



# Landscape edges shape dispersal and population structure of a migratory fish

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Received: 20 February 2019 / Accepted: 17 June 2019 / Published online: 22 June 2019  
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## Abstract

Many freshwater organisms have a life-history stage that can disperse through seawater. This has obvious benefits for colonization and connectivity of fragmented sub-populations, but requires a physiologically challenging migration across a salinity boundary. We consider the role of landscape boundaries between freshwater and seawater habitats, and evaluate their potential effects on traits and developmental histories of larvae and juveniles (i.e., dispersing life-history stages) of an amphidromous fish, *Galaxias maculatus*. We sampled juvenile fish on their return to 20 rivers in New Zealand: 10 rivers had abrupt transitions to the sea (i.e., emptying to an open coastline); these were paired with 10 nearby rivers that had gradual transitions to the sea (i.e., emptying into estuarine embayments). We reconstructed individual dispersal histories using otolith microstructure, otolith microchemistry, and stable isotope analysis. We found that fish recruiting to embayment rivers had distinct dispersal and foraging histories, were slower growing, smaller in size, and older than fish recruiting to nearby non-embayment rivers. Our results indicate that landscape edges can affect dispersal capabilities of aquatic organisms, potentially leading to divergent life-history strategies (i.e., limited- versus widespread-dispersal). Patterns also suggest that dispersal potential among landscape boundaries can create heterogeneity in the traits of individuals, with implications for metapopulation dynamics.

**Keywords** Amphidromy · Dispersal · Habitat edges · Landscape ecology · Seascape ecology

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Communicated by Joel Trexler.

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**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s00442-019-04440-x>) contains supplementary material, which is available to authorized users.

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## Introduction

Dispersal can be risky, but for many species it is an important part of their life cycle. For aquatic organisms that live in streams and rivers (especially if these occur on isolated oceanic islands), a marine life-history stage can facilitate colonization and connectivity between distant sub-populations, and enable individuals to exploit particular conditions to maximize fitness across their life history (Gross 1987). Some well-known examples include anadromous salmon and catadromous freshwater eels that spend a portion of their adult stage at sea. Many amphidromous taxa have adults that reside primarily in freshwater and produce larvae and/or juveniles that migrate downstream to complete a period of development at sea (McDowall 2007; Augspurger et al. 2017). The fates and dispersal potentials of marine larvae are notoriously difficult to study with direct methods, and a long-standing assumption for many amphidromous species (particularly those with long larval durations) is that the majority of individuals disperse widely (McDowall 2010; Waters et al. 2001).

For many organisms, the dispersal potential is a function of edge permeability or the ease at which they can transition through habitat boundaries (Cadenasso et al. 2003). It is important to consider how life-history traits will respond to this variation in edge types. Certain habitat edges may facilitate or impede dispersal (Lidicker 1999; Cadenasso and Pickett 2008) which can be species and context dependent (Bowler and Benton 2005; Stevens et al. 2010). Our current understanding of the relationship between habitat edges and dispersal is largely based upon terrestrial studies (Murcia 1995; Woodroffe and Ginsberg 1998), although several studies have indirectly explored this topic in aquatic systems—particularly concerning Pacific salmon migrations (Groot and Margolis 1991). Terrestrial landscapes and associated habitat edges can profoundly affect ecological flow, access to resources, species interactions, and resource mapping (Ries et al. 2004). Habitat edges undoubtedly play a similarly important role in aquatic environments, though such effects have received little attention (Boström et al. 2011). Further consideration of such edge effects may improve our understanding of marine larval dispersal patterns and evolution of amphidromous life-history strategies (Gross 1987; McDowall 1997).

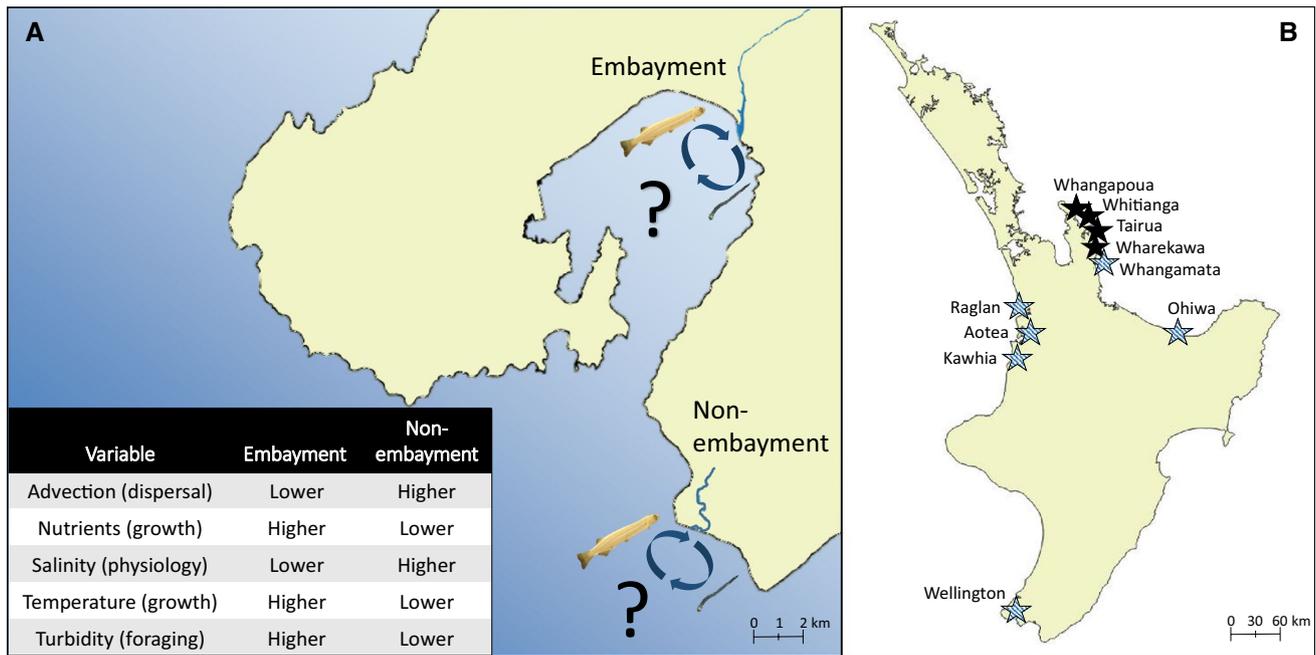
Amphidromous species often disperse through different edge types that connect freshwater and marine environments. For example, some rivers and streams terminate with an abrupt salinity transition to oceanic water, whereas others have a more gradual transition afforded by coastal embayments. Abrupt transitions (or ‘hard’ edges, sensu Duelli et al. 1990) represent steeper watersheds and coastal shelves, where coastal hydrodynamics and bathymetries facilitate rapid mixing and advection (Heath 1985; Hickey and Banas 2003). In contrast, gradual transitions (or ‘soft’ edges, sensu Duelli et al. 1990) are characterized by estuarine conditions, with a gradient in salinity, shallower water depths and reduced advection (Heath 1985; Hickey and Banas 2003). Effectively, these represent distinct edge types between discrete freshwater–marine habitats within a larger landscape context that could affect dispersal. Heterogeneity in freshwater–marine edges may contribute to concomitant variation: in (1) the ease of migration between these habitats (e.g., mediated by osmotic stress)—potentially affecting both the outbound and return journey; (2) larval retention near the natal river (attributable to different advective potentials); (3) traits of the fish that ultimately replenish these rivers (attributable to development in different environments and/or selection during inbound or outbound migration); and (4) landscape-scale patterns of connectivity and trait distributions (including phenotype–environment matches or mismatches). Thus, landscape heterogeneity in aquatic systems could have important consequences for population structure and metapopulation dynamics (Boström et al. 2011).

Here, we evaluate the effects of hard and soft boundaries traversed by amphidromous fish, *Galaxias maculatus*, upon their return to freshwater following a period of larval development at sea. We select two extreme freshwater–marine edge types (i.e., embayments versus non-embayments), that are well known to vary in their biophysical properties, to evaluate their potential influence on dispersal and population structure. We infer patterns and consequences of these landscape features on dispersal processes using otolith (‘ear stone’) microstructure, environmental signatures contained within the otoliths, and stable isotopes of muscle tissue of recruiting individuals. We hypothesize that rivers connected to embayments (with soft edges between habitats) will facilitate divergent developmental and foraging histories compared to nearby rivers connected to non-embayments (with hard edges between habitats). Previous studies have outlined strong associations between life-history traits and dispersal that is largely dependent on habitat type (Grantham et al. 2003; Slade et al. 2013). *Galaxias maculatus* produce much smaller eggs compared to other amphidromous fish species which consequently results in small and poor swimming larvae (Closs et al. 2013). Therefore, our prediction is that differences in advection potential, nutrients, temperature, and salinity (Heath 1985; Largier 1993; Hickey and Banas 2003) between edge types will lead to different dispersal trajectories and concomitant variation in size, age, growth rates, and feeding histories of juvenile recruits. We specifically predict that individuals recruiting to embayment rivers will have a higher likelihood of being retained (or entrained) in a warmer and nutrient-rich environment that will facilitate the development of larger juveniles (i.e., faster growth rates) to more quickly (i.e., younger recruits) return to freshwater (Fig. 1). Variation in dispersal and growth during the early life-history stages has important implications for recruitment (Fogarty 1993; Kaemingk et al. 2014). We consider our findings in the context of the broader metapopulation, where dispersal probabilities, traits of dispersers and asymmetrical patterns in connectivity among the distributions of soft and hard edges could lead to unique life-history strategies.

## Methods

### Study system

We studied the dispersing marine (i.e., larval and juvenile) stages of the amphidromous fish, *G. maculatus*. Adults inhabit lowland rivers and streams throughout New Zealand, and the species is widely distributed around temperate latitudes in the southern hemisphere, including southern Australia and Chile. This distributional pattern is indicative of significant dispersal potential as evidenced by genetic studies (Berra et al. 1996; Waters et al. 2001). Adults typically



**Fig. 1 a** An example of one of our sampled paired systems (Wellington) with a river emptying into a sheltered embayment (a ‘soft’ landscape boundary), and a nearby non-embayment (a ‘hard’ landscape boundary). These coastal geomorphologies are likely to affect dispersers due to differences in advective potential (i.e., exposure to long-shore and tidal currents) and environmental variables (e.g., nutrients, salinity, temperature, and turbidity gradients). This environmental variability at the interface between marine and freshwater

systems may affect hatchlings of amphidromous *Galaxias maculatus* on their outbound journey and/or larvae/juveniles upon their return. **b** Map indicating locations (denoted by hatched blue and solid black stars) of paired systems on New Zealand’s North Island (solid black stars depict systems that were additionally sampled for otolith microchemistry; Whitianga paired system was also sampled for stable isotopes). Additional details of site locations are given in Table S1 (color figure online)

spawn during spring tides, within clumps of riparian vegetation that become temporarily submerged at high tide (McDowall and Charteris 2006). Most spawning occurs at the ‘salt wedge’ interface between freshwater and seawater (i.e., near the mouth of a coastal-flowing river or stream; McDowall and Charteris 2006). Hatchlings from coastal-flowing rivers and streams enter the marine environment and develop as larvae (and then as pelagic juveniles) for up to 6 months (McDowall et al. 1994), before recruiting back to coastal rivers and streams as juveniles to complete their 1–2 year lifespan (Stevens et al. 2016). The returning juveniles form the basis of a culturally and economically important ‘whitebait’ fishery in New Zealand. Recruitment (and hence whitebait fishery yields) are highly variable (McDowall 1984; Jowett et al. 1998). The sources of this variation are poorly known, but recruitment variability in this system is almost certainly shaped by early life-history processes (e.g., larval growth, survival, retention or advection/dispersal).

We evaluate the role of hard and soft boundaries between marine and freshwater habitats on larval development and dispersal histories of *G. maculatus*. We sampled 648 juvenile fish upon their return to 20 rivers distributed around the North Island of New Zealand (Fig. 1; Table S1): 10 rivers had abrupt transitions to the sea (i.e., emptying to an open

coastline—subsequently referred to as a non-embayment edge type); these were paired with 10 nearby rivers (separated by < 30 km) that had gradual transitions to the sea (i.e., emptying into estuarine embayments—subsequently referred to as an embayment edge type). Each paired system was sampled within 24 h; all paired systems were sampled over a span of 10 days during peak *G. maculatus* migration (23 September–3 October 2014). *G. maculatus* recruits were collected using commercially available ‘whitebait nets’, modified fine-meshed fyke nets, or long-handled dip nets. All fishing was conducted over 4-h periods centered on high tides during daylight hours, and at sites located ≤ 3 km from river mouths. All collected fish were unpigmented (indicative of a recent migration from the sea; McDowall and Eldon 1980) and were immediately preserved in analytical-grade ethanol (99.9%) for subsequent laboratory processing and analysis.

**Size, age, and growth rates of dispersers**

We evaluated phenotypic traits of dispersers collected upon their return to rivers emptying to sheltered embayments (*n* = 10) and paired (i.e., nearby) non-embayments (*n* = 10; Fig. 1). We measured the total length (TL) of all

sampled *G. maculatus* ( $n = 648$ ), and estimated age and growth rates of a randomly selected subsample ( $n = 500$  fish in total) using otolith microstructure. Sagittal otoliths were cleaned (using methods of Shima and Swearer 2009a, b), embedded in cyanoacrylate, and polished to expose a complete record of daily growth increments along the sagittal plane, using diamond lapping films (3–9  $\mu\text{m}$ ) affixed to a lapping wheel (Model 920; South Bay Technology, San Clemente, CA, USA). Prepared otoliths were photographed at  $400\times$  magnification and the Caliper Tool package of ImagePro Plus v7.0 (MediaCybernetics, Bethesda, MA, USA) was used to count and measure increments along the postrostral axis.

We identified a conspicuous ‘hatch check’ as an abrupt change in increment widths near the otolith core and used this to estimate size-at-hatch as the distance from the otolith core to the hatch check (measured along the postrostral axis). We estimated pelagic larval duration (PLD) as the number of daily growth increments from hatch check to otolith edge. We estimated growth rates as the mean width of daily growth increments across the PLD. We used paired  $t$  tests to evaluate variation in size, age, and growth rates as a function of habitat-edge type (i.e., differences between traits of fish recruiting to rivers connected to embayments and nearby non-embayments).

### Reconstructing dispersal histories

We used otolith microchemistry to reconstruct dispersal histories of fish entering both embayment and non-embayment edge types. We subsampled 99 fish captured from 8 of the 20 rivers (i.e., 4 paired systems; Fig. 1). We quantified concentrations of 12 minor and trace elements ( $^7\text{Li}$ ,  $^{11}\text{B}$ ,  $^{24}\text{Mg}$ ,  $^{31}\text{P}$ ,  $^{34}\text{S}$ ,  $^{39}\text{K}$ ,  $^{55}\text{Mn}$ ,  $^{63}\text{Cu}$ ,  $^{66}\text{Zn}$ ,  $^{88}\text{Sr}$ ,  $^{138}\text{Ba}$ ,  $^{208}\text{Pb}$ ; all standardized to  $^{48}\text{Ca}$ ) using a Varian 7700  $\times$  Inductively Coupled Plasma Mass Spectrometer (ICP-MS) fitted with a RESolution (Resonetics, Nashua, NH, USA) laser ablation (LA) system constructed around a Compex 110 (Lambda Physik) excimer laser operating at 193 nm. Elemental ratios (hereafter elements) were selected based on their putative utility to explain dispersal patterns (Shima and Swearer 2009a; Shima and Swearer 2016). We analyzed elemental concentrations along the transverse axis (from core to edge), and used daily increments to bin successive LA-ICP-MS scans by day of development (following methods of Shima and Swearer 2009a). Samples were run in blocks of 9, bracketed by analyses of NIST 610 and 612 calibration standards and MACS3 consistency standard, and randomly assigned to a block. Internal and external precision estimates for all trace elements were below 10%.

### Identifying a subset of trace elements that discriminate geographic locations

Elements may be incorporated into otoliths via a variety of pathways, and in some cases, with significant time lags (Campana and Thorrold 2001). We reasoned that a subset of the 12 measured elements might provide a useful geographic signature for our particular application (e.g., Shima and Swearer 2016). Consequently, we conducted a preliminary MANOVA to identify trace elements at the otolith edge that differed between (1) paired systems and (2) edge types (embayment versus non-embayment) nested within paired systems. We sampled the final three growth increments at the otolith edge, where we had reason to believe that fish had been in different geographic locations given their recent return to freshwater following an obligate larval development period at sea (Hickford and Schiel 2016). We considered edge type to be nested within paired systems because they represent two different spatial scales. Paired system and edge type were treated as fixed effects in the model considering the number of sampled paired systems and their location compared to the number of possible sites containing populations of *G. maculatus* (Quinn and Keough 2002). All elements were  $\ln(x + 1)$  transformed prior to analysis to meet statistical assumptions. This analysis suggested a subset of seven elements ( $^7\text{Li}$ ,  $^{24}\text{Mg}$ ,  $^{31}\text{P}$ ,  $^{55}\text{Mn}$ ,  $^{63}\text{Cu}$ ,  $^{66}\text{Zn}$ , and  $^{208}\text{Pb}$ ) could be used to discriminate fish between edge types (Table S2).

### Evaluating evidence for different developmental histories

We used this subset of seven elements to evaluate a set of hypotheses that fish recruiting to rivers with/without embayments have distinct developmental histories. As above, we used log-transformed data in a MANOVA that included the effects of (1) paired systems and (2) edge types (embayment versus non-embayment) nested within paired systems. We evaluated average trace element concentrations from three different time spans in the developmental history of dispersers: (1) for the final  $\sim 10$  days of dispersers’ development prior to recruitment to rivers; (2) for the initial  $\sim 10$  days of larval development (i.e., just after hatching); and (3) for the dispersers’ complete developmental duration. We also performed canonical correlation analysis for each time span and report the respective element loadings (Table S3). To facilitate visualization of trace element profiles for fish with a range of PLDs, we standardized elemental time series to a common length scale (i.e., set by youngest fish in the sample) and plotted mean  $\pm 95\%$  confidence interval (CI) of elemental concentration; our formal MANOVA analyses were based on pre-determined spans of time series (in units of days) for replicate fish that varied in PLD.

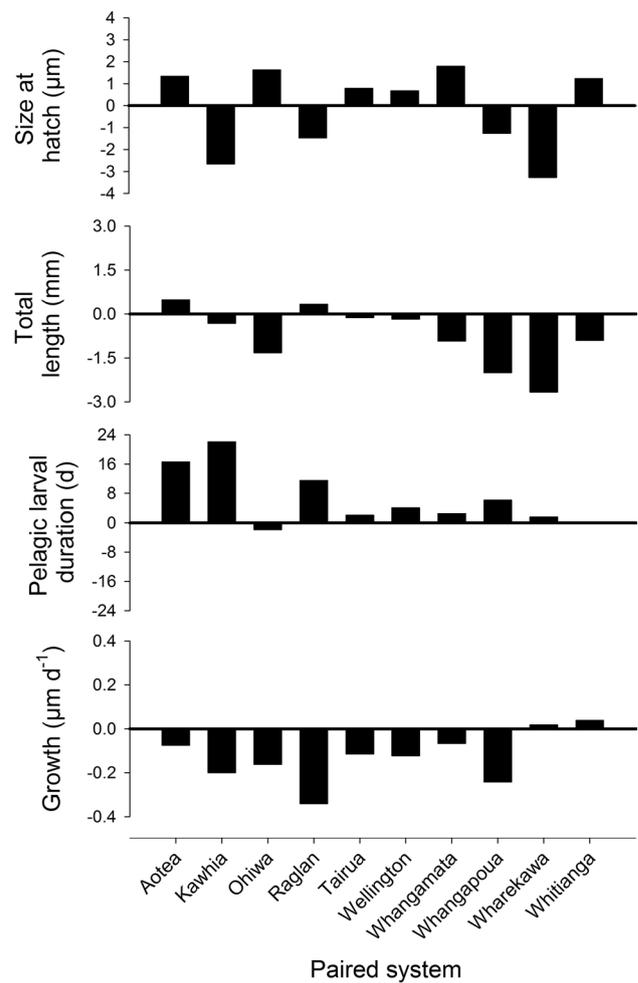
### Reconstructing feeding histories

We used stable isotopes ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) to reconstruct recent feeding histories of a random subsample of 20 fish that recruited to a paired system ( $n = 10$  fish per river; from the Whitianga paired system, Fig. 1). Fish were stored on ice immediately following capture, and were subsequently processed. Body tissue (excluding the head and gut) was dissected, freeze-dried, ground to a fine powder with a mortar and pestle, and weighed to the nearest 0.001 mg. We quantified carbon and nitrogen isotopes of each fish using a DELTA<sup>Plus</sup> (Thermo-Fisher Scientific, Bremen, Germany) continuous flow, isotope ratio mass spectrometer linked to an NA 1500 elemental analyser with an AS200-LS autosampler (Fisons Instruments, Rodano, Italy), located at the National Institute of Water and Atmospheric Research Environmental and Ecological Stable Isotope Facility in Wellington, New Zealand. Each sample was preceded by internal  $\text{CO}_2$  and  $\text{N}_2$  reference gas standards and calibrated against National Institute of Standards and Technology standards, providing  $\delta$  values accurate to within  $\pm 0.20\text{‰}$  (1 SD) and with a precision better than  $\pm 0.14\text{‰}$  (1 SD) for both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ . We used ANCOVA to evaluate variation in  $\delta^{15}\text{N}$  or  $\delta^{13}\text{C}$  values between embayment and non-embayment edge types (fixed effect) and as a function of fish total length (TL; the covariate). We evaluated a full model that included an interaction between fish size and edge type, and where this interaction was not significant, we removed it and interpreted a reduced model.

### Results

#### Variation in size, age, and growth rates of dispersers

*Galaxias maculatus* entering rivers connected to embayments and non-embayments varied in size, age, and growth rates. Size-at-hatch did not vary among fish that recruited to embayment rivers (mean across embayment sites: 22.6  $\mu\text{m}$ ; range 18.4–25.4  $\mu\text{m}$ ) and non-embayment rivers (mean across non-embayment sites: 22.7  $\mu\text{m}$ ; range 20.0–25.4  $\mu\text{m}$ ;  $t = -0.20$ ,  $p = 0.85$ ). However, fish that recruited to rivers connected to embayments tended to be smaller (mean across embayment sites: 44.8 mm; range 39.3–50.9 mm) compared to fish that recruited to rivers without embayments (mean across non-embayment sites: 45.6 mm; range 39.9–51.0 mm;  $t = -2.38$ ,  $p = 0.04$ ; Fig. 2). Fish entering embayment rivers were also older (mean across embayment sites: 98.1 days; range: 73.8–132.9 days) in contrast to fish that entered rivers without embayments (mean across non-embayment sites: 91.6 days; range 70.6–126.1 days;  $t = -4.21$ ,  $p < 0.01$ ;

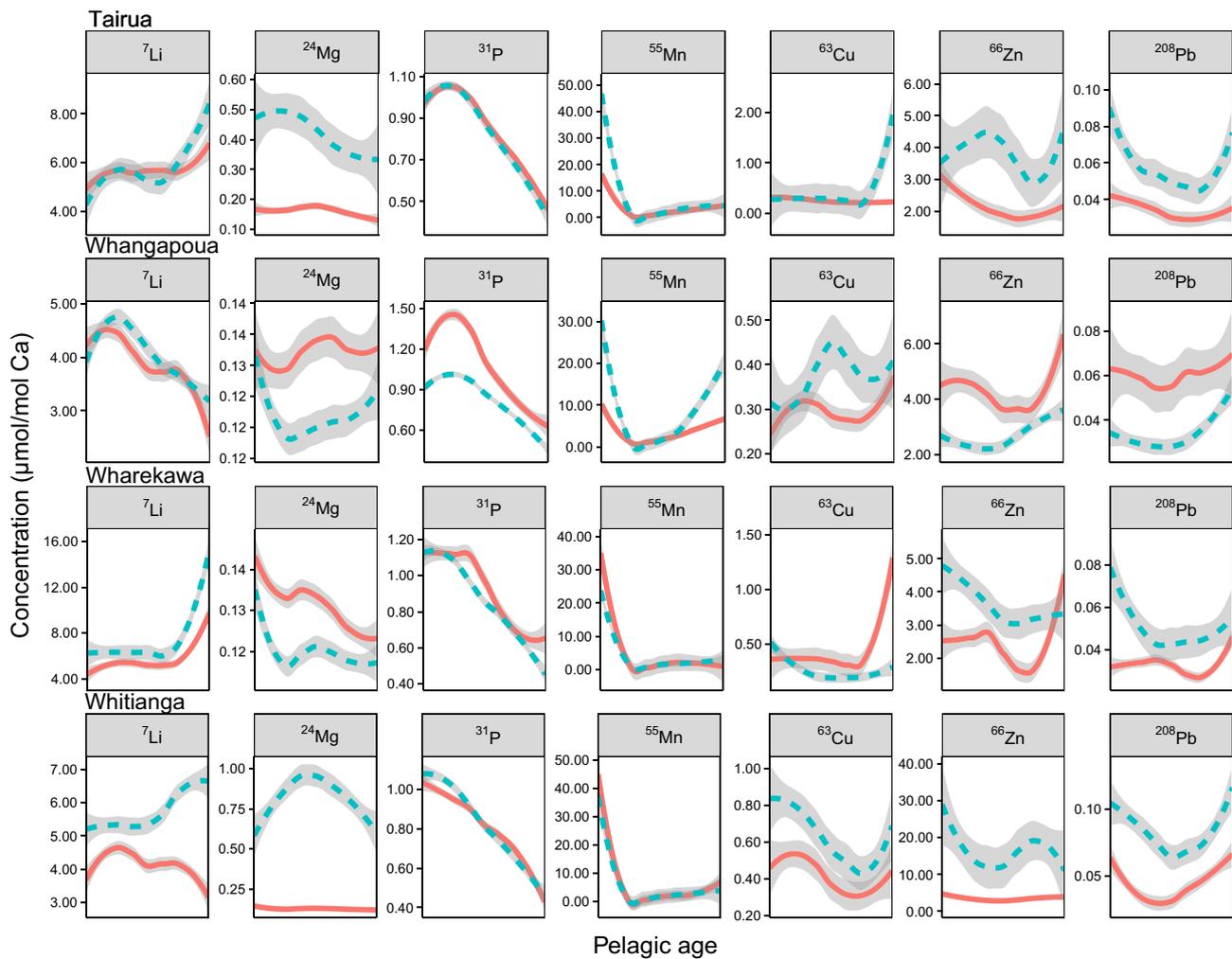


**Fig. 2** Disparity in size, age, and growth of *G. maculatus* recruiting to rivers with embayments versus nearby (paired) rivers without embayments. The mean differences in traits (positive values indicate larger trait values associated with embayments) are given for ten paired systems. Total length, pelagic larval duration, and growth rates exhibit significant differences with respect to the presence/absence of embayments, based on paired  $t$  tests (see text for statistical reporting)

Fig. 2). In addition, fish that recruited to rivers connected to embayments grew more slowly (mean across embayment sites: 2.3  $\mu\text{m/day}$ ; range: 1.9–2.6  $\mu\text{m/day}$ ) in relation to fish recruiting to nearby rivers without embayments (mean across non-embayment sites: 2.4  $\mu\text{m/day}$ ; range 2.0–2.7  $\mu\text{m/day}$ ;  $t = -3.47$ ,  $p < 0.01$ ; Fig. 2).

#### Variation in dispersal histories

Trace element profiles differed markedly between fish recruiting to rivers with an embayment (solid red lines, Fig. 3) versus fish that recruited to rivers without embayments (dotted blue lines, Fig. 3).



**Fig. 3** Age-related variation in trace element concentrations within otoliths of *G. maculatus* collected from Tairua, Whangapoua, Wharekawa, and Whitianga paired systems. Profiles for seven trace elements (mean  $\pm$  95% CI) are depicted from hatch to freshwater recruitment (left to right on x-axis; note fish of variable ages were standardized to a common temporal scale [a percentile of developmental duration], so units of x-axis are arbitrary). Graphs depict

changes ( $\pm$  95% CI) in seven trace element concentrations ( $^7\text{Li}$ ,  $^{24}\text{Mg}$ ,  $^{31}\text{P}$ ,  $^{55}\text{Mn}$ ,  $^{63}\text{Cu}$ ,  $^{66}\text{Zn}$ ,  $^{208}\text{Pb}$ ), presented relative to Ca concentrations) between embayment and non-embayment edge types (embayment = solid red line; non-embayment = dotted blue line). Plots were generated using ggplot2 and the geom\_smooth option using the loess function in R (color figure online)

#### For the final 10 days of pelagic development

MANOVA analyses indicate that the chemical profiles of fish in their 10-day lead-up to recruitment differed among paired systems (Wilk's Lambda = 0.19,  $F_{3,91} = 9.01$ ,  $p < 0.0001$ ) and between edge types (Wilk's Lambda = 0.24,  $F_{4,91} = 5.31$ ,  $p < 0.0001$ ). Associated univariate analyses suggest that these overall patterns may be largely attributable to three of the seven elements ( $^7\text{Li}$ ,  $^{24}\text{Mg}$ , and  $^{55}\text{Mn}$ ) that differed among the paired systems, and five elements ( $^7\text{Li}$ ,  $^{24}\text{Mg}$ ,  $^{31}\text{P}$ ,  $^{55}\text{Mn}$ , and  $^{63}\text{Cu}$ ) that differed between edge types (Fig. 3; Table S4).

#### For the first 10 days of pelagic development

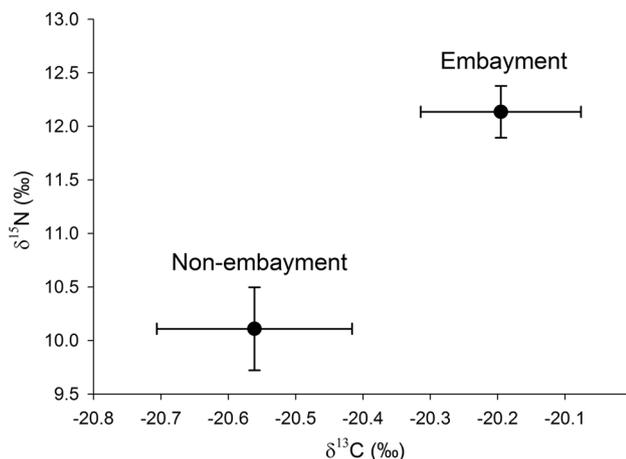
MANOVA analyses indicate that the chemical profiles of fish in their first 10 days of pelagic development (i.e., as hatchlings) differed among paired systems (Wilk's Lambda = 0.37,  $F_{3,91} = 4.81$ ,  $P < 0.0001$ ) and between edge types (Wilk's Lambda = 0.30,  $F_{4,91} = 4.36$ ,  $P < 0.0001$ ). Associated univariate analyses suggest that these overall patterns may be largely attributable to three of the seven elements ( $^7\text{Li}$ ,  $^{24}\text{Mg}$ , and  $^{55}\text{Mn}$ ) that differed among the paired systems and four elements ( $^7\text{Li}$ ,  $^{24}\text{Mg}$ ,  $^{31}\text{P}$ , and  $^{55}\text{Mn}$ ) that differed between edge types (Fig. 3; Table S4).

## For the entirety of pelagic development

MANOVA analyses indicate that the chemical profiles of fish across their full pelagic developmental duration differed among paired systems (Wilk's Lambda = 0.28,  $F_{3,91} = 6.57$ ,  $P < 0.0001$ ) and between edge types (Wilk's Lambda = 0.26,  $F_{4,91} = 5.03$ ,  $P < 0.0001$ ). Associated univariate analyses suggest that these overall patterns may be largely attributable to four of the seven elements ( $^7\text{Li}$ ,  $^{24}\text{Mg}$ ,  $^{31}\text{P}$ , and  $^{55}\text{Mn}$ ), that varied both among the paired systems and between edge types (Fig. 3; Table S4).

## Variation in feeding histories

Dietary characteristics of *G. maculatus* differed between the two edge types. An interaction between edge type and fish size was not significant for either  $\delta^{15}\text{N}$  ( $F_{1,16} = 0.36$ ,  $p = 0.56$ ) or  $\delta^{13}\text{C}$  ( $F_{1,16} = 0.58$ ,  $p = 0.46$ ) values, indicating consistent stable isotope trends between edge types for the Whitianga paired system (Fig. 4). Fish recruiting to rivers through an associated embayment had higher  $\delta^{15}\text{N}$  values than fish recruiting to rivers without an embayment ( $F_{1,17} = 34.87$ ,  $p < 0.001$ ), and  $\delta^{15}\text{N}$  values decreased with increasing fish size for both embayment and non-embayment fish ( $F_{1,17} = 14.86$ ,  $p < 0.01$ ). Similarly, fish recruiting to rivers through an associated embayment had elevated  $\delta^{13}\text{C}$  values ( $F_{1,17} = 5.08$ ,  $p = 0.04$ ), and  $\delta^{13}\text{C}$  values decreased with increasing fish size for both embayment and non-embayment fish ( $F_{1,17} = 7.20$ ,  $p = 0.02$ ).



**Fig. 4** Stable isotope values ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ;  $\pm$  SE) for *G. maculatus* collected at an embayment and non-embayment edge type from our Whitianga paired system

## Discussion

Extensive dispersal is considered a primary advantage of adopting the amphidromous life-history strategy, which is predicted to facilitate colonization and connectivity among distant island populations (McDowall 2007, 2010). Genetic and microchemistry studies have supported this notion (Waters et al. 2001; Hickford and Schiel 2016). However, more recently, several studies have challenged this paradigm to suggest that many amphidromous species have limited-dispersal and do not leave their natal site (Hogan et al. 2014; Hicks et al. 2017). Landscape edges or features offer an explanation for this apparent discrepancy among studies and further advances our understanding of the amphidromous life-history strategy. We posit that landscape features in aquatic systems could facilitate or impede dispersal (Huey et al. 2014), similar to findings in terrestrial systems (Ries et al. 2004). In our study, rivers connected to embayments may retain more individuals compared to rivers connected to open coastlines. Therefore, we may expect to see evidence for wide- and limited-dispersal strategies, depending on the landscape context.

Variation in dispersal histories, feeding histories, and phenotypes were strongly associated with the presence or absence of an embayment connecting rivers to the sea. This suggests that landscape features, and in particular the characteristics of the boundary conditions between fresh water and the marine environment, shape demographic heterogeneity among sub-populations. Rivers without embayments may have sharper environmental discontinuities, and hydrodynamic conditions at the river mouth may be more advective. In contrast, embayments may soften the boundary between river and sea, facilitating a gradient in environmental (e.g., salinity, temperature, turbidity, productivity) and hydrodynamic conditions (Heath 1985; Largier 1993; Hickey and Banas 2003) that may more readily retain or entrain dispersers for extended periods (Shima and Swearer 2009a; Huey et al. 2014). Given the biophysical conditions of a softer boundary (e.g., lower advection, more nutrients, higher temperature, lower salinities), we expected divergent dispersal histories, but did not expect recruits to be smaller (with slower growth rates) and to return later (i.e., be older) than fish returning to rivers lacking embayments.

Several non-mutually exclusive hypotheses may account for variation in disperser traits associated with the presence/absence of embayments. Dispersal may be limited in one or both edge types. Larvae may take advantage of local hydrodynamic conditions [e.g., stratified flows, eddies (Cowen et al. 2000)] to remain near river mouths (Closs et al. 2013). This could facilitate retention near the natal river, and self-recruitment (sensu Hicks et al. 2017;

Hogan et al. 2014; Swearer et al. 2002). We suspect that embayments may promote natal retention or larval entrainment after an initial period of dispersal. Rivers associated with embayments may be replenished by a higher proportion of retained (or entrained) larvae, whereas rivers without an embayment may be replenished by larvae that dispersed over greater distances and/or had more heterogeneous developmental histories.

Selection processes may also drive spatial variation in disperser histories and traits. For example, Pacific salmon are predicted to experience strong selective forces caused by climatic changes to their physical environment (Crozier et al. 2008). Species with complex life histories could especially be vulnerable to selection pressures as they must disperse through multiple environments to complete their life cycle (Robinson et al. 2009; Hegg et al. 2013). In our example, embayments may moderate selection on dispersers, because environmental gradients may ease the physiological transition between seawater and fresh water. In addition, retentive hydrodynamic conditions due to a more sheltered environment, may reduce energetic requirements for an upstream migration, and/or enable fish to remain in a desirable location (e.g., fish recruiting through embayments are older). Rivers without embayments may provide a greater challenge to recruiting fish, and recruitment may only be possible for a subset of dispersers (e.g., fish recruiting to rivers without embayments are larger and faster growing).

Aquatic landscape features appear to drive heterogeneity in dispersal probabilities and phenotypic traits of fish that replenish sub-populations. Variable developmental histories and resulting phenotypic mixtures of recruits (e.g., Shima and Swearer 2009a, b) can have important consequences for performance in later stages (Shima and Swearer 2010; Shima et al. 2015). Phenotypic mixtures can also affect sub-population stability (Noonburg et al. 2015) and metapopulation dynamics (Shima et al. 2015). For *G. maculatus* in particular, phenotypic traits of marine recruits may affect the probability of survival to reproductive age in the freshwater environment (Neilson 2016). *G. maculatus* recruiting to a river with an embayment were more phenotypically diverse compared to those recruiting to a river without an embayment. Variation in size, age, and growth rates between these two nearby rivers corresponded to different adult survivorship patterns with low survival of early hatched fish in the river with an embayment (Neilson 2016). We presume that the consequences of trait variation are context dependent. If river systems with embayments differ markedly in attributes of upstream freshwater adult habitats (e.g., typically these will be larger watersheds with shallower elevation gradients) and the traits of recruiting fish vary with respect to the presence/absence of embayments (e.g., due to asymmetrical patterns in connectivity and/or selection), this creates opportunities for phenotypic-environment matches/mismatches

(sensu Edelaar et al. 2017). In addition, phenotypically diverse recruits may vary in their response to freshwater predator avoidance and survival (Moody et al. 2014).

Rivers in close proximity to each other are replenished by amphidromous fish with different developmental histories, different feeding histories, and different phenotypes. Collectively, our data strongly suggest population structure at the scale of individual watersheds for *G. maculatus*—at least for fish recruiting to embayment rivers. Fish recruiting to four pairs of nearby rivers (i.e., separated by < 30 km) on the North Island of New Zealand acquire distinct trace element signatures in otoliths in the 10-day preceding settlement, suggesting that dispersers may aggregate in distinct locations (and possibly near river mouths) before undergoing an upstream migration. Carbon and nitrogen stable isotope data reinforce this inference: fish sampled from two nearby rivers differed markedly in their isotopic values, indicating distinct feeding histories and/or variation in their environment (Post 2002). Fish collected from the embayment river had enriched  $\delta^{15}\text{N}$  values, which is characteristic of estuaries that experience high nutrient loading from adjacent urbanized areas (McClelland et al. 2003). Similar aggregations are common for anadromous species including salmon (Keefer et al. 2008) and this behavior pattern likely enables individuals to adjust their physiology to a lower salinity environment (Bystriansky and Schulte 2011). As alluded to above, our data also suggest that variation in dispersal history is manifested as early as the first 10 days after hatching (i.e., immediately upon entry into the marine environment). This indicates that dispersers recruiting at the same time, but to different (nearby) rivers, have distinct dispersal trajectories very early in their development. For cohorts recruiting to a given river, these results could reflect a shared dispersal history (e.g., Shima and Swearer 2016), and/or retention near the natal environment (Hicks et al. 2017), or early entrainment in chemically distinct environments (Huey et al. 2014). Perhaps due to their extended separation, fish recruiting to nearby rivers varied significantly in age, size, and growth rates. Collectively, these results support significant spatial structure in the demographic properties of nearby sub-populations.

Lastly, we note that our findings demonstrate population structuring at the watershed scale for this migratory species. If many river systems are self-recruiting, then perhaps we should revisit current management strategies for the imperiled New Zealand whitebait fishery (which targets recruiting *G. maculatus*). Uniform management and conservation strategies are applied irrespective of habitat type and landscape–seascape transition zones. We demonstrate a strong link between habitat heterogeneity or edge types, dispersal, and phenotypes for this migratory species that has conservation implications. For example, if larvae of *G. maculatus* (and potentially, those of many other amphidromous species)

are entrained near river mouths, it may be necessary to manage watersheds for water quality that influences the development and fitness of the early life stages of amphidromous species.

**Acknowledgements** We acknowledge funding from the National Science Foundation (DBI 1306226) and Victoria University of Wellington; logistic support from Victoria University Coastal Ecology Laboratory; and research assistance from J. Bottcher, C. McDowall, C. Neilson, V. Wood, T. Bates, B. Focht, D. McNaughton, B. Moginie, D. Crossett, B. Focht, A. Kaemingk, A. Kilimnik and J. Brown. We thank C. Chizinski for statistical advice and three anonymous reviewers for improving this manuscript.

**Author contribution statement** MK and JS jointly obtained funding, designed the study, supervised technicians, and drafted the paper with input from the other coauthors. MK analyzed the data. SS conducted LA-ICP-MS analysis. MK and SB conducted stable isotope analysis.

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