



# Connectivity of fish communities in a tropical floodplain river system and predicted impacts of potential new dams

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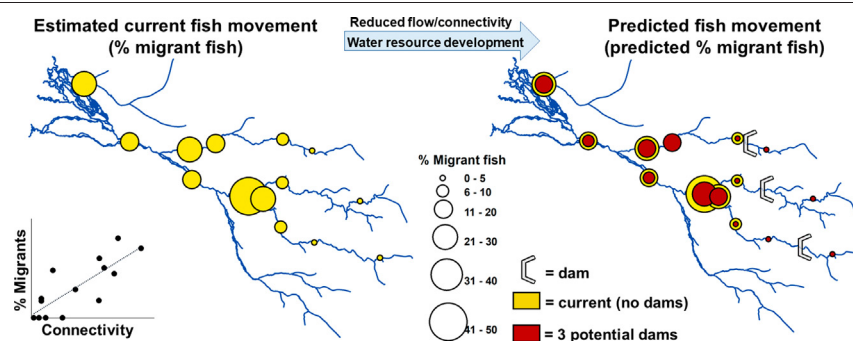
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## HIGHLIGHTS

- We used sulfur stable isotopes to study fish movement in a tropical river system.
- Fish movement varied spatially across the river system with changes in connectivity.
- We developed a method for predicting impacts of potential dams on fish movement.
- The location of the dam influenced the severity of the impact on fish movement.
- This quantitative method is a tool that can be used to guide sustainable development.

## GRAPHICAL ABSTRACT



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## ABSTRACT

Longitudinal and lateral connectivity is important for mobile aquatic species in rivers for reproductive migrations, recruitment, gene flow and access to food resources across habitat types. Water resource developments such as dams and levees may disrupt these connections, causing river fragmentation and loss of access to highly productive habitats such as floodplain wetlands. We used sulfur stable isotopes as a tracer to estimate patterns of fish movement in an unregulated river in tropical northern Australia, taking advantage of observed spatial variation in sulfur isotope values of their food resources across the catchment. We also modelled the flow and barrier related impacts of potential dam development scenarios on fish movement. Fish with isotope values significantly different from local prey values were determined to be migrants. In the 'no dams' scenario, movement varied among fish species (0–44% migrant fish within species where  $n > 5$ ) and sites (0–40% migrant fish within sites where  $n > 5$ ), and immigration was higher in more connected sites. Impacts of water resource development on fish movement varied between dam scenarios, with predictions that a dam on the main channel of the Mitchell River would have the highest impact of the three individual dam scenarios. This study provides critical information on how flow-mediated connectivity supports patterns of fish community movement in an unregulated river system. The generic quantitative approach of combining tracers of fish movement with connectivity modelling provides a powerful predictive tool. While we used sulfur stable isotopes to estimate fish movement, our approach can be used with other tracers of movement such as otoliths and acoustic telemetry, making it widely applicable to guide sustainable development in other river systems.

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## 1. Introduction

Lateral and longitudinal connectivity of habitats in a river network facilitates the movement of organisms, transfer of nutrients, and flow of energy across the landscape (Opperman et al., 2010). Fish use connectivity for reproductive migrations, recruitment and recolonization, and access to subsidies from the floodplain and the ocean (Pettit et al., 2017). Connectivity is mediated by river flow, which varies naturally between seasons and years (Warfe et al., 2011). Water resource developments are a global threat to river connectivity, with less than half of the world's large river systems remaining free flowing (Grill et al., 2019). Biodiversity loss increases when multiple barriers to flow (such as dams) are present along a river due to loss of access to habitats used for spawning, foraging and refuge (Liermann et al., 2012). River fragmentation consequences extend beyond environmental impacts, since free-flowing rivers also provide important economic and societal ecosystem services, including productive fisheries (Grill et al., 2019; Vörösmarty et al., 2010).

Highly seasonal precipitation in the wet-dry tropics of Australia causes high river flow in summer that progressively recedes throughout the winter, and in some rivers, flow ceases prior to the next wet season (McJannet et al., 2014). In free-flowing rivers, the flow regime provides lateral connectivity to seasonally inundated habitats, including creeks and floodplain wetlands, and longitudinal connectivity of in-channel habitats and the ocean (Pettit et al., 2017; Stoffels et al., 2014). Tropical floodplain wetlands can be highly productive habitats and may serve as aquatic refugia for organisms during the dry season and drought (Pettit et al., 2011; Waltham et al., 2014). The reconnection of in-channel habitats following seasonal river flows provides opportunities for local and large-scale movements by fish for different aspects of their life history, such as refuge migrations to areas with permanent water and catadromous movements to the sea for spawning (Benitez et al., 2018; Bond et al., 2015).

Climate change is likely to disrupt the natural flow regime through changes to the frequency and timing of floods and droughts, as well as long-term temperature, precipitation and vegetation cover changes (Jaeger et al., 2014; Olmstead, 2014). Increased demand for dams and other water resource developments as a result of climate change can also severely disrupt the natural flow regime (Bunn and Arthington, 2002; Cramer et al., 2018). Not only can changes affect the timing and magnitude of seasonal flow pulses, they may also alter the connectivity of river networks which causes river fragmentation (Ward and Stanford, 1995). River fragmentation may result in loss of genetic structuring and isolation from productive habitats and aquatic refugia, and may limit migrations essential to fulfil important life stages (Gido et al., 2016). Food web structure and function may also change with reduced connectivity, through changes in primary production and invertebrate community composition (Leigh and Sheldon, 2009). Preserving and, where needed, restoring connectivity in freshwater ecosystems is identified as one of the critical actions to slowing the alarming rate of freshwater habitat and biodiversity loss (Tickner et al., 2020). Understanding how aquatic species use the variability in flow and connectivity to move and feed throughout a river system is important for informing sustainable water resource management.

Fish movement through river systems is often studied by capture and release of tagged individuals (Lucas and Baras, 2000). However, it is also possible to use natural chemical (e.g. strontium isotopes in fish otoliths) or biochemical signatures to distinguish between resident fish and fish that have migrated to their capture location from elsewhere. Stable isotopes are biochemical markers that fish integrate from their environment (mostly through diet), and spatial variation in background values caused by variations in chemical, hydrological and geological conditions can be used to infer movement or geographical origins (Rasmussen et al., 2009; Rubenstein and Hobson, 2004). Sulfur stable isotopes of freshwater vary spatially with changes in underlying geology (Burke et al., 2018) and show little fractionation between

food sources and consumers (MacAvoy et al., 2000), meaning a fish's muscle tissue will reflect the location where feeding took place. Sulfur stable isotopes can therefore be used to determine fish residency in catchments with spatial variation in sulfur isotopes by assessing whether the sulfur isotope values of fish match the local prey sulfur isotope signal (Fry and Chumchal, 2011).

In this study, we used sulfur stable isotopes to explore movement and residency among fish populations across the Mitchell River catchment, a largely free-flowing river in the wet-dry tropics of northern Australia. We also developed an index of connectivity using stream gauge data for river channel sites throughout the catchment with the aim of assessing the importance of flow-mediated connectivity for fish movement. We then used this information to predict how the construction of dams for water resource development may affect fish movement potential via the evaluation of several modelled scenarios. We hypothesized that fish known to move to reproduce would show evidence of movement at most sites, and non-migratory reproducers would show little evidence of movement. We further hypothesized that reductions in connectivity due to the potential construction of dams would reduce the extent of movement evident at sampling sites.

## 2. Materials and methods

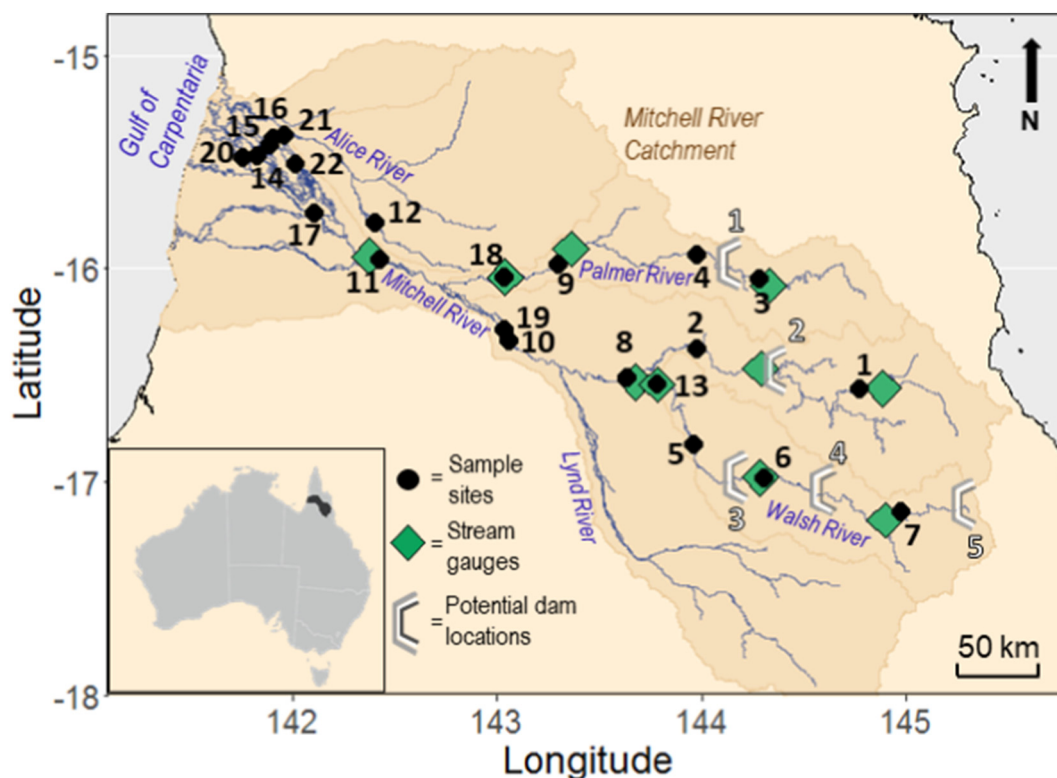
### 2.1. Study location

The Mitchell River catchment is situated in the wet-dry tropics of northern Queensland, Australia, and covers an area of approximately 72,000 km<sup>2</sup> (Petheram et al., 2018). The westward flowing main channel of the Mitchell River stretches from the headwaters in the Daintree rainforest in the east to the river mouth in the Gulf of Carpentaria in the west. Major tributaries that flow into the Mitchell River include the Walsh, Lynd, Alice and Palmer rivers (Fig. 1). Geology and river form vary throughout the catchment, with the eastern third comprised of bedrock varying between sedimentary, granitic and volcanic lithology (Batlle-Aguilar et al., 2014). An alluvial delta megafan at lower elevation spreads west from the confluence of the Mitchell and Palmer Rivers, producing a network of braided channels and creeks on the floodplain (Rustomji et al., 2010).

Rainfall in the Mitchell catchment is highly seasonal, with only 4% of annual rainfall (on average) falling across the catchment during the dry season, from May to October (Petheram et al., 2018). Historical flow data shows that the main channel of the Mitchell River experiences perennial flow most years, while the Palmer and Walsh rivers experience cease to flow conditions in most years (an average of 45 and 33 zero flow days per year, respectively). With mostly unmodified flow, the Mitchell River catchment has a high diversity of fish, with 46 species recorded (including two exotic species of tilapia), many of which move between habitats in the catchment (Jardine et al., 2017; Pusey et al., 2004). Few barriers to fish movement currently exist within the catchment, including a natural rock cascade downstream of Site 2, and one dam in the headwaters which is considered to have a hydrological impact (Southedge Dam at Lake Mitchell; Marshall, 2016). However, the Mitchell River catchment has received considerable attention for expansion of irrigated agriculture that would require new water infrastructure development (Commonwealth of Australia, 2015).

### 2.2. Sample collection

To explore movement of fish communities over a large scale (throughout most of the Mitchell River catchment), collection sites were spread across geological regions and varied in hydrological characteristics to include river channel, floodplain creek, and wetland sites. Most of the wetlands were permanent waterbodies that become periodically connected to other parts of the river network during large wet season floods. Sites throughout the catchment are hydrologically connected during the wet seasons and, given the lack of instream



**Fig. 1.** Mitchell River catchment and river network. Symbols represent fish and invertebrate collection site locations (black points), stream flow gauge locations (green diamonds) and potential dam locations (grey and white dam symbols) identified in the CSIRO Northern Australia Water Resource Assessment (Petheram et al., 2018). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

barriers (natural or artificial) and floodplain development, we assumed mobile fish are able to move freely throughout the system. Sampling was limited to the late wet/early dry season (May to July) and because of large distances between sites and difficulty in accessing remote areas, was conducted over three consecutive years. Most sites were sampled on only one occasion, with the exception of Sandy Creek and Yelko Waterhole, which were sampled in two consecutive years (2018 and 2019; Table S1).

Fish and invertebrates were collected from 22 sites within the Mitchell catchment (Fig. 1, Table S1). Invertebrates were collected with dip nets to provide isotope values of the local prey items for fish, since invertebrates and small fish are the primary prey of these fish species (unpublished data). Invertebrate taxa varied based on what was present at each site at the time of sampling. These included aquatic insects, mussels, shrimp and terrestrial insects (grasshoppers). While a variety of invertebrate taxa were collected at each site during the 2017 and 2018 trips, only bivalves were collected from some sites in 2019. Invertebrates were chosen to represent the local sulfur isotope signal because they integrate isotopes from their food over time and therefore show less temporal and spatial variation than short-lived phytoplankton and periphyton (Hecky and Hesslein, 1995).

Fish were collected by boat or backpack electrofishing during the 2017 and 2018 trips. Cast nets were used to collect fish in 2019. Because we studied whole fish communities, sampling targeted all habitat types present and effort was allocated to each habitat based on its relative area within the site ( $n = 10$  to 48 fish per site). Fish were euthanized, measured and muscle tissue was extracted in the field. All specimens were immediately placed in vials in liquid nitrogen containers for transport to Griffith University where they were stored in a  $-20^{\circ}\text{C}$  freezer.

### 2.3. Sample preparation and analysis

Fish and invertebrate samples were freeze dried for 48 h and ground into a fine powder using a stainless-steel ball mill grinder. Ground and

dried tissue was weighed (9–10 mg) into tin capsules and an oxidizing agent (vanadium pentoxide) was added to aid combustion of S for  $\delta^{34}\text{S}$  analysis. A total of 246 invertebrates and 571 fish samples were analysed using a Sercon Europa EA-GSL elemental analyzer and a Hydra-20-20 continuous flow isotope ratio mass spectrometer. Stable isotope ratios were expressed in  $\delta$  notation as deviations from standards in per mil (‰):  $\delta X = [(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 1000$ , where X is  $^{34}\text{S}$ ,  $R_{\text{sample}}$  is the ratio ( $^{34}\text{S}/^{32}\text{S}$ ) in the sample, and  $R_{\text{standard}}$  is the ratio in the standard. Although carbon isotopes were also measured in these analyses, we chose to use only a single tracer ( $\delta^{34}\text{S}$ ) because of large variation among sites in local invertebrate  $\delta^{34}\text{S}$  compared with  $\delta^{13}\text{C}$  (Fig. S1). Laboratory and National Institute of Standards and Technology (NIST) standards were analysed to estimate analytical precision and accuracy. The reference materials for  $\delta^{34}\text{S}$  was Vienna Cañon Diablo troilite (VCDT). The analytical precision (standard deviation) for NIST standard NBS 1577 (bovine liver,  $n = 6$ ) and NBS 127 ( $n = 6$ ) was  $<0.5\text{‰}$  and  $<0.6\text{‰}$ , respectively.

### 2.4. Data analysis

All data analysis was performed using the software Microsoft Excel and R (R Core Team, 2020). Maps and figures were created in R using the package 'ggplot2' (Wickham, 2016). Maps were created using georeferenced shapefiles downloaded from the Queensland Spatial Database (<http://qldspatial.information.qld.gov.au>). River distance between sites was calculated using the package 'Riverdist' (Tyers, 2017) in R.

#### 2.4.1. Site residency of large fish using sulfur isotopes

Sulfur isotopes can be influenced by the underlying geology present (including the distribution of light and heavy sulfides in bedrock), atmospheric deposition, and aerobic or anaerobic sediment conditions (Krouse, 1991). Sulfate can be removed under anaerobic conditions via sulfate reduction to sulfide, followed by sulfide product formation

(Schoepfer et al., 2014). Larger amounts of sulfur may be introduced into freshwaters that have underlying ancient marine geologies compared to non-marine geologies (Hitchon and Krouse, 1972), since seawater has 10–1000 times more sulfate than freshwater (Lamers et al., 2013).

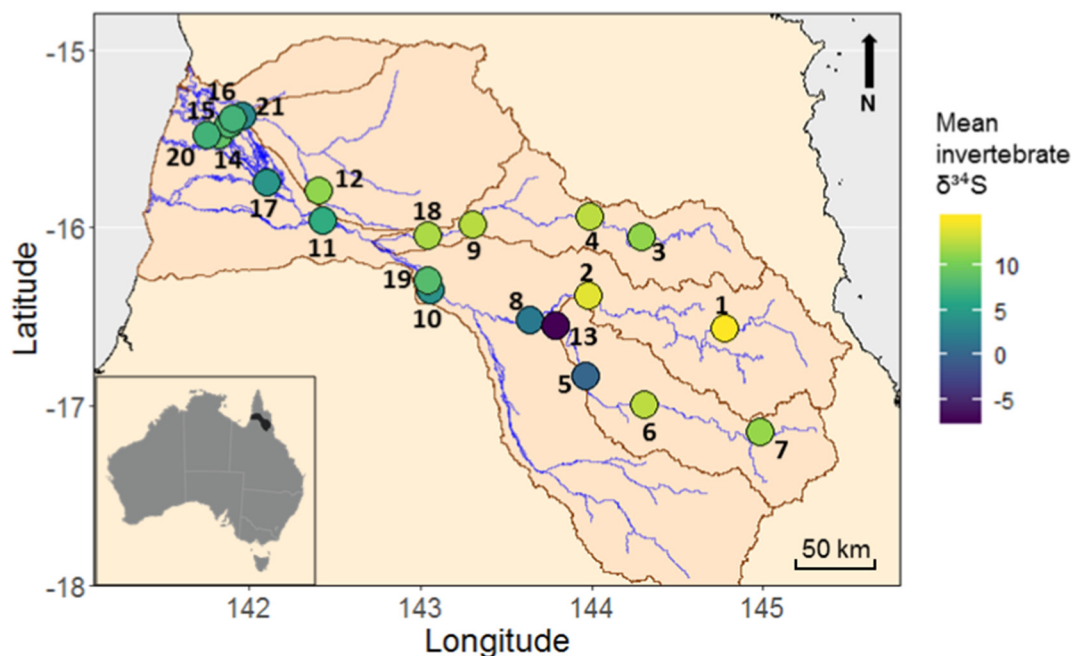
Variation in invertebrate  $\delta^{34}\text{S}$  across sites (Fig. S1) suggested that prey were local and site-specific, since little to no variation in prey  $\delta^{34}\text{S}$  values between sites would be expected if there was mixing of prey between sites or prey flowing into downstream sites from upstream sites. No differences in  $\delta^{34}\text{S}$  among invertebrate taxa across all sites provided evidence that any of the invertebrate taxa could be used and all taxa within each site were therefore pooled (Fig. S2). The sites in this study do not represent defined spatial changes in  $\delta^{34}\text{S}$ , but rather show overall zones of varying  $\delta^{34}\text{S}$  across the catchment (Fig. 2). These zones of different invertebrate  $\delta^{34}\text{S}$  values provided evidence that there was sufficient spatial variation to use  $\delta^{34}\text{S}$  as a chemical marker for distinguishing resident fish from migrant fish, where migrant fish would be considered to have recently immigrated from areas of the catchment other than the zone of capture, which includes the site of capture and any directly adjacent sites with a similar local  $\delta^{34}\text{S}$  signal.

In addition, strong correlations between mean aquatic invertebrate and mean small fish (total length < 10 cm)  $\delta^{34}\text{S}$  provided evidence that small fish were feeding locally with little movement between sites and were also suitable to use as a prey source for large piscivorous fish (Fig. S3). The small fish species analysed included glassfish *Ambassis macleayi*, fly-specked hardyhead *Craterocephalus stercusmuscarum*, goby *Glossogobius giurus*, and rainbowfish *Melanotaenia splendida inornata*. Small individuals (<10 cm total length) of other larger growing species were also included in the 'prey fish' data set.

To distinguish between resident and migrant large fish, the  $\delta^{34}\text{S}$  value of each individual ( $n = 299$ ) was standardized to the measured  $\delta^{34}\text{S}$  distribution of relevant invertebrate or small fish prey species at the site in which it was caught (using a prey-standardized Z-score:  $(\delta^{34}\text{S}_{\text{consumer}} - \text{site mean } \delta^{34}\text{S}_{\text{prey}}) / \text{site SD } \delta^{34}\text{S}_{\text{prey}}$ ). Z-scores were used to assess where the  $\delta^{34}\text{S}$  values of large fish fit in relation to the distribution of measured  $\delta^{34}\text{S}$  values in site prey collected at the same time. The  $\delta^{34}\text{S}_{\text{prey}}$  groups used to calculate Z for each large fish species were chosen based on its known trophic ecology,

taken from Sternberg and Kennard (2014). In summary,  $\delta^{34}\text{S}_{\text{prey}} =$  small fish when  $\delta^{34}\text{S}_{\text{consumer}} =$  large piscivorous fish,  $\delta^{34}\text{S}_{\text{prey}} =$  secondary consumer and omnivorous aquatic invertebrates when  $\delta^{34}\text{S}_{\text{consumer}} =$  omnivore or invertivore fish, and  $\delta^{34}\text{S}_{\text{prey}} =$  primary consumer, secondary consumer and omnivorous aquatic invertebrates when  $\delta^{34}\text{S}_{\text{consumer}} =$  herbivore/detritivore fish (Table S2).

One-sample Kolmogorov–Smirnov tests (KS test) were performed to obtain a  $p$ -value for each individual large fish that indicated whether the prey-standardized Z-score of its  $\delta^{34}\text{S}$  value was from the same statistical distribution as its prey sources. Migrants were defined as individuals with  $p < 0.05$ . A significant difference between  $\delta^{34}\text{S}$  of the consumer and the prey at the site in which the fish was caught suggests recent immigration to the site from elsewhere (recent being described as being within the sulfur isotope turnover rate of fish muscle in tropical waters which varies from weeks to months (Barnes and Jennings, 2007; MacAvoy et al., 2001)). Isotopic turnover refers to the rate at which the isotope value of the fish tissue reaches equilibrium after switching to a different isotopically distinct food source (Herzka, 2005). Turnover is a function of somatic growth and metabolism, whereby juvenile fish exhibit faster turnover than adults through addition of biomass (Herzka, 2005). It is therefore difficult to predict the time of immigration to a site by large migrant fish, though we estimate it to be within six months based on fish size, water temperature and seasonal flow regimes. Residents were defined as fish that were not significantly different to the local  $\delta^{34}\text{S}$  prey signal, since they had likely been within the local  $\delta^{34}\text{S}$  zone long enough to reflect the local prey. A limitation of this approach was that spatial resolution for distinguishing migrant fish changed across the catchment with variation in local  $\delta^{34}\text{S}$  signals. Movement may be underestimated at some sites that had adjacent sites with similar 'local'  $\delta^{34}\text{S}$  signals. However, the identification of high percentages of migrants at some sites with similar prey  $\delta^{34}\text{S}$  values to adjacent sites suggested that this was unlikely to be a major concern. We did not determine migrant source locations or distance travelled by migrants because there were separate areas of the catchment that had similar local  $\delta^{34}\text{S}$  signals e.g. some off-channel wetlands had similar values to river channel sites on the Mitchell River, meaning that we could not assign source locations with confidence. Therefore, our use of the term 'movement' refers to the number (percentage) of migrant fish.



**Fig. 2.** Spatial variation of  $\delta^{34}\text{S}$  of invertebrates at sites (numbered) where invertebrates were collected across the Mitchell River catchment. Purple points indicate low  $\delta^{34}\text{S}$  and yellow points indicate high invertebrate  $\delta^{34}\text{S}$  values. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



#### 2.4.2. Connectivity analysis and predicted changes in fish movement under potential dam scenarios

A site connectivity index (connectivity of a site to the rest of the river network) was created to assess whether the percentage of migrant fish at a site (from  $\delta^{34}\text{S}$  analysis in Section 2.4.1) was influenced by flow-mediated spatial connectivity of the location of capture to the rest of the river network. Fifteen years (2000–2015) of modelled daily flow (discharge) data were obtained (Hughes et al., 2017) for nine stream gauges in the Mitchell River catchment (Fig. 1). These data were modelled from decades of recorded discharge at each stream gauge and were used because there are gaps in the daily records for some of the gauges. A depth of 10 cm was chosen as the minimum water depth required for large fish (>10 cm total length) to pass a gauge, and the flow ( $\text{m}^3 \text{s}^{-1}$ ) at 10 cm depth for each gauge was set as the minimum flow required for connection between gauges (DSITIA, 2013).

First, we calculated pairwise proportions of days that flow was above the passable depth at each of the gauges the fish needed to pass to reach the second gauge in the pair. For example, for a fish to have opportunity to move from the upper Palmer River to the upper Mitchell River, this pair of gauges, as well as all the gauges passed on the way, had to have flow rates above the minimum passable depth of 10 cm on a given day to be counted as connected for that day. A value of one was assigned for days where gauges were above this minimum flow, and a value of zero was assigned for days where one or more gauges in the connection pathway had flow below this minimum flow. Each main channel site was assigned to the nearest gauge in the same sub-catchment, and because there were more main channel sites than gauges, some gauges were assigned to two sites. Because Site 5 was positioned halfway between two gauges, the proportion of days Site 5 was connected to other sites was calculated for both gauges and the average of these proportions was assigned to Site 5. Because connectivity is also influenced by distance and elevation, the pairwise proportions of days sites were connected were tabulated in a matrix and divided by the river distance between sites (km). Second, these pairwise distance-weighted values were divided by the slope between sites (obtained from GIS digital elevation model layers).

Lastly, the final connectivity index for each site was calculated by dividing the mean site connectivity (average connectivity of a site with all other sites) by the river distance to mouth, to anchor the site connectivity network to the actual river network and ensure that connectivity was not just between sites, but to the rest of the river network. The main Mitchell River mouth was used for this rather than each sub-catchment headwaters, because the mouth has a more clearly defined location and uses a single distance for each site, rather than multiple distances for each headwater location. By taking the average of the pairwise connectivities and anchoring them in the network in relation to the river mouth, we seek to show how connected a site is to the rest of the network, rather than to other specific sites. Floodplain creek and wetland sites were not included in this analysis, since flow at the stream gauges does not accurately represent connectivity to these off-channel habitats. These three steps can be represented in the following three equations:

$$DWC = \frac{PFC}{PD} \quad (1)$$

where *DWC* is distance weighted connectivity, *PFC* is the pairwise site flow connectivity, defined by the proportion of days a pair of sites are connected by flow and *PD* is the pairwise river distance between sites.

$$SDWC = \frac{DWC}{S} \quad (2)$$

where *SDWC* is the slope and distance weighted connectivity between a pair of sites and *S* is the average slope between the same pair of sites.

$$C_x = \frac{(\text{mean } SDWC \text{ of site } x)}{DM} \quad (3)$$

where  $C_x$  is the overall connectivity index for site *x* and *DM* is the distance between site *x* and the Mitchell River mouth.

We used a logit regression to quantify the relationship between the index of connectivity and the percentage of migrants at each site. We then used this model to predict impacts of reductions in connectivity under five scenarios of dam infrastructure development, where dams act as absolute barriers to movement and also affect connectivity via reduced flows. For these scenarios, modelled flow data for the same 15 year period (2000–2015) was downloaded from the NAWRA river model app (<https://nawra-river.shinyapps.io/river/>) (Hughes et al., 2017). The river model data is a prediction of what historical flow would have been under scenarios selected by the model user, including a change in flow at all sites downstream of a potential dam. Petheram et al. (2018) identified five potential dams in the Mitchell catchment and we modelled five unique scenarios based around them:

- 1) All dams (all five potential dams; Fig. 1).
- 2) Three dams only (the three with lowest predicted cost per ML yield (Petheram et al., 2018): Palmer dam (dam 1, Fig. 1), Pinnacles dam (dam 2, Fig. 1) and Chillagoe dam (dam 4, Fig. 1)).
- 3) Chillagoe dam only.
- 4) Palmer dam only.
- 5) Pinnacles dam only.

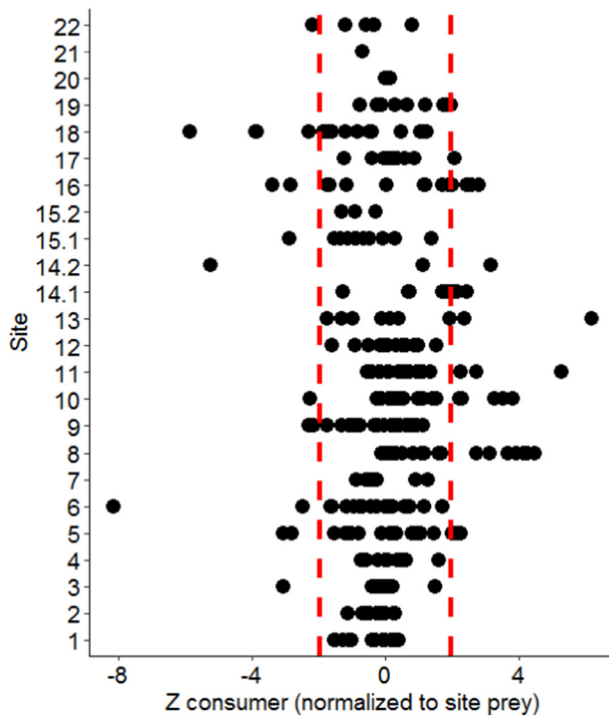
No methods of water extraction other than directly from the dams were included in these river models. Site connectivity was recalculated for the new data modelled from each dam scenario using the same methods as the original site connectivity index described above (see Table S5 for site connectivity under each scenario). Additionally, any sites above dams included in the model were assigned a connectivity of zero to sites downstream of modelled dams, assuming the dams were impassable by all fish species. As such, these scenarios were implemented as “worst-case” without any assumptions around potential risk mitigation via fish passage facilities or flow releases for downstream agricultural or environmental uses. Having recalculated connectivity under these scenarios, the logit regression model was used to predict the percentage of migrants (with prediction intervals) that would be lost from each site, due to the reduction in connectivity under each scenario. Our index of connectivity is a measure (or more specifically an indicator) of how connected a given site is to the rest of the river network, not how connected it is to another specific site. Reductions in the mean connectivity does not imply a reduction in migration opportunities among our sampling sites but rather, a reduction in the opportunity for fish to move into or out of the site more generally, from anywhere in the river network. More details of model assumptions are provided in Supporting Information.

### 3. Results

#### 3.1. Large fish site residency analysis — $\delta^{34}\text{S}$ values

Across the catchment, 16% (48 of 299) of all large fish in this study were identified as recent immigrants to their site of capture, however, this varied on a site-by-site basis, with immigration percentages ranging between zero and 67% (zero to seven individual migrant large fish per site; Figs. 3 & 4, Table S3). There was also evidence for wet season movement to floodplain wetlands, with at least one migrant fish found in three out of five wetlands (Yelko Waterhole, Leichardt Waterhole, and White Water). Movement into Yelko Waterhole was particularly high, where 30% of the fish were found to be migrants in 2018 and two out of three fish were found to be migrants in 2019.

At the species level, evidence for recent movement was apparent for 13 of the 17 large fish species collected in this study, though the



**Fig. 3.** Z scores of individual large fish (fish > 10 cm) at each site. Points outside of dashed lines were considered migrant fish because they had significantly different  $\delta^{34}\text{S}$  values from prey  $\delta^{34}\text{S}$  at that site. Points between the two dashed lines were not significantly different from the local prey at that site and those fish were therefore considered residents. Sites 14.1 and 14.2 represent Yelko Waterhole samples from 2018 and 2019, respectively, and Sites 15.1 and 15.2 represent Sandy Creek samples from 2018 and 2019, respectively.

percentage of migrants for each species varied, ranging between zero and 44% (for species with  $n \geq 5$ ). As expected, many individuals of catadromous species were migrants, and unexpectedly, most fish species that were not known to make reproductive migrations also showed evidence of movement (Table 1). For example, 43% of freshwater longtom and 27% of salmon catfish individuals, respectively, were found to be migrants and these species are not considered to be reproductive migrators.

### 3.2. Connectivity analysis and predicted changes in fish movement under potential dam scenarios

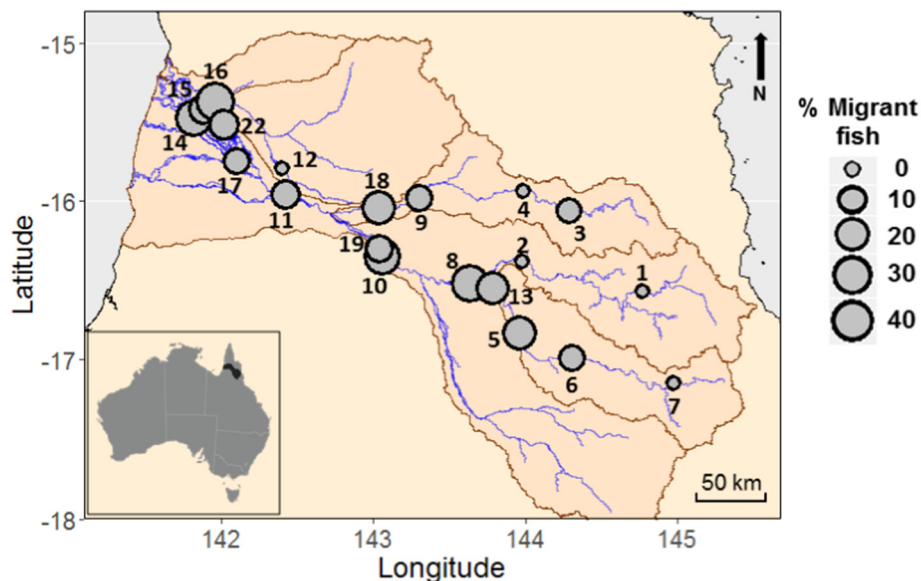
Movement of large fish (percentage of migrant fish at a site, determined from  $\delta^{34}\text{S}$  analysis) was higher at river channel sites that were more connected to the rest of the river network (Fig. 5). In fact, over half of the variation in large fish movement across sites was explained by flow-mediated site connectivity. The logit regression of this relationship ( $y = -3.15 + 0.21x$ ,  $df = 12$ ,  $F = 16.45$ ,  $R^2 = 0.58$ ,  $p = 0.002$ ) was used to predict the change in the number of migrants from the fitted values at each site/sub-catchment under five dam scenarios (Table S4).

Each of the dam scenarios resulted in appreciable reductions in predicted migration. The largest predicted change in the percentage of migrants was under the *all five dams* scenario, with movement potential into sites in the Mitchell sub-catchment from elsewhere in the catchment predicted to decrease by a mean of 45% (Fig. 6, Table 2). There was little difference in predicted decrease in movement potential between the *all five dams* and the *three main dams* scenario with both scenarios resulting in reductions approximately ranging between 20% and 40%. The individual dam scenarios (Chillagoe, Palmer or Pinnacles) were predicted to most affect the movement potential of fish within the sub-catchment in which they were located. However, the *Pinnacles dam only* scenario had a similar predicted effect on fish movement potential in the Palmer sub-catchment to the *Palmer dam only* scenario, through changes in connectivity of downstream Palmer River sites with the rest of the river network (Tables S4 & S5). Predicted values for individual dam scenarios showed that the Pinnacles dam is likely to have a greater effect on fish movement potential across more sites than the Chillagoe dam or the Palmer dam (Table 2).

## 4. Discussion

This study demonstrated that large-scale hydrological connectivity, both lateral and longitudinal, supported movement of fish assemblages in a free-flowing tropical river. Contrary to our first hypothesis, our results showed that fish movement occurred (to varying degrees) across most species, regardless of their reproductive life history. Therefore, physical barriers and reduced connectivity are likely to have a larger negative effect on the movement of more species than originally anticipated.

Fish movement studies often share a common finding that approximately 10–30% of fish in a community are migrants (Davis et al., 2015;



**Fig. 4.** Percentage of migrants (indicated by size of grey points) at sites with  $n > 5$  large fish.

**Table 1**

$\delta^{34}\text{S}$  analysis results for large fish species. Fish species with individuals collected from wetlands that were significantly different from the wetland prey  $\delta^{34}\text{S}$  are indicated in the "migrated to wetlands?" column. Species are grouped by reproductive movement classifications from Sternberg and Kennard (2014). P = piscivore/invertivore, I = invertivore, O = omnivore, HD = herbivore/detritivore.

Reproductive movement classification	Trophic guild	Species	% migrants	n	Migrated to wetlands?
Catadromous	P	Tarpon <i>Megalops cyprinoides</i>	33	15	Y
	P	Barramundi <i>Lates calcarifer</i>	44	23	Y
Potamodromous	I	Toothless catfish <i>Anodontiglanis dahli</i>	0	10	
	I	Hyrtl's tandan <i>Neosilurus hyrtlii</i>	0	5	
	I	Black catfish <i>Neosilurus ater</i>	18	17	
	O	Spangled perch <i>Leiopotherapon unicolor</i>	13	16	Y
	O	Sooty grunter <i>Hephaestus fuliginosus</i>	7	29	
	HD	Gulf grunter <i>Scortum ogilbyi</i>	14	22	
No movement	P	Sleepy cod <i>Oxyeleotris lineolatus</i>	7	44	Y
	P	Shovel-nosed catfish <i>Neoarius midgleyi</i>	9	11	
	P	Salmon catfish <i>Neoarius graeffei</i>	27	34	Y
	P	Northern saratoga <i>Scleropages jardinii</i>	0	1	
	P	Mouth almighty <i>Glossamia aprion</i>	0	15	
	P	Giant gudgeon <i>Oxyeleotris selheimi</i>	17	6	
	P	Freshwater longtom <i>Strongylura krefftii</i>	43	14	
	I	Seven-spot archerfish <i>Toxotes chatareus</i>	0	11	
	HD	Bony bream <i>Nematolosa erebi</i>	9	22	

Griffiths, 2003; Skov et al., 2008), and our overall figure of 16% (from  $\delta^{34}\text{S}$  analysis) fell within this range. Residency is highly variable between species and can be dependent on adult size, and reproductive and feeding strategies (Fry and Chumchal, 2011; Schmetterling and Adams, 2004). Furthermore, individual fish movement and residency behaviour within a species may be influenced by social hierarchy, and feeding specialization (Akbaripasand et al., 2014; Harrison et al., 2017).

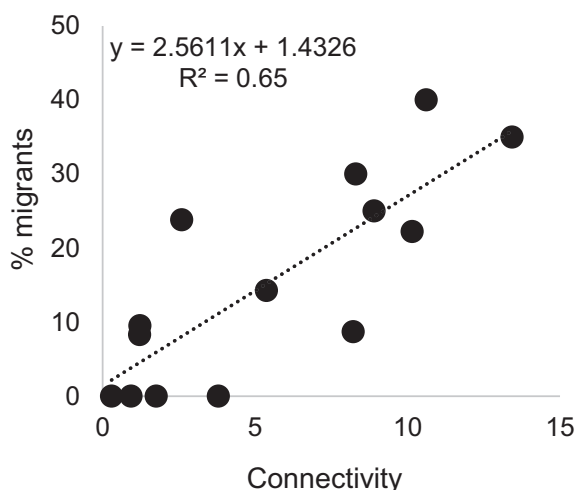
This study explored the catchment scale movement of an entire large fish assemblage and found that connectivity of river channel sites was significantly positively correlated with the percentage of migrant fish within a site, suggesting that realized movement is a function of opportunity. Kaus et al. (2018) identified two periods of increased movements of a potadromous salmonid *Brachymystax lenok* in a Mongolian river. The first related to movement into tributaries when flow began to increase in late spring and the second related to movement into deeper overwintering pools as flow subsided in autumn (Kaus et al., 2018). The latter may reflect fish behaviour exhibited in our results, which showed movement to more connected sites (with samples collected in late autumn/early winter) as flow subsided.

In this study, barramundi and tarpon were found to be two of the most mobile species, which was expected given their catadromous life history. However, otolith microchemistry studies have found that most barramundi do not migrate to the sea each year to breed, and

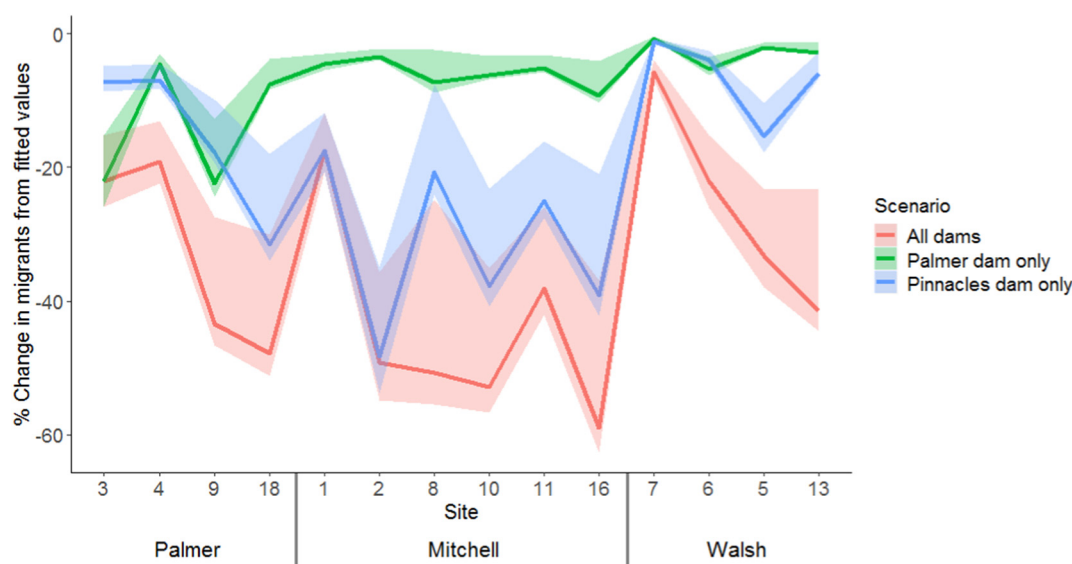
most sub-adult tarpon (tarpon in this study were all in the sub-adult size range of 12–35 cm) would have not yet migrated to the sea to spawn (Crook et al., 2017; Milton and Chenery, 2005; Shen et al., 2009). Therefore, movements of barramundi and tarpon found in this study may represent foraging for food or movement to more permanent habitats, rather than reproductive migrations. Migrant barramundi were found only in deeper sites (>2 m depth) and it is possible that they move to these deeper habitats to ensure they have enough water to survive the dry season (Moore and Reynold, 1982) and/or to increase their chances of success in foraging for prey fish. While salmon catfish and freshwater longtom are not considered to be reproductive migrators (Sternberg and Kennard, 2014), they were found in this study to be among the most mobile species (indicated by high percentages of migrants). More mobile species are likely to be most impacted by reductions in connectivity.

The relationship observed between fish movement and connectivity suggests that fish movement is likely to be impacted by climate change and water resource developments, which can both alter river flows (Jaeger et al., 2014). Reduced river flows can lead to earlier disconnection of habitats, and water resource development in the form of dams and other infrastructure also add the direct effect of a barrier across the channel (Branco et al., 2014). As highly connected habitats are an important refuge for fish during the dry season, fish may be driven towards fewer of these habitats, and competition for food and/or stress of predation may increase (Mazumder et al., 2016; Robertson et al., 2008). Our connectivity-movement model predicted that dams would have a negative impact on the movement potential of large fish across river channel sites, which was consistent with our second hypothesis. These dam scenarios are examples of extreme development impacts and present worst-case scenarios. Some of these impacts may be mitigated by the use of fish passages on dams, or substituting potential dams for off-channel water storage (Harris et al., 2017). Our connectivity-movement model provides a tool that can be used in optimization models to determine if there are infrastructure solutions that have minimal impact on fish movement but are also viable for agriculture.

Migrant fish were found in three out of five wetlands sampled, indicating that wet season connectivity is important for access to floodplain wetland habitats. The timing of seasonal flows has been shown to be a strong predictor of fish movement into and out of floodplain wetlands (Marshall et al., 2016) and if water resources are further developed in the Mitchell River catchment, it is critical that not only enough flow remains to inundate floodplains, but also that this occurs at suitable times. Wetland connections to channels and tributaries of the Mitchell River usually persist for only a short period under high wet season flow (Warfe et al., 2011). Therefore, it is possible that water resource developments will reduce



**Fig. 5.** Relationship between mean site connectivity (weighted by slope, distance between sites, and distance to river mouth) and percentage of migrants at the same site, for river channel sites.



**Fig. 6.** Percentage change from current migrant percentages under three different dam scenarios at each site with 95% prediction intervals. Only three scenarios were plotted for clarity of the plot.

the permanence of floodplain wetlands turning them into temporary wetlands or drying them completely (Reid et al., 2012). Wetland loss not only reduces the availability of highly productive habitat for fish, but also threatens food security for many Indigenous Australians (Kingsford, 2015; Pyke et al., 2018). Indigenous Australians from several communities make up ~23% of the catchment population and harvest fish, turtles and other resources from wetlands, creeks and river channels as an important part of their diet (Jackson et al., 2014).

The relationship between connectivity and fish communities has been examined previously (Fullerton et al., 2010), including the impact of existing dams and altered flow regimes using species reproductive traits (Rolls et al., 2014). Subsequently, trait-based approaches have been used to qualitatively predict the likely impacts of new water resource developments (Arantes et al., 2019; Cheng et al., 2015; Rolls and Sternberg, 2015), while predictive modelling of fish responses to reduced connectivity has been less explored (Teichert et al., 2020). Our approach identified movements of fish that appear to be largely unrelated to reproductive traits but facilitated by connectivity in an unregulated river. We used a model of the relationship between connectivity and movement to quantitatively predict the impacts of reduced connectivity. These predictions can be directly integrated into management decision making tools, such as ecological risk assessments (e.g. McGregor et al., 2018). While we used sulfur stable isotopes to estimate fish movement, our approach can be used with other tracers of movement such as otoliths and acoustic telemetry, making it widely applicable to other river systems.

Most studies using  $\delta^{34}\text{S}$  as a movement tracer have focused on movement between freshwater and marine environments (Fry and Chumchal, 2011; Herzka, 2005; Moore et al., 2016), but here we demonstrated that  $\delta^{34}\text{S}$  can be also used to study movement within freshwater reaches of a river system, given the natural variation in  $\delta^{34}\text{S}$  values within the system. Similar to fish movement studies based on strontium ratios (e.g. Brennan et al., 2015), the presence of multiple different underlying geologies within a catchment is likely to be a good indicator of whether  $\delta^{34}\text{S}$  will be an effective tracer of movement in that system (Burke et al., 2018).

The variable geology in the Mitchell catchment creates spatial variation in background strontium (Batlle-Aguilar et al., 2014) and sulfur isotopes, supporting their use as tracers of movement in this system. In this way our approach provides a complementary method of fish movement analysis to quantify flow related movement across a catchment.

## 5. Conclusion

In summary, this study quantified seasonal movement of an entire fish community in a free-flowing river system. While movement varied between species, it was not limited to species that move to reproduce. Fish used connectivity to move both in the river and on the floodplain and dams are predicted to reduce movement throughout the catchment. Northern Australia is not the only tropical region under pressure of water resource development. Southeast Asia, Africa and South America are under pressure of agricultural expansion and hydropower development (Laurance et al., 2014; Zarfl et al., 2015). These regions, particularly the Amazon and Central Africa, have been rated as the ecoregions in the world with the highest fish species diversity and endemism (Liermann et al., 2012). Developing approaches to understand ecological responses to natural variations in flow and connectivity, such as that reported here, is important for predicting changes that are likely to occur with climate change and water resource development and developing management strategies that aim to conserve biodiversity (Tickner et al., 2020). A global history of over a century of river and catchment modifications and subsequent declines in biodiversity and fisheries resources serve as an important reminder of the consequences of anthropogenic alterations to natural systems that do not adequately factor connectivity pathways into their design.

## CRedit authorship contribution statement

**Kaitlyn O'Mara:** Data curation, Formal analysis, Writing – original draft, Validation. **Michael Venarsky:** Investigation, Data curation,

**Table 2**

Sub-catchment mean  $\pm$  SD percentage change in migrants from current (no dam) percentages. The three main dams scenario includes the potential Chillagoe, Palmer and Pinnacles dams.

Sub catchment	All five dams	Three main dams	Chillagoe dam only	Palmer dam only	Pinnacles dam only
Mitchell	$-45 \pm 15$	$-42 \pm 14$	$-8 \pm 6$	$-6 \pm 2$	$-31 \pm 12$
Palmer	$-33 \pm 15$	$-31 \pm 14$	$-5 \pm 2$	$-14 \pm 9$	$-16 \pm 12$
Walsh	$-26 \pm 15$	$-20 \pm 12$	$-15 \pm 10$	$-3 \pm 2$	$-7 \pm 6$



Writing – original draft, Validation. **Ben Stewart-Koster**: Investigation, Data curation, Writing – original draft, Validation. **Glenn B. McGregor**: Investigation, Writing – original draft, Validation. **Cameron Schulz**: Investigation, Writing – original draft, Validation. **Martin Kainz**: Data curation, Writing – original draft, Validation. **Jonathan Marshall**: Conceptualization, Methodology, Writing – original draft, Validation. **Stuart E. Bunn**: Conceptualization, Methodology, Writing – original draft, Validation.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2021.147785>.

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