associated with changing environmental conditions over time. This knowledge is crucial for identifying suitable interventions and restoration activities in the Burdekin's heavily modified landscape. Additionally, considering interannual variation in environmental conditions such as rainfall, river flow volume and climatic indices is essential, as these factors likely enable or trigger *L. calcarifer* movement (Balston, 2009; Leahy & Robins, 2021; Meynecke et al., 2013). Identifying the environmental factors involved in *L. calcarifer* movement will inform management interventions for the sustainable management of this population.

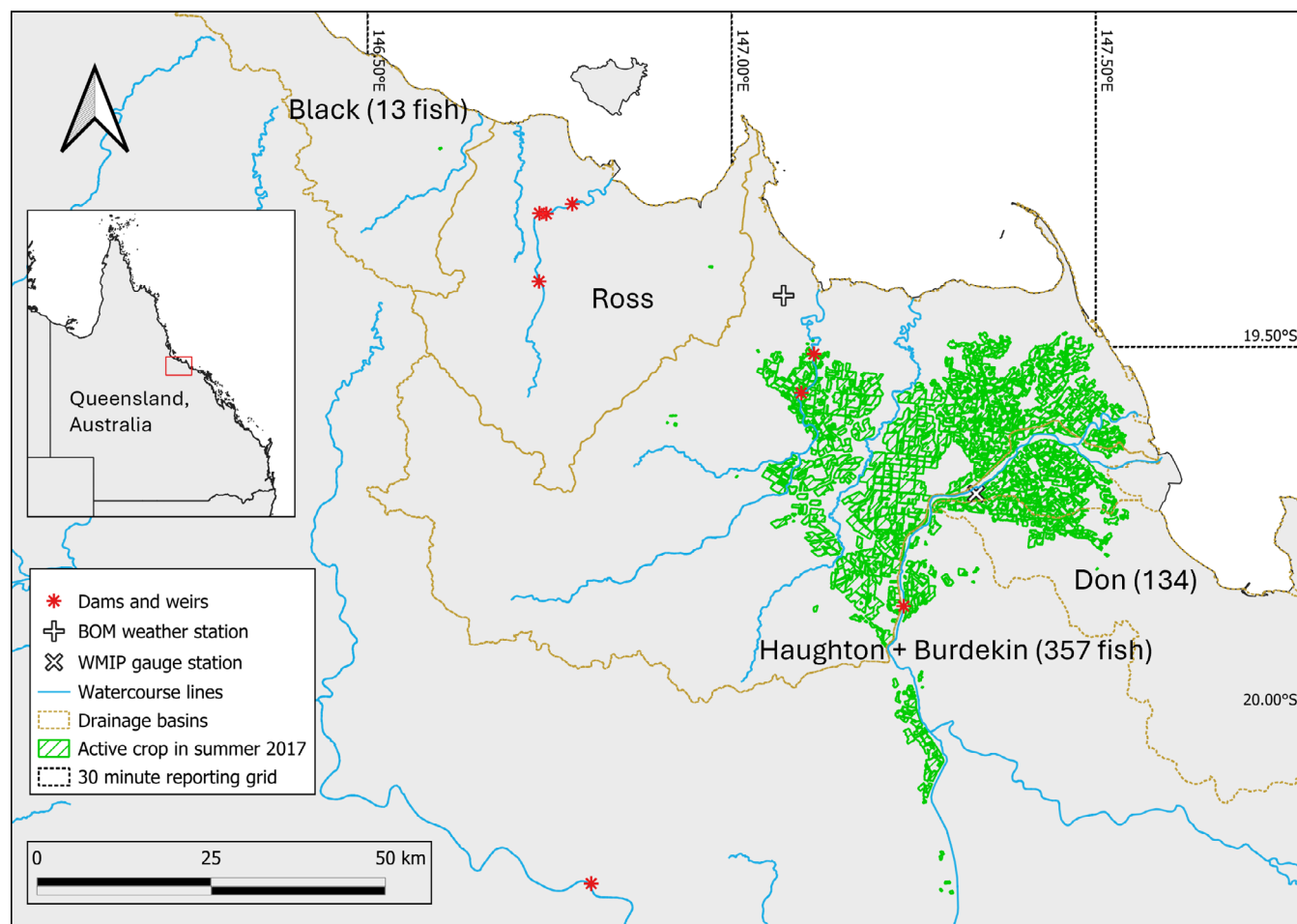


FIGURE 1 Study region including key river basins and number of fish sampled (in brackets) in North Queensland, Australia. Locations of weather stations and river gauge stations are indicated. Habitat modifications for crops are highlighted, and major barriers to fish movement (dams and weirs) are shown.

The current study quantifies the movement strategies of *L. calcarifer* in a heavily modified landscape and identifies the environmental parameters that influence the prevalence of each movement strategy. The specific objectives were to determine: (1) when *L. calcarifer* change habitats; (2) what proportion of each movement strategy occurred through time; and (3) what environmental conditions influence the timing of movement and the proportion of the population adopting particular movement strategies. We address these objectives using change point analysis of an extensive *L. calcarifer* otolith microchemistry dataset. Our findings on *L. calcarifer* life-history flexibility are important for understanding this iconic species' complex ecology and adaptability to anthropogenic habitat changes.

2 | MATERIALS AND METHODS

2.1 | Ethics statement

Fish were collected by the Department of Agriculture and Fisheries, Queensland (DAF) from commercial and recreational fishers (Fisheries

Queensland General Fisheries Permit 200672) and targeted scientific collection (Fisheries Queensland General Fisheries Permit 186281) in line with DAF Animal Ethics permit SA-2018-12-671.

2.2 | Study area

The sampling areas were in the bays and river mouths of the Dry Tropics of Queensland from 18.7 to 20° S between February 2019 and September 2020 (Figure 1). The region experiences a warm and wet summer (November to March) influenced by monsoonal rains and occasional cyclones, and cool and dry austral winter conditions (April to October). The El Niño Southern Oscillation (ENSO) phenomenon also influences annual variation in environmental conditions in this region. The study region encompasses the Black River, Ross River, Haughton River and the Burdekin River basins. These basins contain a mix of urban areas, grazing land, conservation areas, irrigated sugar cane, several dams and weirs and some earthen bund walls at the intertidal zone. These modifications have resulted in a heavily changed landscape (GBRMPA, 2013; Gunn & Manning, 2009; Queensland

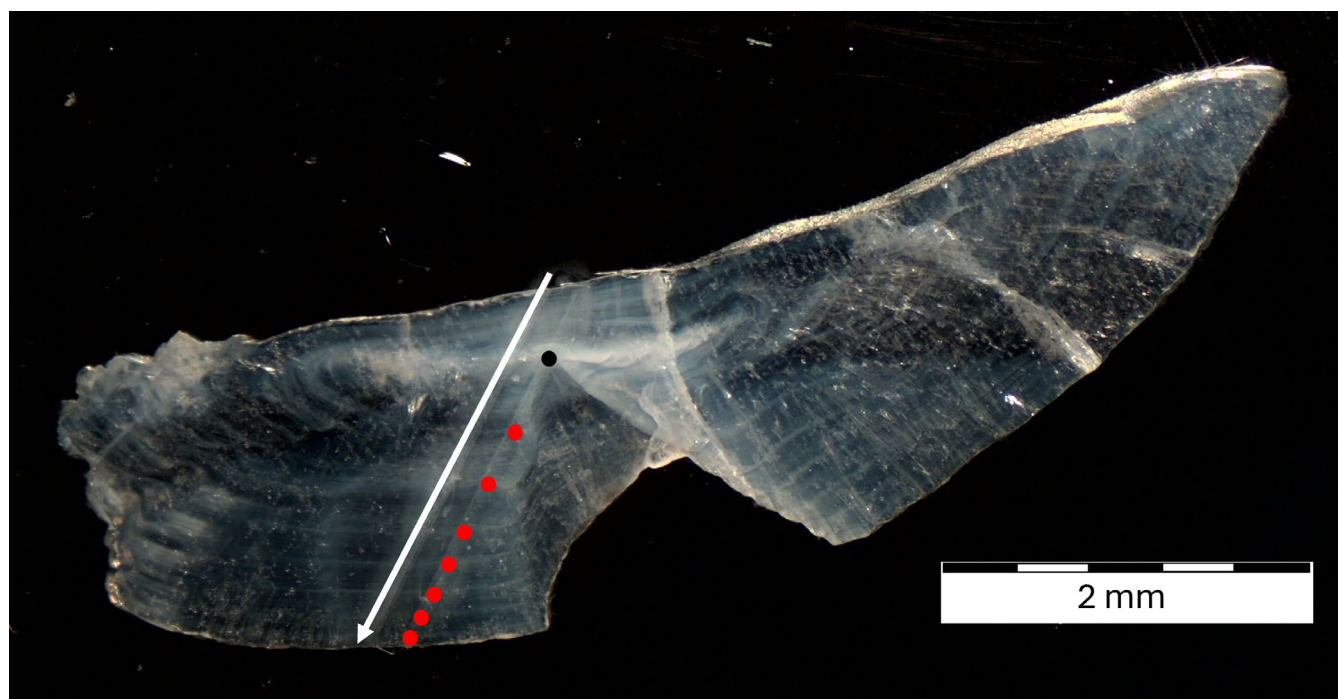


FIGURE 2 A 15 \times magnification of a sectioned *Lates calcarifer* otolith showing the laser ablation track and annotation of increments (fish ID 01-0d, 7 years old, 59 cm total length). The black dot indicates the core area (primordium or increment zero), the red dots indicate annual increments and the white arrow indicates laser transect direction.

Government, 2022), inundation patterns (Waltham, Adame, et al., 2020) and reduced accessibility of juvenile fish and crustaceans to freshwater habitats (Waltham, 2017).

2.3 | Otolith microelement profiles

Sectioned otoliths and microchemical profiles were produced during prior research exploring *L. calcarifer* natal origins in this region (Leahy et al., 2022; Leahy et al., 2023). Sagittal otoliths were extracted, cleaned, embedded in epoxy resin, sectioned and affixed to microscope slides as described in Leahy et al. (2022). The concentration of 15 elements including strontium (Sr) was measured as a ratio to calcium (Ca) (mmol mol^{-1}) using laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) at the University of Western Australia (Perth, Western Australia). Although this study focuses on Sr:Ca ratios, the concentrations of 14 other elements relative to Ca were also measured to assess the alignment between annuli and chemical profiles. This provided a means of validating traditional age estimation and increment markers, as further detailed in the Supplementary section (Appendix S1). Elemental values that exceeded six standard deviations from the mean were excluded. Data processing and analyses were conducted in R Studio (version 2023.06.0, build 421) using R software version 4.3.1 (R Core Team, 2022).

Detailed otolith preparation methods are provided in Leahy et al. (2022). In short, all otoliths were pre-ablated four times using a 50–150 μm wide swath to remove any potential surface contamination. A

30 μm wide laser track was then ablated from the distal to the proximal edge of the sectioned otolith at a speed of 5 $\mu\text{m/s}$ to capture the chemical concentration along the clearest growth axis of the otolith. The track included the primordium area where the fish's early life history is recorded and continued along the reading plane where increment rings are most visible next to the sulcal groove (Figure 2). The Sr:Ca ratio was recorded at each laser ablation spot along the track. Ablation speed and time were used to calculate the ablation distance. Ablated otoliths were photographed (Olympus EP 50) using a light-reflecting stereomicroscope (Olympus SZ 40) at 15 \times to 25 \times magnification, depending on the otolith size. Live view images were visualised and controlled via EPView software (version 1.4, Olympus Life Science).

2.4 | Biochronological features

Each otolith was photographed twice under two settings to capture different aspects of the ablated otoliths. In the dry setting, otolith slides were placed directly on a dry white background. The external light source from a dual gooseneck illuminator was set to emphasise the edge of the ablation path and otolith boundaries. In the wet setting, otolith slides were placed on a black background. Ultrapure water (18.2 M Ω cm) was added below and above the slide and then covered using a clean glass coverslip. The angle of the external light source was adjusted to produce the most explicit image of the otolith annuli (Fisheries Queensland, 2020).

Annuli counts and position were determined following previously established *L. calcarifer* ageing protocols (Fisheries Queensland, 2020). The alternating pattern of narrow opaque and wide translucent zones representing slow and fast growth occurring in dry and wet seasons was counted and measured. The open-source software FIJI (Schindelin et al., 2012) was used to visualise otolith images and measure increment distances. The distance between otolith microstructures was measured from the beginning of the laser track (distal edge, Figure 2). The point on the laser path where it passed through the primordium was considered 'increment 0'. Points where the laser path intersected with subsequent opaque zones were marked in red and named chronologically (Figure 2). Additionally, an extra increment named 'increment 0.5' was added at the halfway point between the otolith core and the first annulus to capture any microchemical changes occurring during very early life. The alignment between annuli and chemical profiles was also investigated (Figure S8 and Appendix S1).

The birth year was inferred from each fish's age (increment count and edge type) and catch date following established protocols for East Coast barramundi (Fisheries Queensland, 2020). Based on the spawning season of *L. calcarifer* in the study area, for convenience, all fish were assumed to have the same birth date of 1 January (Fisheries Queensland, 2020; Russell & Garrett, 1985). A hypothetical increment, 'increment 0.5', was generated for each individual, at the midway point between the core (formed 1 January) and increment 1 typically formed between May and September in neighbouring Central Queensland (Robins et al., 2006). The period captured by increment 0.5 is therefore likely to be during the late wet season (approximately March).

2.5 | Inferring habitat usage and movement

To understand patterns of *L. calcarifer* habitat use, otolith Sr:Ca ratio was used as a proxy for salinity and habitats the fish experienced. The concentration of otolith Sr:Ca has a non-linear relationship with salinity; it increases sharply between 0 and 5–8 PSU, after which the curve becomes less steep and approaches a plateau at higher salinity levels (Hicks et al., 2010; Hüsey et al., 2020; Lin et al., 2007). Otolith Sr:Ca has previously been used as a proxy for salinity exposure in barramundi in this study region (Leahy et al., 2022; McCulloch et al., 2005) and has been demonstrated to be as effective as strontium isotopes at distinguishing the transition from fresh water to estuarine/marine water (McCulloch et al., 2005). The precise otolith Sr:Ca concentration to use as a threshold between high and low salinity exposure was determined by examining the frequency distribution of otolith Sr:Ca concentration at each increment. Distinctly bimodal distributions were observed at every increment (Figure S1). The lowest point between the two modes occurred at or near $2.0 \text{ mmol} \cdot \text{mol}^{-1}$ for all increments and was therefore used as a salinity threshold to distinguish low from high salinity exposure in subsequent analyses. We identified otolith Sr:Ca concentration at $2.0 \text{ mmol} \cdot \text{mol}^{-1}$ as a threshold for salinity levels in this dataset. Fish with mean otolith Sr:Ca greater than the

threshold were interpreted as having exposure to brackish or saltwater conditions, and those lower than the threshold were interpreted as having freshwater exposure. Upon examining mean Sr:Ca at the otolith core, we found 36 individuals had values below the threshold, indicating the ablation track did not successfully capture otolith material from their primordium, and were therefore excluded from the analyses. Another 14 fish were excluded because the corresponding birth years were represented by fewer than 15 fish. As a result, 530 fish were retained for further analyses.

To visualise fish movement history across habitats and salinity levels using otolith Sr:Ca, a change point analysis was carried out on each fish using the *changepoint* package in R (Killick & Eckley, 2014). The Akaike information criterion (AIC) penalty method was used with a pruned exact linear time (PELT) search method and no additional manual penalty. This approach produces mean values for sections of multipoint data that are more objective and replicable than visual classification methods (Killick & Eckley, 2014) and are well suited to large datasets. The change point analysis parameters were tuned to de-emphasise seasonal variability and instead detect major and persistent habitat changes. The calculated mean Sr:Ca value from the *changepoint* package was extracted at each increment and compared with the value at adjacent increments to identify changes in salinity exposure and to infer potential habitat use (Figure 3). Several possible salinity and habitat change scenarios were identified based on the habitat use thresholds identified above.

2.5.1 | Movement direction

Any difference in mean Sr:Ca value between two increments indicates a 'salinity change', which we infer as potential fish movement. Types of salinity changes are: (1) a *decrease*, which is a change from a higher to a lower ambient salinity level, such as experiencing a flood pulse in a wet season, or an actual movement to a low salinity habitat such as a freshwater lagoon; (2) an *increase*, which is a change from lower to higher salinity conditions, such as downstream movement from freshwater habitats to the estuarine environment, or dissipation of flood conditions; and (3) *no change*, which indicates continued exposure to the same salinity level.

Changes in salinity levels indicate only the direction of movement but not the magnitude of movement. Only changes in salinity levels across the salinity threshold were classified as potential movement between habitats. A decrease in salinity across the threshold is classified as a 'downstream movement' and vice versa for an 'upstream movement'.

2.5.2 | Habitat use and habitat-use strategies

Mean Sr:Ca served to identify the habitat type a fish was potentially using at a particular time (increment). The habitat each *L. calcarifer* used ('habitat use') was categorised using the mean Sr:Ca at a particular increment. The early life-history model of *L. calcarifer* indicates that

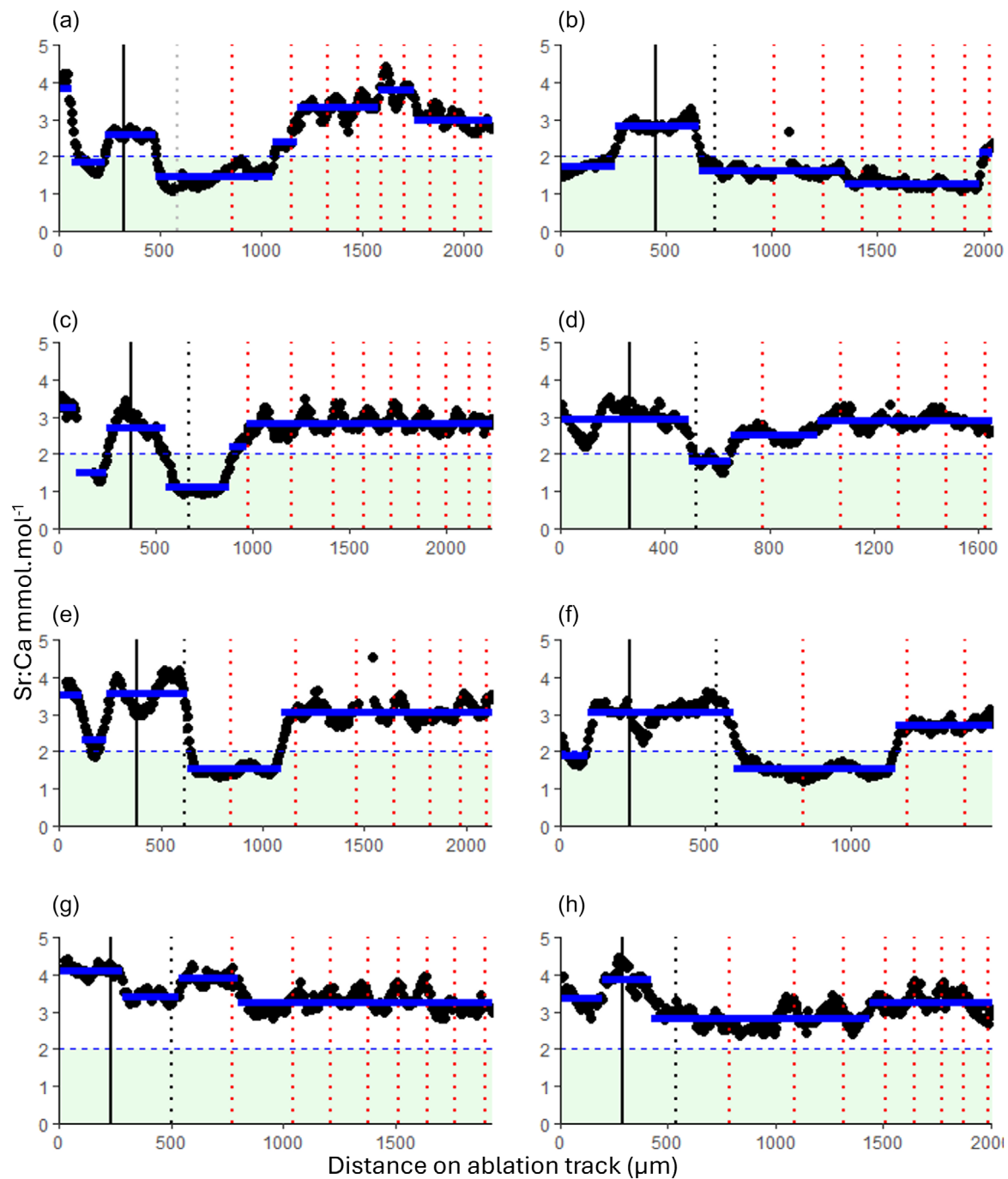


FIGURE 3 Example of a Sr:Ca ratio along ablation transects revealing historical habitat use and four habitat use strategies (in brackets) of eight adult *Lates calcarifer*: (a) ID 03-0c (S/F/F), (b) ID 05-0b (S/F/F), (c) ID 02-0p (S/F/S), (d) ID 05-0c (S/F/S), (e) ID 01-0d ID 05-0c (S/S/F), (f) ID 01-0n (S/S/F), (g) ID 01-0f (S/S/S) and (h) ID 05-0a (S/S/S). The distance on the x-axis starts from the beginning of the laser track, through the primordium, and ends at the otolith edge. Black vertical lines indicate the otolith core, red vertical dotted lines indicate each annual increment and a black vertical dotted line indicates a hypothetical 'increment 0.5' described in-text. Solid blue horizontal lines indicate the duration and mean Sr:Ca value calculated by the change point analysis. The horizontal blue dotted line indicates the locally defined, species-specific salinity threshold for fresh and saltwater habitats ($2.0 \text{ mmol} \cdot \text{mol}^{-1}$).

egg development and larval hatching occur in saltwater (McCulloch et al., 2005; Milton et al., 2008). *L. calcarifer* can then migrate upstream when the floodplain is connected during the wet season, typically within their first year and as early as 3 months of age (Milton

et al., 2008; Roberts et al., 2024). This movement to persistent freshwater habitats can be confounded with prolonged exposure to wet season flooding, both of which would result in otolith Sr:Ca $< 2.0 \text{ mmol} \cdot \text{mol}^{-1}$ at increment 0.5. Freshwater occupancy may

persist for one or more years and would be identified by otolith Sr:Ca $< 2.0 \text{ mmol} \cdot \text{mol}^{-1}$ at increment 1, 2, etc. Simplifying to two possible habitat uses [fresh water (F), and brackish/saltwater (S)] at each increment, four different habitat-use strategies can be expected from young *L. calcarifer* at increments 0, 0.5 and 1: S/F/F, S/F/S, S/S/F and S/S/S (Figure 3). The prevalence of each strategy was quantified across the sampled population.

2.6 | Environmental drivers of habitat-use strategy

Historical environmental data were collected from open-access online databases for the period from 2008 to 2017 to include all *L. calcarifer* birth years in the dataset. Climatic data were retrieved from the Ayr weather station (station number 033002) operated by the Australian Bureau of Meteorology (BOM, 2023b). Environmental datasets included total monthly rainfall (mm) – Rain, monthly mean maximum temperature ($^{\circ}\text{C}$) – Tmax and monthly mean minimum temperature ($^{\circ}\text{C}$) – Tmin. To investigate the impact of regional climatic conditions on the movements of *L. calcarifer*, two climatic indices were also included. The Southern Oscillation Index (SOI) indicates the intensity of El Niño or La Niña events in the Pacific Ocean. SOI data were obtained from BOM (2023a). The standard Australian Monsoon Index (AMI) measures average rainfall anomalies on land north of 25° S in Australia (Marshall & Hendon, 2015). These data were obtained from the Predictive Ocean Atmosphere Model for Australia (POAMA, 2024).

Mean river discharge volumes (Megalitres day^{-1}) – River – from the three major river systems in the study region (the Ross River, the Haughton River and the Burdekin River) were obtained from the Water Monitoring Information Portal service (WMIP, 2023). The relevant monitoring stations are Alligator Creek at Allendale (118106A), Haughton River at Powerline (119003a) and Burdekin River at Clare (120006B). Due to its large catchment area, the mean river discharge volume from the Burdekin River at Clare (gauge station 120006B) was chosen to represent the overall variation in river flow in the study region. All parameters were defined using hydrological years (November to October) (Lough, 2007) and were trimmed to the wet summer season in a hydrological year (November to April) to capture the conditions most relevant to *L. calcarifer* movements, which occur in wet months (Crook et al., 2016; Crook et al., 2020). Pearson's correlation showed that environmental parameters in hydrological years were strongly correlated to environmental parameters in the wet season (0.58 to 1.0, Table S1); therefore, only parameters in the wet season were retained for further analyses.

Next, we examined the influence of environmental factors on the movement behaviours of *L. calcarifer* using correlation analyses to identify potential relationships between environmental variables in the wet season (e.g., Rain, Tmax, Tmin, SOI, AMI and River) and the proportion of fish displaying each life-history strategy (S/F/F, S/F/S, S/S/F and S/S/S). Similarly, we assessed the association of these environmental parameters to the proportion of freshwater habitat use at particular life-history stages (increment 0.5 and increment 1). Using the proportion of fish in each cohort displaying each life-history

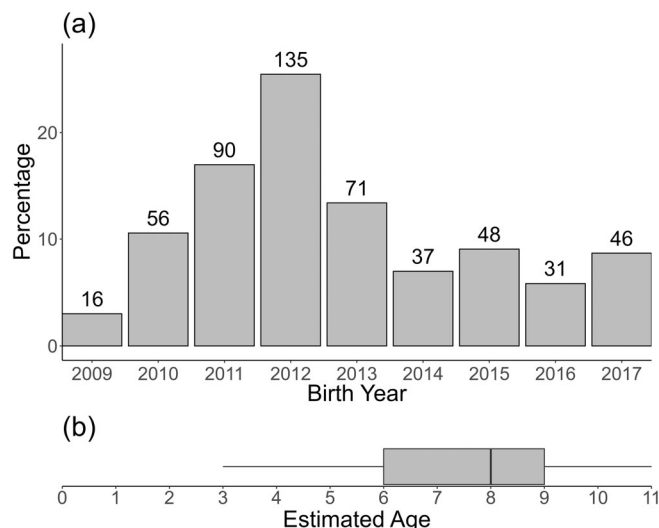


FIGURE 4 The distribution of birth year and fish age for all 530 retained samples. (a) Frequency histogram of birth year. (b) Box-and-whisker plot of age distribution: The whiskers indicate the data range, the box represents the interquartile range and the solid bar inside the box represents the median.

strategy as the response variable accommodates uneven sample numbers from each birth year. To reduce the likelihood of inferring false positives (Type I error) from multiple comparisons, the significance level was adjusted using the Bonferroni correction method (Armstrong, 2014; Cabin & Mitchell, 2000).

Environmental variables were checked for collinearity to reduce redundancy and improve accuracy in the analyses (Table S1). Variables with a moderately high correlation ($r > 0.6$) with multiple variables or that were conceptually redundant were excluded (sensu Dormann et al., 2013). Rain, Tmax, SOI, AMI and River were strongly collinear. We chose total rainfall across the wet season (Rain) to represent parameters that reflected water availability in the basin. Only two environmental parameters were retained in subsequent analyses: Rain and minimum temperature across the wet season (Tmin).

Binomial generalised additive models (GAMs) were used to model the likelihood of *L. calcarifer* adopting either freshwater or saltwater habitats based on Tmin and Rain in a particular wet season. GAMs are less sensitive than GLMs to heterogeneity of variances between groups of *L. calcarifer* occupying freshwater and saltwater habitats, which was detected in our dataset using a Levene's test. Four GAM configurations were tested (Table S2), and the best-performing model was selected based on the lowest AIC (Akaike, 1974). Residual analyses of environmental variables were used to check model validity.

3 | RESULTS

3.1 | Estimated age and birth year

The estimated age of the 530 adult *L. calcarifer* was between 3 and 11 years, with birth years ranging from 2009 to 2017 (Figure 4). Mean

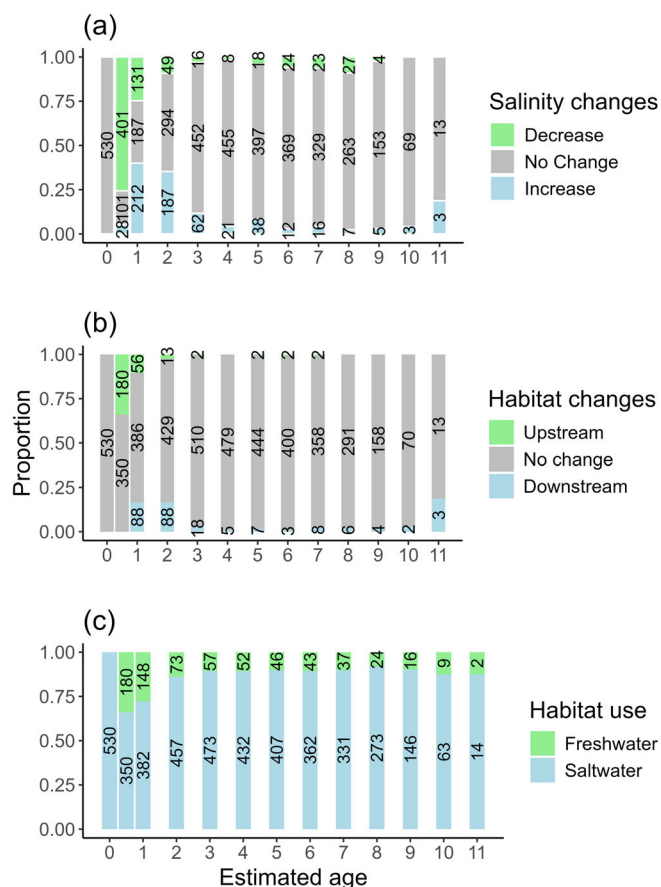


FIGURE 5 The proportion of otoliths showing (a) salinity change, (b) potential habitat change and (c) habitat use at each increment (i.e., estimated age). The number of samples available at each increment is labelled on the plot. Changes in salinity and habitat are inferred from changes in mean otolith Sr:Ca using change point analysis. In this context, a freshwater habitat is defined as a habitat that causes the mean otolith Sr:Ca to be lower than $2.0 \text{ mmol mol}^{-1}$ and vice versa for saltwater habitats. 'Saltwater habitat' includes a salinity range found in estuarine and marine habitats (details in-text).

and median ages were 7.2 and 8 years, respectively. Around half of the fish (55.9%) were born between 2011 and 2013. A limited number of fish born in 2009 were caught in this study. We suspected that most of the fish of this age class may have either been removed from the fishery during previous fishing years or exceeded the maximum legal size for barramundi in this jurisdiction [120 cm (Queensland Government, 2024)].

3.2 | Movement patterns

3.2.1 | Timing of movements

Change point analysis of *L. calcarifer* otolith Sr:Ca profiles showed that 97.2% of fish (515 fish) experienced changes in salinity levels (not necessarily change habitat types) at least once in their lifespan (before the point of capture) and 92.8% (492 fish) experienced it within their

first year. The most common salinity change event in their first year of age was a decrease in salinity at increment 0.5, that is during the first wet season (75.7%, 401 out of 530 fish, Figure 5a). Indications of increasing salinity were often observed immediately thereafter (increment 1, 212 out of 401 fish, 52.8%). This pattern indicates a brief period of seasonal exposure to flooding or a short visit to a lower salinity habitat before returning to higher salinity habitats. The majority of salinity increases occurred within the first 3 years of life (76.8%, 407 out of 530 fish) (Figure 5a).

A similar pattern was observed when we assessed the proportion of fish that experienced sufficiently large changes in salinity to be deemed to have potentially changed habitats (Figure 5b). Interpretation of Sr:Ca profiles showed that 46.6% of *L. calcarifer* (247 out of 530 fish) potentially experienced habitat changes to a lower salinity, indicating an upstream movement or exposure to a major and prolonged flood pulse, at least once in their lifetime. Among those that experienced a reduction in salinity sufficiently large to indicate a potential habitat change, 95.5% (236 out of 247 fish) did so within their first year (i.e., at increment 0.5 or 1, Figure 5b). The highest percentage occurred at increment 0.5 (180 out of 247 fish, 72.9%) during their first wet season (Figure 5b,c).

Changes to higher salinity habitats (i.e., brackish or marine environments), due to a downstream movement or receding flood water, mostly occurred between 1 and 3 years of age (194 movements, 86.2% of downstream events). Unlike changes to a lower salinity habitat, which were concentrated in a narrow age range (0.5 to 2 years old), changes to a higher salinity habitat were observed in a broader age range (1 to 11 years old). These timings suggest that individual choices in the timing of downstream migration may contribute to the wide range of duration of freshwater residency in barramundi.

Ninety-one per cent of individuals that showed a sign of upstream migration showed a corresponding sign of downstream migration (225 fish). However, even though all samples were collected from saltwater habitats, 9% of individuals that showed signs of upstream migration did not have corresponding signs of downstream migration. Lacking a sign of downstream migration is most likely the result of very recent downstream migration that did not leave enough time to accumulate a saltwater signature in the otolith at the time of capture (Gu et al., 2022).

3.2.2 | Habitat-use strategies

Signs of freshwater habitat use were observed most frequently at increment 0.5 (34.0% of all fish) and increment 1 (27.9% of all fish) (Figure 5c). The proportion of freshwater habitat use gradually declined with age but persisted among older fish at an average of $10.9\% \pm 1.6\%$ from increments 2 to 11 (Figure 5c). Among the 530 fish in the study, 16.6% potentially experienced a freshwater environment at increment 0.5 but returned to a saltwater environment by increment 1 (S/F/S strategy, $N = 88$ fish), indicating seasonal exposure to fresh water, but not persistent occupancy in fresh water. About 17.4% moved to fresh water at increment 0.5 and stayed there at

increment 1 (S/F/F strategy, $N = 92$ fish), and 10.6% remained in saltwater at increment 0.5, but had moved to fresh water by increment 1 (S/S/F strategy, $N = 56$ fish), both of which indicate persistent occupancy in fresh water over at least one dry season. About 55.5% remained in saltwater habitats at increments 0.5 and 1 (S/S/S strategy, $N = 294$ fish), indicating no use of fresh water as juveniles. These habitat-use strategies of young *L. calcarifer* are equivalent to 33.9% of fish experiencing freshwater flooding during their first wet season (S/F/F + S/F/S strategies), and to 27.9% of fish residing in freshwater habitats during their first dry season (S/F/F + S/S/F strategies).

3.3 | Use of freshwater habitats

In general, the proportion of *L. calcarifer* experiencing or occupying freshwater environments was positively correlated, though not statistically significant, with the total amount of rainfall and mean daily river discharge during the wet season. The strategies in which fish experience fresh water in their first wet season (S/F/F and S/F/S) showed moderate to strong positive associations with rainfall and river discharge (Table 1 and Figure S3). Conversely, the opposite relationship was observed for fish experiencing saltwater in their first wet season (S/S/F and S/S/S).

Although the S/S/F strategy involves occupying fresh water during the dry season, it showed a negative correlation with most of the tested environmental variables except for mean maximum temperature. The S/S/F strategy was the least common and was even absent in one of the study years (2016, Figure 6). The observed negative correlations with rainfall and mean minimum temperature for the S/S/F strategy are counterintuitive with established barramundi biology and may be attributed to a statistical artefact due to the limited number of fish exhibiting this strategy.

The correlations between environmental parameters and the proportion of fish experiencing fresh water during their first wet season (increment 0.5) and dry season (increment 1) exhibited similar trends, but none were statistically significant (Table 1 and Figure S5). Proportions of freshwater habitat use for both periods (increments 0.5 and 1) were positively associated with rainfall, river flow and climatic indices, and negatively associated with temperature variables. The correlations with the use of freshwater habitats tended to be stronger during the first wet season (increment 0.5) compared to the first dry season (increment 1). Among the variables representing freshwater availability, local variables (rainfall and mean river discharge) showed stronger associations than regional variables such as climatic indices (SOI and AMI).

The proportions of some strategies changed noticeably across the study period (Figure 6) but were not statistically significant after applying the Bonferroni correction. The proportion of *L. calcarifer* that resided exclusively in marine habitats (S/S/S strategy) distinctly increased between 2009 and 2017 ($r = 0.72$), in contrast to strategies in which fish experienced fresh water in their first wet season (X/F/X), which declined across that same period ($r = -0.72$ to -0.67 , Figures 6 and S4).

The probability of freshwater habitat use during the first wet season of *L. calcarifer* (increment 0.5) was best explained using a GAM that included total wet season rainfall (*Rain*) and minimum wet season temperature (*Tmin*) and no interaction term (Table 2 and Table S2). *Tmin* had a significant non-linear relationship with the probability of freshwater habitat use (Table 2 and Figure 7b), and *Rain* showed a borderline-significant non-linear relationship with the choice of habitat use ($p = 0.0521$, Figure 7a). Cooler wet season temperature and greater total rainfall play important roles in juvenile barramundi exposure to fresh water during their first wet season.

During the first dry season of *L. calcarifer* (increment 1), *Tmin* significantly affected the choice of habitat use (Figure 7d). Although *Rain* showed a positive relationship with the probability of *L. calcarifer* using freshwater habitats, it was not statistically significant (Table 2; Figure 7c). Our models indicate that *L. calcarifer* are significantly more likely to reside in fresh water during their first dry season (increment 1) following particularly cool wet seasons. The choice of occupying freshwater habitats during their first dry season may have been influenced by other factors that were not included in the models.

4 | DISCUSSION

In the current study, otolith Sr:Ca ratio from a large sample size (530 fish) provided valuable insight into the life history of *L. calcarifer* in a heavily modified floodplain. The wide range of year classes in this study (2009 to 2017) allowed us to capture a broad range of interannual environmental variation. Such a wide range of observations has not always been available, which may be responsible for weak environmental correlations noted in previous studies (McCulloch et al., 2005; Milton et al., 2008). Evidence of *L. calcarifer* movement from otolith microchemistry is concentrated in their early years and is associated with cooler and wetter years. Management interventions should focus on facilitating catadromy in young *L. calcarifer*, such as through improving habitat connectivity, to maintain both life-history strategies in this population and encourage more productive catadromous strategy in this species.

4.1 | Timing and prevalence of *L. calcarifer* migration

The majority of *L. calcarifer* in this study changed salinity levels within their first year of life (92.8%), whereas a notable proportion experienced sufficient change in salinity level to indicate a potential transition between salt and freshwater habitats (44.6%). A third of all the samples (33.8%) potentially moved upstream during their first wet season. Probable upstream movement of juvenile *L. calcarifer* was indicated by the presence of a freshwater signature in either their first wet or dry season.

Early age of upstream migration in *L. calcarifer* is consistent with findings from other studies. The upstream movements of *L. calcarifer* at an early age are supported by observations of juvenile *L. calcarifer*,

TABLE 1 Correlation coefficients between different movement strategies and environmental parameters (in the wet season).

Environmental parameters	Habitat-use strategy at inc. 0/0.5/1				Freshwater habitats use at inc.	
	S/F/F	S/F/S	S/S/F	S/S/S	Inc 0.5	Inc. 1
Rainfall (mm)	0.69	0.57	−0.73	−0.59	0.71	0.50
Mean maximum temperature (°C)	−0.31	−0.62	0.18	0.54	−0.51	−0.38
Mean minimum temperature (°C)	0.29	−0.25	−0.70	0.20	0.04	−0.12
Southern Oscillation Index (SOI)	0.23	0.53	−0.54	−0.41	0.42	0.23
Australian Monsoon Index (AMI)	0.02	0.30	−0.56	−0.15	0.18	0.00
Mean river discharge (ML day ^{−1})	0.53	0.47	−0.71	−0.44	0.57	0.34
Year	−0.72	−0.67	0.43	0.72	−0.78	−0.63

Notes: None of the correlations were statistically significant after Bonferroni corrections. The adjusted significance levels for the ‘Habitat-use strategy’ and ‘Freshwater habitats use at increments’ are $p = 0.0018$ and 0.0036 , respectively. Bold numbers indicate strong correlations ($|r| > 0.6$) but not statistical significance after the Bonferroni correction.

Abbreviations: F, freshwater; Inc, increment; S, seawater.

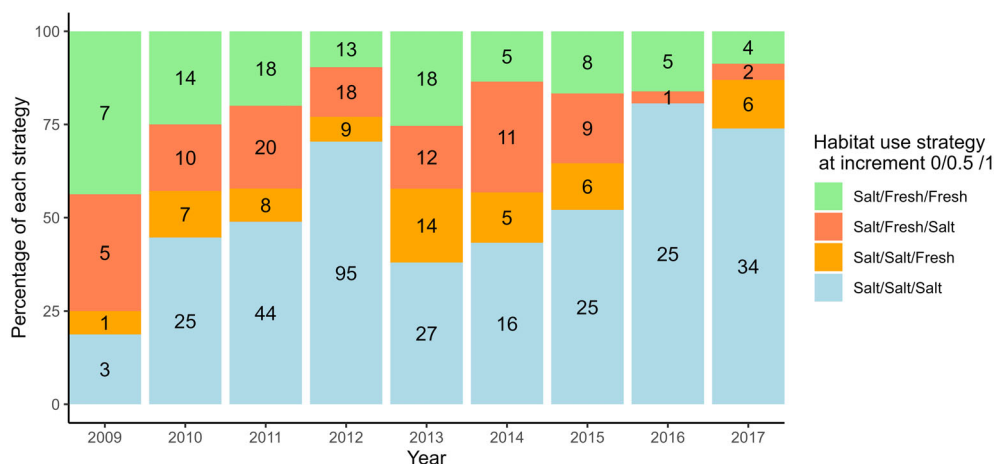


FIGURE 6 Percentage of habitat-use strategies by year-class. The number of observations of each strategy is labelled on the plot.

TABLE 2 Summary of the best-performing GAMs testing the influence of environmental conditions on the probability of *L. calcarifer* experiencing freshwater habitats during their first wet season (increment 0.5) and their first dry season (increment 1).

Model formula	Habitat_Use ~ s(Rain_wet, k = 9) + s(Tmin_wet, k = 9)				
Responses	Predictors	Eff. df	Ref. df	χ^2	p-value
Freshwater habitat use during first wet season (increment 0.5)	Rain	2.668	2.805	8.506	0.0521
	Tmin	4.897	5.126	14.545	0.0215
Freshwater habitat use during first dry season (increment 1)	Rain	1.001	1.001	1.46	0.2269
	Tmin	4.939	5.794	22.3	0.0007

Abbreviations: Eff.df, effective degree of freedom; GAM, generalised additive model; Rain, total wet season rainfall; Ref. df, reference degree of freedom; Tmin, mean minimum temperature in the wet season.

as small as 30–101 mm total length, moving upstream to freshwater habitats in central Queensland (Power et al., 2019). Indeed, the timing of freshwater accession of juveniles in our study agrees with results from other rivers in Queensland (Milton et al., 2008) and the Northern Territory (Roberts et al., 2024). However, our data contradict a result from Papua New Guinea, where *L. calcarifer* stayed much longer (3 to 8 years) in the marine environment before entering freshwater habitats (Milton & Chenery, 2005). The possible factors contributing to

variations in the timing of freshwater accession merit further investigation.

It is important to note that evidence of exposure to fresh water in their first wet season at increment 0.5 may be confounded. The microchemical signatures herein are the combination of an actual movement of juvenile *L. calcarifer* to a lower salinity habitat and a reduction in ambient salinity due to wet season flood pulses. *L. calcarifer* exposed to a freshwater environment for an extensive

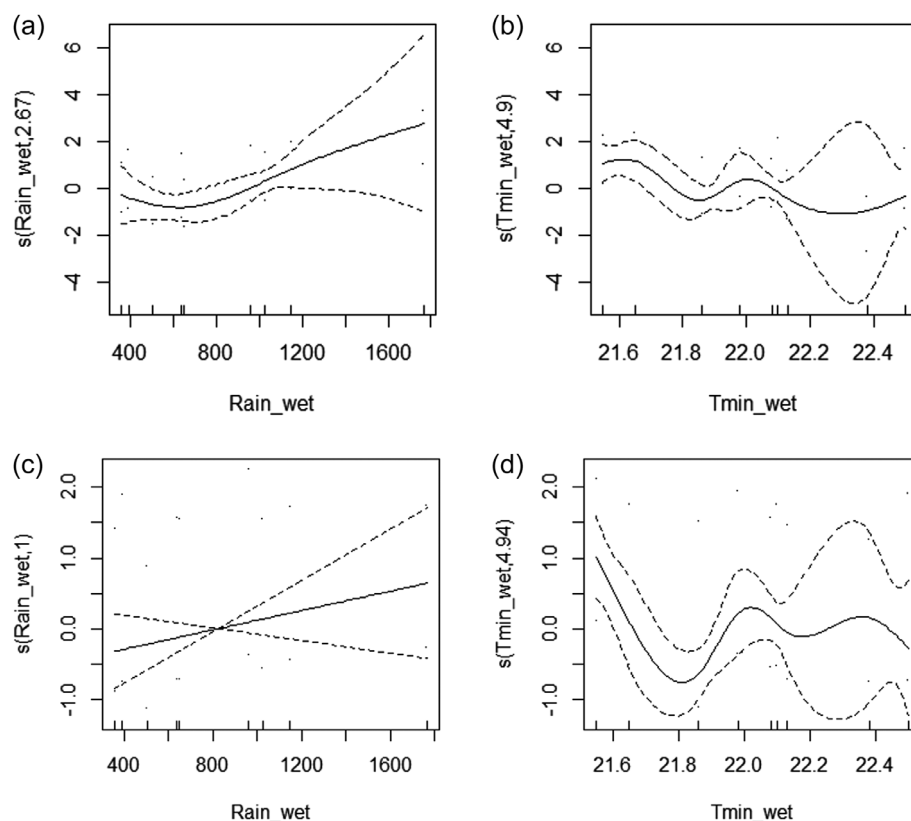


FIGURE 7 The relationships between environmental variables and the probability of *Lates calcarifer* selecting freshwater habitat at different periods (top panels for increment 0.5 and bottom panels for increment 1). The left column shows relationship with *Rain*: Total rainfall in wet season, and the right column shows relationships with *Tmin*: Mean minimum temperature in wet season.

period develop signs of fresh water in their otoliths. The rate of otolith Sr deposition depends on ambient concentration and exposure time (Gu et al., 2022). To equilibrate to the ambient concentration, otolith Sr needs 1–3 days of exposure to a higher concentration (Bernat et al., 1972; Gu et al., 2022; Liu et al., 2022) and 10–40 days of exposure to a lower concentration (Macdonald & Crook, 2010). The actual proportion of young *L. calcarifer* migrating to and remaining in the freshwater habitat cannot be distinguished solely by interpreting signs of low otolith Sr:Ca in their first wet season (increment 0.5). However, we can infer freshwater residency more reliably by examining the freshwater signature during their first dry season (increment 1), when flood pulses do not occur.

4.2 | Habitat-use strategies

Of the 530 fish in this study, 46.6% of *L. calcarifer* potentially utilised freshwater habitats at least once in their life. Among those that encountered prolonged and distinct freshwater exposure, 72.87% (192 fish) did so during their first wet season. As discussed earlier, this number combines indiscernible groups (actual movements and merely experiencing floods). An unconfounded count of freshwater utilisation should be assessed during the dry season. In this study, we found that

only 27.9% of *L. calcarifer* utilised freshwater habitats during their first dry season (S/F/F + S/S/F strategies).

The overall proportion of juvenile catadromous *L. calcarifer* (juveniles that resided in freshwater habitats) in this study is 27.9% ($n = 530$), ranging from 16.1% to 50% between 2009 and 2017. This overall proportion is generally lower than that reported in other studies (Table 3). Other studies on *L. calcarifer* collected from estuarine and marine habitats in Queensland and the Northern Territory, Australia, found proportions of catadromous individuals ranging from 40% to 61.5% (Table 3). The lower proportion of catadromous *L. calcarifer* in this study could be attributed to several factors, such as methodological differences in the definition of freshwater residency, focal age and sample size, as well as true ecological differences arising from habitat modification, climatic conditions or genetic stock.

The lower proportion of catadromous *L. calcarifer* in this study could be influenced by the varying levels of landscape modifications among the study areas. The Burdekin and nearby basins in our study have undergone significant modifications (GBRMPA, 2013). Several dams and weirs have been installed (GBRMPA, 2013; Gunn & Manning, 2009), large areas are dedicated to flood-irrigated agriculture (Queensland Government, 2022) and bund walls have been constructed at the fresh/saltwater interface (Karim et al., 2021). These changes can alter natural hydrology and reduce the accessibility of

TABLE 3 Proportions of catadromous *Lates calcarifer* from fish that were sampled from different estuarine and marine habitats across northern Australia and Papua New Guinea.

	Authors (year)	Basins	Sample size	Catadromy	
				Count	Percentage
1	Crook et al. (2016)	NT, Australia	22	13	59.1
2	Roberts et al. (2019)	NT, Australia	64	n.p.	61.5
3	Roberts et al. (2024)	Four basins, NT, Australia	168	105	62.5
		Fitzroy River, NT, Australia	63	43	68.3
		Daly River, NT, Australia	46	35	76.1
		Mary River, NT, Australia	35	14	40.0
		Roper River, NT, Australia	24	13	54.2
4	Milton and Chenery (2005)	Fly River, PNG	11	1	9.1
5	Milton et al. (2008)	Fitzroy River, QLD, Australia	20	8	40.0
6	McCulloch et al. (2005)	Burdekin River, QLD, Australia	4	2	50.0
7	Current study	Burdekin River, QLD, Australia	530	148	27.9

Note: 'n.p.' means 'not provided'.

freshwater habitats due to the presence of barriers to fish movements. Such modifications likely contribute to the reduced proportion of catadromous *L. calcarifer* observed in our study compared to other regions.

The less disturbed and more intact habitats of the Northern Territory may allow barramundi to access wetlands even in the dry season (Roberts et al., 2024), whereas the existing barriers (physicals and chemicals) in our study region may prevent upstream migration. During the wet season, particularly in extremely wet years, previously disconnected habitats can be reconnected. The proportion of catadromous barramundi in our study is moderately associated with the amount of rainfall, river flow and temperature during the wet season, especially during extreme wet events such as the one in 2009. In that year, rainfall was double the average and five times greater than the driest year (2015) within the study period (BOM, 2023b). Even though the sample size in 2009 is limited, we retained this data point to represent an extreme wet event in the study region. Long-term monitoring of migratory behaviour in relation to climatic cycles such as La Niña could shed light on how barramundi in the modified habitats adapt their migratory patterns in response to the extreme climate events.

We suspect that significant wet events play a crucial role in facilitating barramundi migration in modified habitats by improving habitat connectivity and helping fish overcome barriers. Similar trends have been observed in other regulated river systems, where greater river flow increased upstream movements of catadromous (Amtstaetter et al., 2021), amphidromous (Amtstaetter et al., 2021), as well as freshwater migratory species (Carpenter-Bundhoo et al., 2023).

The weaker environmental correlations at increment 1 compared to increment 0.5 may indicate the impact of a modified landscape on barramundi catadromy. All correlation and GAM analyses indicated that wetter and cooler wet seasons increased the proportion of *L. calcarifer* experiencing flood plumes during the wet season (increment 0.5) but did not necessarily increase the proportion of those

residing in freshwater habitats (catadromy) during their first dry season (increment 1). This discrepancy may be due to the presence of physical (Abbott et al., 2020) or chemical barriers (Waltham, Coleman, et al., 2020) in this modified habitat that prevented *L. calcarifer* from migrating upstream to forage, reside and persist in freshwater environments. Although we cannot directly test these mechanisms with the current dataset, previous restoration efforts, such as the removal of aquatic weeds (Waltham, Pyott, et al., 2020) and earthen bund walls (Karim et al., 2021; Waltham, Adame, et al., 2020) have allowed natural tidal water ingress and promoted the reappearance of migratory fish in wetlands in this region. Further targeted studies are needed to evaluate the role of such barriers in limiting catadromous behaviour in *L. calcarifer* within this system.

Correlation analyses indicated that local measures of freshwater availability (rainfall and river flow) were more important than regional climatic predictors for predicting young *L. calcarifer* access to freshwater habitats. This result contrasts with other studies, such as in the Northern Territory, where AMI was strongly correlated with year class strength and migration patterns of *L. calcarifer* (Crook et al., 2022; Roberts et al., 2024). In addition, two climatic indices, the Madden-Julian Oscillation and SOI, significantly correlated with *L. calcarifer* catch volume in Princess Charlotte Bay, North Queensland (Meynecke et al., 2013). Our study shows that accession of *L. calcarifer* to fresh water had stronger correlations to rainfall and river flow rate than to the SOI and AMI. In contrast to other parts of Northern Australia, the landscape of Far North Queensland and the Burdekin floodplain in particular have been heavily modified by agricultural and urban development (Wolanski & Ducrotoy, 2014). Climatic indices such as SOI and AMI, which capture broad-scale regional phenomena, may not be as relevant in modified systems where water may be retained or extracted before reaching the lower catchment. On the contrary, rainfall and river flow at monitoring stations closer to the river mouth are more locally relevant parameters.

These parameters, especially in the wet season, indicate the abundance of fresh water that potentially reconnects habitats and allows young *L. calcarifer* to access their prospective nursery grounds. We acknowledge that this interpretation is based on correlational patterns and that further research is needed to disentangle the specific mechanisms limiting freshwater use in modified catchments. Nevertheless, our findings highlight the importance of considering fish life-history constraints when designing environmental flow strategies. Suitable interventions such as timing and allocations to environmental flows should ensure the optimum water level to reconnect supratidal habitats to allow access for young *L. calcarifer* in the wet season.

The declining proportion of catadromy observed in our study over time may have negative impacts on the growth rate of *L. calcarifer* in this region, as the growth rates of young *L. calcarifer* are known to correlate with their choice of habitat use and rate of river flow (Roberts et al., 2019; Robins et al., 2006). From 2009 to 2017, the proportion of marine residents (S/S/S) steadily increased, whereas the proportion of freshwater occupants (S/F/F and S/S/F) declined (Figure 6). It was speculated that the lower proportion of catadromous individuals could be biased by the limited number of samples born in the later years (2014 to 2017) or by some catadromous individuals still occupying freshwater habitats and not being sampled. However, sample size-related bias is unlikely, as the proportion of catadromy during 2014 to 2017 was similar to or greater than that in 2012, which had the greatest number of fish born. Downstream movement opportunity bias is also unlikely to be a major influence in this dataset, as most *L. calcarifer* in this region only occupy freshwater habitats for a year before returning to saltwater habitats (Munpholsri et al., in preparation). Because of the strong correlation between the proportion of catadromous individuals and precipitation, we suspect that the observed trend of a reduced proportion of catadromy can be attributed to the reduced precipitation in the region during that same period (Figure S7, BOM, 2023b). The implications of this shift in hydrological conditions and life-history strategies over time on local *L. calcarifer* growth rates merit direct investigation.

4.3 | Considerations regarding salinity threshold and change point analysis

The current study classified habitats into two categories based on the mean otolith Sr:Ca threshold (fresh water $<2.0 \text{ mmol} \cdot \text{mol}^{-1} \leq$ saltwater). These criteria oversimplify the complexity of *L. calcarifer*'s potential habitats, which are on a spectrum ranging from fully fresh water, through brackish, to fully saltwater. A simplified binary habitat classification (fresh and marine habitats) has been applied in other *L. calcarifer* studies (Milton et al., 2008; Milton & Chenery, 2005) and other species (Honda et al., 2012; Milton & Chenery, 2003). Although several studies have attempted to correlate the concentration of otolith Sr with water salinity, this proxy is more reliable for distinguishing salinity gradients below 5 ppt. Beyond this range, the Sr mixing model curves flatten, making interpretation of higher salinity levels more challenging (Crook et al., 2016; Milton & Chenery, 2005). For our purpose of distinguishing

persistent residency in freshwater habitats, we consider a binary classification of habitats appropriate.

The otolith Sr:Ca threshold for freshwater exposure varies between study regions and species. For example, in *L. calcarifer*, the criteria for freshwater habitat were defined as $<1.5 \text{ mmol} \cdot \text{mol}^{-1}$ in the Ross River (Cappo et al., 2005) and Fitzroy River (Milton et al., 2008), $<1.6 \text{ mmol} \cdot \text{mol}^{-1}$ in Papua New Guinea (Milton & Chenery, 2005), $<1.81 \text{ mmol} \cdot \text{mol}^{-1}$ in the Burdekin and $<1.89 \text{ mmol} \cdot \text{mol}^{-1}$ in the Barrattas (Cappo et al., 2005). The criterion for freshwater threshold for brown trout, *Salmo trutta*, in Japan was $<3.0 \text{ mmol} \cdot \text{mol}^{-1}$ (Honda et al., 2012), whereas the criteria for threshold for eels, *Anguilla* spp., in Southeast Asia and Canada were $<2.0 \text{ mmol} \cdot \text{mol}^{-1}$ (Arai & Chino, 2019) and $<3.5\text{--}4 \text{ mmol} \cdot \text{mol}^{-1}$ (Thibault et al., 2007), respectively. A previous study recommended that the criterion should be tailored specifically for each study system or species (Cappo et al., 2005). To improve the accuracy of salinity criteria for future studies, a combination of methods could be considered, such as standardising salinity levels with Sr isotopes (Crook et al., 2016; Milton & Chenery, 2005), comparing Sr:Ca, Ba:Ca and Sr:Ba (Cappo et al., 2005; McCulloch et al., 2005) and checking otolith element frequency distributions as was done in the current study (Appendix S1).

We found that change point analysis was a helpful tool for handling complex multipoint data from the otolith mass spectrometry analysis, as has been found in other otolith studies (de Maichak Carvalho et al., 2020; Gonzalvo et al., 2021). Using a mathematical model to calculate mean otolith Sr:Ca is objective, quantitative and replicable compared to visually estimating a representative value at an increment, which can be somewhat subjective. In addition, using a mean value can minimise the number of samples discarded due to gaps in ablation data. In our study, 6.2% of otoliths had increment positions falling in a data gap in an ablation transect (Figure S6a,b). These gaps are typically attributed to instrument errors and removing outliers during data cleaning. It is important to note that change point analysis parametrisation, such as penalties and search methods, can produce different results. Parameters should therefore be fine-tuned to individual studies, and interpretation of change point analysis results should be done with this in mind. Future studies could improve the detection sensitivity of a change point analysis by incorporating multiple elements. Although *changepoint* can only analyse univariate data, a nonparametric approach such as the *ecp* package can detect changes in both univariate and multivariate data (James & Matteson, 2015). Incorporating both Sr and Ba and detecting changes in both mean and variance of those elements could reveal fine-scale changes that mean Sr alone may not be able to detect.

It is possible that the change point analysis approach may have underestimated freshwater exposure at increment 0.5. This is because some mean Sr:Ca values at the increment 0.5 might have been exaggerated (i.e., overestimation of saltwater exposure, underestimation of freshwater exposure) due to the use of mean values for such a narrow time period. The hypothetical increment 0.5 was generated to capture observed Sr:Ca variations before the first increment and is positioned at the halfway point between the core and the first annual increment.

However, a brief exposure to fresh water (low mean Sr:Ca) that might occur slightly before or after this position can be missed by the change point analysis approach (Figure S6c,d). In addition, if the actual value of otolith Sr:Ca at increment 0.5 was at or below the freshwater threshold, but Sr:Ca values at neighbouring ablation points were higher (i.e., more saline), then the averaging process of the change point analysis would lead to an incorrect interpretation of saltwater habitat signature (Figure S6c-f).

In conclusion, this study demonstrates that the movement strategies of *L. calcarifer* in the northeast coast of Queensland, though flexible, are lower than other studies for this species, with less than one-third of the population following a catadromous life history (i.e., persistent residency in fresh water across at least one dry season, S/F/F or S/S/F). The remaining individuals in our sample population lived only in brackish and marine habitats (S/S/S) or visited fresh water briefly during their first wet season (S/F/S). Among those individuals that moved upstream, most movements occurred very early in life, within 1 to 2 years. Environmental parameters indicating cooler temperatures and locally increased water availability, such as rainfall and river flow, were positively associated with the movement of young *L. calcarifer* into freshwater habitats. Maintaining habitat connectivity and suitable river flows are key to the viability of the wild *L. calcarifer* population in this region.

5 | LAY SUMMARY

The chemical composition of *L. calcarifer* ear bones showed historical movement between salt- and freshwater habitats. In North Queensland, less than one-third of juvenile *L. calcarifer* resided in fresh water, which is lower than other regions. Their upstream movement into fresh water was linked to the amount of rainfall and temperature. Connectivity between estuaries and freshwater wetlands enables *L. calcarifer* movement and should facilitate population growth.

AUTHOR CONTRIBUTIONS

Nut Munpholsri: data analysis, data visualisation and preparation of manuscript. Naomi M. Gardiner and Nathan J. Waltham: conceptualisation, interpretation of data, editing and reviewing the manuscript. Susannah M. Leahy: conceptualisation, data collection, generations and analysis, funding acquisition, interpretation of data, editing and reviewing the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

According to the data transfer agreement with the Department of Agriculture and Fisheries, Queensland (DAF) (Ref. No. AS10910_6533), DAF is the owner of the dataset. Data are provided for the purpose of a PhD thesis and related publications of Nut Munpholsri. Any inquiry to access to the data should directly contact DAF.

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SUPPORTING INFORMATION

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