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ORIGINAL ARTICLE

Ecology of FRESHWATER FISH WILEY

Inter-decadal variation in diadromous and potamodromous fish assemblages in a near pristine tropical dryland river

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Abstract

Freshwater ecosystems are both incredibly biodiverse and highly threatened globally. Variation in environmental parameters including habitat and flow can substantially affect many ecological processes within riverine aquatic communities, but the ties between such parameters and ecology are neither well studied nor understood. In highly variable tropical dryland river systems, assessing such relationships requires data collection over inter-decadal time scales, which is not typically permitted on development schedules driven over short periods (including election and funding cycles). Here, we used seine net sampling data collected over an 18-year period in the tropical dryland Fitzroy River, Western Australia, to assess how environmental and temporal factors including habitat, seasonality, and inter-annual variation in wet season magnitude affect the community assemblage structure, recruitment, and growth of aquatic species in dryland rivers. Results demonstrated that macrohabitat (main channel vs floodplain creek) and the magnitude of wet season rains and resultant flooding both had a substantial influence on biotic communities, alongside seasonal and diel variation. The magnitude of wet season flooding (measured as river discharge volume) had the greatest impact on assemblage composition within floodplain creek habitats and was a significant driver of recruitment rates and growth of recruits and adults of several species examined. This study highlights key considerations for conserving dryland river systems and constituent biota. Specifically, these are maintaining (a) rhythmicity of flow within each year, (b) diversity of flow volume between years, and (c) a variety of habitat types including ephemeral, semi-permanent, and permanent shallow floodplain and deeper main channel pools, in order to support a diverse array of generalist and specialist diadromous and potamodromous fishes.

KEYWORDS
Fitzroy River, flow, recruitment, seine, water resource development

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1 | INTRODUCTION

Freshwater ecosystems worldwide are some of the most biologically diverse and notably some of the most threatened. Freshwater ecosystems are relatively rare (0.8% of earth's surface; Gleick, 1996), and pristine systems are especially uncommon as these ecosystems are threatened by a plethora of factors including water resource development, pollution, harvest, habitat destruction, and climate change (Dudgeon et al., 2006; Sala et al., 2000; Vörösmarty et al., 2010). As a result, freshwater ecosystems are considered some of the most imperilled in the world, with biodiversity loss and destruction of habitats occurring at accelerated rates compared to marine and terrestrial ecosystems (He et al., 2019; McRae et al., 2017; Sala et al., 2000; Strayer & Dudgeon, 2010). As human populations continue to expand and climate change disrupts weather patterns, these threats are likely to increase (Carpenter et al., 2011; Strayer & Dudgeon, 2010; Vörösmarty et al., 2010). It is therefore essential that we understand how water resource developments, climate change, and other threats affect freshwater ecosystems in order to enact effective conservation measures for our remaining freshwater biodiversity.

Concomitant pressures on freshwater ecosystems are particularly prevalent and concerning in arid environments; here, human needs for freshwater are high, harnessing freshwater resources for human use often requires substantial alteration of natural flow regimes, and climate change is likely to increase the extreme conditions inherent of these often highly dynamic systems (Arthington & Balcombe, 2011; Jaeger et al., 2014; Sandi et al., 2020; Sheldon et al., 2010; Strayer & Dudgeon, 2010). Arid freshwater environments are typically characterised by dryland river systems, which host cycles of flood and drought that can be predictable on an annual basis or highly variable from year to year. These climatic cycles result in extreme natural variation in flow rates and durations, water levels, and habitat quality and quantity for freshwater biota (Tooth, 2000; Warfe et al., 2011). This typically creates “boom-or-bust” cycles where productivity is high during and after flood events when terrestrial nutrients are pulled into aquatic systems, and low during energy-limited drought periods when aquatic habitats shrink or in some cases disappear (Arthington & Balcombe, 2011; Bunn, Thoms, et al., 2006). Aquatic species in dryland rivers must cope with these highly variable conditions in habitat and resource accessibility and quality. In fact, many have adapted to rely on the cyclic conditions for different aspects of their life history including migration, recruitment, life-stage transitions, and spawning and reproductive cycles (Bunn & Arthington, 2002; Gido et al., 2013; Jenkins & Boulton, 2003; King et al., 2003; Lear et al., 2019; Sheldon et al., 2010; Tyler et al., 2021). Additionally, it is likely that many dryland species rely on productive wet season periods to restore body condition and to increase growth, while little growth occurs during the energy-limited dry season (e.g. Balcombe et al., 2012; Junk et al., 1989; Lear et al., 2021). Because of the inherent connection between ecological processes and flood regimes in these systems, dryland river ecosystems and biota are highly vulnerable to any alteration of flow regimes, such as that driven by water resource developments or climate change, which makes arid region dryland rivers some of the most threatened freshwater systems globally (Vörösmarty et al., 2010). The natural variability in flow in dryland rivers also makes them good study systems to assess how impending changes in flow or other hydrological and environmental characteristics might affect other more stable river systems in the future.

While the threats of water resource development, climate change, and other factors on arid river systems are clearly consequential, the exact mechanisms and pathways by which such threats affect freshwater ecosystem processes or specific biota are not always well-known. This can make it difficult to predict effects of proposed developments or other stressors on specific communities or ecosystems, in turn compromising environmental management. One of the reasons that these processes remain relatively understudied is that there has often been little opportunity to survey these systems prior to major disturbance, as many systems throughout the world have already been heavily altered for decades or centuries (Nilsson et al., 2005; Nilsson & Berggren, 2000; Vörösmarty et al., 2010). This makes it challenging to empirically compare biodiversity, community structure, or ecosystem processes from before and after disturbance. Furthermore, the extraordinary variation in flow between years in many dryland systems means that studies must occur over extended time scales to capture the full natural variation in flood and drought levels inherent in these systems. However, this is generally financially prohibitive, and not permitted on the fast-track scale of many impending developments or the 1–3 year funding cycles typical of research grants. As a result, there is little information available describing how environmental and hydrological variation influences freshwater communities in natural systems, making it difficult to predict how proposed water resource developments, climate change, or other factors will influence biotic communities (Shenton et al., 2012).

The present study aims to assess how environmental parameters including flow, habitat type, and seasonality affect the composition, recruitment, and diversity of freshwater and diadromous fish assemblages in the lowland main channel and floodplain creek of the Fitzroy River catchment (in Western Australia), based on directed fish surveys conducted over a period of 18 years. Situated in a sparsely populated region, the Fitzroy River is a relatively pristine and undeveloped dryland river with predictable annual cycles of wet season flood and dry season drought, as well as substantial interannual variation in the volume of flooding experienced during the wet season (Lear et al., 2019; Morgan et al., 2004). The river also lacks alien fishes (Morgan et al., 2004). This makes it an excellent model system for investigating ties between natural ecological processes and flow. Results are discussed in relation to how natural variation in fish communities may be affected by widespread threats to freshwater environments including water resource developments. This discussion is highly relevant not only to conservation of the Fitzroy River catchment, for which water resource developments are proposed for the near future, but also to other dryland or seasonally variable river systems under pressure from anthropogenic threats.

2 | METHODS

All work with animals was conducted under permits granted by Western Australia Department of Fisheries and Murdoch University's Ethics Committee.

2.1 | Study area

The Fitzroy River in the Kimberley region of Western Australia is a dryland river system subject to a monsoonal climate. During the wet season (approximately December – May), the river is generally fully connected and flowing, with discharge rates of up to 986 Gl per day recorded over the last 20 years (Government of Western Australia River Monitoring Stations; http://kumina.water.wa.gov.au). During the dry season (June – November), typically river flow gradually and predictably subsides and the river recedes into disconnected permanent pools, with river discharge generally ceasing between August and September (Whitty et al., 2017). Habitat and water quality conditions vary substantially between the wet season and dry season as well as within the dry season, where water temperatures range between approximately 18 and 35°C. Additionally, there is high inter-annual variation in wet season flow in the Fitzroy River, with the river sporting the fifth most variable annual discharge rates worldwide (Puckridge et al., 1998); total wet season flow has varied more than 30-fold over the past 20 years (Government of Western Australia River Monitoring Stations; http://kumina.water.wa.gov.au). This results in high inter-annual variation in water levels, flow, and aquatic habitat characteristics during both the wet and dry seasons.

The Fitzroy River is also relatively undeveloped compared to many other rivers in the region. Along its over 700 km course, it has three major structures: two river crossings (Myroodah Crossing and Fitzroy Crossing) and the Camballin Barrage, built in the 1960s for irrigation purposes but abandoned shortly thereafter. At present, there is some small-scale water abstraction for local irrigation purposes, but flow regimes in the river are relatively unaltered.

Sampling in the current study was conducted during the dry season in several locations in the main channel of the Fitzroy River and in a floodplain creek system, Uralla Creek, which runs parallel to the main channel for over 70 km (Figure 1). Uralla Creek floods during the wet season from water which naturally diverts from the main channel, and both Uralla Creek and the main channel of the river recede to disconnected permanent pools during the dry season.

2.2 | Fish sampling methods

Fish assemblage sampling was conducted over a period of 18 years, between 2004 and 2021. Sampling was most consistent in Uralla Creek, where sampling occurred each year between 2008 and 2021, except in 2011 when early flooding prohibited access (Figure 2). Sampling in the main channel of the Fitzroy River was conducted in 2004, 2005, 2007–2010, 2014, and 2021. Main channel sampling was conducted in Myroodah Pool, Camballin Pool, and the pools immediately above and below the Camballin Barrage (Figure 1), although not all sites were sampled in each year. In most cases, if a location was sampled during a year, sampling was conducted in both the early (June–July) and late (October–November) dry season.

On each sampling occasion, fish were captured using a 26 m seine net, which contained a 10 m pocket of 3 mm woven mesh and two 8 m wings of 6 mm woven mesh, and which fished a depth of up to 1.5 m. Three replicate seines were conducted during the day and during the night on each occasion. Each individual fish caught was identified to species level, the total number of each species caught in each seine was counted, and the total length (TL) of the first 100 individuals of each species caught in the three sets was measured to the nearest 1 mm. The orbital carapace length (OCL) rather than TL was measured for crustaceans that were caught. It is notable that this method of sampling surveys only a small proportion of each location (river pools sampled can be >2 km long), and largely excludes fish that use deeper habitats (e.g. *Carcharhinus leucas* (bull shark), *Pristis pristis* (freshwater sawfish), and large *Lates calcarifer* (barramundi)), but produces relatively standardised comparative samples of the small-bodied teleost and crustacean assemblages present in shallow water.

2.3 | Wet season characteristics

Several factors relating to wet season discharge and river stage height were used to describe the wet season in each year. Discharge and stage height data from the Fitzroy River were collected from the Department of Water and Environmental Regulation river monitoring stations (kumina.water.wa.gov.au/waterinformation/telem), with parameters extracted from Willare (monitoring station 802008) in the lower Fitzroy Catchment. Overall, the total volume of water discharged from the Fitzroy River during the wet season (the sum of all river discharge recorded between December and May) was used to categorise the wet season as either low volume (<2000 Gl), medium volume (2000–7000 Gl), or high volume (>10,000 Gl) based on natural breakpoints in wet season discharge volumes. Wet season discharge volumes between 7000 and 10,000 Gl did not occur during the study period. This qualitative wet season descriptor was used as a categorical predictor in modelling analyses assessing drivers of fish assemblage structure (see following section).

Additionally, several other wet season characteristics were extracted to determine which factors contributed most to observed patterns in recruitment and growth of fish, to be used as continuous predictors in modelling recruitment patterns of specific species (see following section). These characteristics included the total, early, or late wet season discharge (summed discharge from December–May, December–February, or March–May, respectively), the number of days where main channel river stage height was <1 m, 1–2 m, 2–4 m, 4–6 m, 6–8 m, or >8 m above the point at which river flow ceases, the number of days since main channel stage height dropped below 1 m, and the maximum river stage height and maximum river

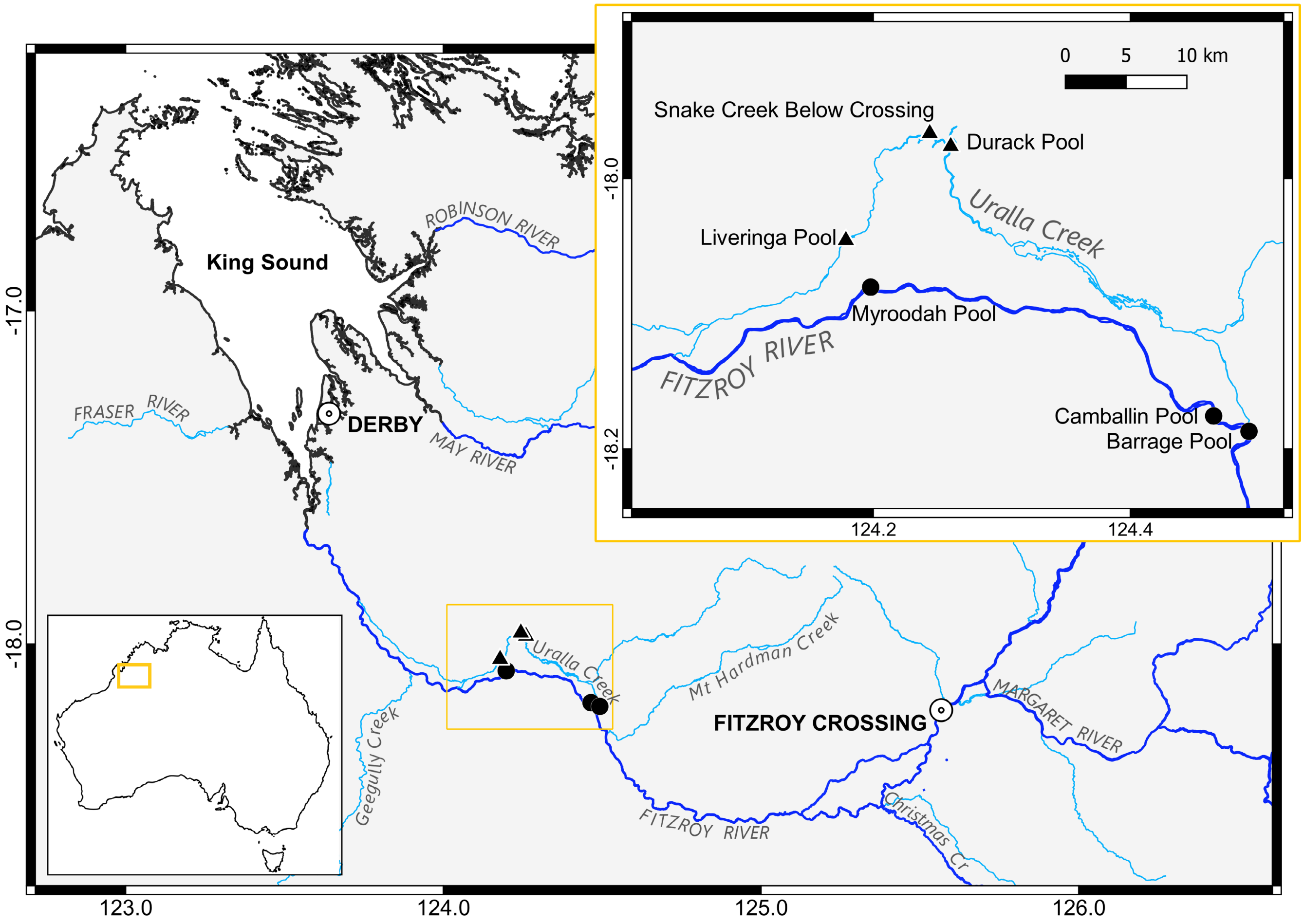
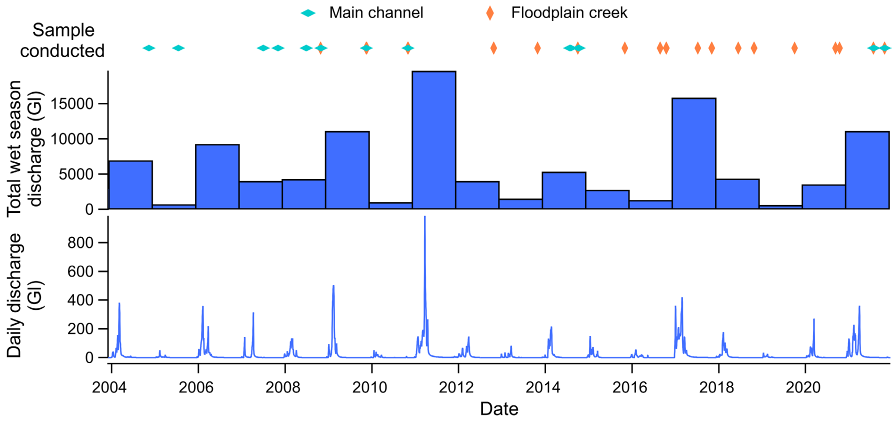


FIGURE 1 Map of the Fitzroy River, with the seine net sampling sites in the main channel (circles) and Uralla Creek (triangles) identified.

FIGURE 2 Hydrograph depicting variation in discharge of the Fitzroy River during the 18-year sampling period. Timing of discharge was predictable across years, but total volume was highly variable. Top points show the times when fish sampling was conducted throughout the study in either main channel or floodplain habitats.



discharge rate recorded during a given wet season. At a stage height of over approximately 8 m, there is inundation of the floodplain, and at stage heights below 1 m, there is low to negligible flow in many floodplain systems and the main channel.

2.4 | Fish assemblage characteristics and analyses

Each group of three replicate seines conducted was combined into one sampling set. Taxonomic diversity of faunal assemblages caught in each set was calculated using Hill numbers (Chao et al., 2014). The total number of individuals caught in each sampling set (abundance) and total number of species caught in each set (species richness) were also determined. Each sampling set was described by time of day (day or night), time of the year (early or late dry season), and habitat type (main channel or creek) in further analyses.

Diversity, fish abundance, and species richness were compared across samples using permutational multivariate analyses of variance (PERMANOVAs) in R (v. 3.6.3; R Foundation for Statistical Computing, Vienna, Austria), using the “predictmeans” package (Luo et al., 2014) and "lme4" package (Bates et al., 2015). An initial set of PERMANOVAs was run to compare the diversity, abundance, and species richness between Uralla Creek and main channel sites using only data from years where both locations were surveyed (2008–2010, 2014–2015, and 2021), and a subsequent set of models were run on the two habitat types separately using all data collected during the full study duration. Habitat type (for the initial model set), time of day, time of year, preceding wet season volume, and interactions between these variables were included as fixed predictors in these models, with sampling site included as a random effect. To limit the possibility of false positive results with the use of multiple tests, fixed predictors with a PERMANOVA *p*-value <.01 were considered significant predictors of diversity, fauna abundance, or species richness.

The drivers of community composition of fish assemblages were examined using nonmetric multi-dimensional scaling (NMDS). This was conducted using the "vegan" package in R (Oksanen et al., 2013). Rare species occurring in <5% of sampling sets were excluded from analyses. Species counts were square-root transformed to reduce variance between species with consistently high counts and those with consistently low counts and were then transformed using a Wisconsin double standardisation to equalise emphasis among sampling points and species. A Bray–Curtis dissimilarity matrix was constructed from these transformed data, which was then used to assess differences in community structure through analyses of similarity (ANOSIMs). Single-factor ANOSIMs were first run with data from all sampling sets from all sites and compared community composition between locations, day and night samples, the early and late dry season, and years with low-, medium-, and high-volume wet seasons. Subsequently, samples from the main channel and the floodplain creek were separated, and ANOSIMs were run on each subset of data to determine whether assemblage composition specifically in the main channel or creek differed between day and night, early and late dry season, and wet seasons with low, medium, and high discharge volumes. These analyses were visualised using NMDS plotting, and the significance and relative contribution of each factor to community composition were assessed by the relevant ANOSIM *p*-value and $\bar{R}$ statistic.

2.5 | Recruitment, growth, and wet season volume

Following analyses describing overall patterns in the sampled fish assemblages, several specific species were selected to identify trends in size, recruitment, and abundance throughout the study period. All species were characterised by guilds dependent on spawning period: either spawning perennially, in the dry season only, in the late dry season only, or in the wet season only. The most abundant species of each guild was selected for recruitment and growth analyses, including *Nematolosa erebi* (bony bream; perennial spawner), *Craterocephalus lentiginosus* (Prince Regent hardyhead; dry season spawner), *Ambassis* spp. (glassfish, *Ambassis* sp. 1 and *Ambassis* sp. 2 in Morgan and Hammer (2018); late dry season spawner), *Leiopotherapon unicolor* (spangled perch; wet season spawner), *Glossamia aprion* (mouth almighty; dry season mouth brooder), and *Macrobrachium spinipes* (cherabin; amphidromous wet season spawner). Length-at-age data for these species were largely unavailable in the literature for this catchment, and therefore, length-frequency distributions of individuals in the current study were examined to determine the size cut-off representing the maximum size of new recruits (<1 year old) compared to individuals born in previous years. This size limit was readily apparent in *M. spinipes* (≤25 mm OCL), *N. erebi* (≤80 mm TL), and *Ambassis* spp. (≤30 mm TL), where a bimodal length-frequency distribution was present, and the smaller of the two distributions was assumed to represent new recruits (see Figure S1). *Craterocephalus lentiginosus* and *L. unicolor* both showed a right-skewed unimodal size-frequency distributions, and the recruitment size limit was assumed to be prior to the trailing end of the distribution, at ≤50 mm TL for *C. lentiginosus* and ≤100 mm TL for *L. unicolor* (see Figure S1). These estimated size cut-offs for 1-year-old fish roughly agree with limited published length-at age or growth data for these species in similar catchments, where available (Beesley et al., 2022; Bishop et al., 2001; Llewellyn, 1973).

The catch per unit effort of new recruits ($CPUE_R$) of each of the model species was used to examine patterns in recruitment rates dependent on wet season discharge volume. For these analyses, only data collected in the floodplain creek in the late dry season were used, as early dry season and main channel sampling efforts were less consistent. For each year, $CPUE_R$ was calculated as the total number of new recruits caught in Uralla Creek in the late dry season (including both night and day seines) divided by the total number of seine replicates conducted. Regression analyses were used to determine whether $CPUE_R$ varied with characteristics of wet season volume described previously in section 2.3. Each of these wet season characteristics was examined using a separate regression model, as all showed high collinearity with each other. The R^2, Akaike's information criterion corrected for small sample size (AICc), and log-likelihood of each model were compared to determine which wet season characteristic best predicted each species' annual recruitment. Additionally, the median size (TL or OCL) of new recruits and the median size of age 1+ individuals was run through a similar regression analysis as with $CPUE_R$, and the same model descriptors used to determine if the size of new recruits or age 1+ individuals varied depending on wet season characteristics. In all chosen models, temporal autocorrelation was tested for using the Durbin-Watson test, but was not detected in any case, and therefore corrective factors for autocorrelation were not included.

3 | RESULTS

The timing of wet season discharge in the Fitzroy River was predictable across years, but the volume was highly variable between years, ranging approximately 30-fold in volume throughout the study period from 646 Gl (2019) to nearly 20,000 Gl (2011) (Figure 2). Three years where sampling occurred were determined "high-volume" years with total discharge >10,000 Gl (2009, 2017, and 2021; sampling was not conducted in 2011 due to excessive flooding), 7 years were determined "medium-volume" years with total discharge 2000–7000 Gl (2004, 2007, 2008, 2012, 2014, 2018, and 2020), and 6 years determined "low-volume" years with total discharge <2000 Gl (2005, 2010, 2013, 2015, 2016, and 2019).

In total, 24 teleost species, two crustaceans, and one elasmobranch were captured during seine net sampling in dry season refuge pools (Table 1), including nearly 50,000 individual fish and crustaceans. The most commonly caught species was *N. erebi*, which constituted nearly a quarter of seine net catches between 2004 and 2021. *Craterocephalus lentiginosus*, *Ambassis* spp., *Melanotaenia australis* (western rainbowfish), *G. aprion*, *M. spinipes*, *L. unicolor*, *Glossogobius giuris* (flathead goby), and *Amniataba percoides* (barred grunter) were also relatively common, with all other species each constituting <2% of the total catch (Table 1). CPUE of individual species ranged from 0 to 432 individuals per seine (maximum CPUE measured in *N. erebi*), and overall CPUE including all species ranged from 0 to 609 individuals per seine.

3.1 | Drivers of dry season refuge pool assemblage structure

Habitat type had the most consistent effect on species richness, fauna abundance, and diversity (Hill number), which were higher in creek habitats compared to channel habitats in almost all cases regardless of time of day, season, or the preceding wet season volume (Figure 3). Because of the varied effects of other parameters on diversity, abundance, and species richness between habitats, separate models for creek and main channel habitats were adopted for further examination of predictors. Within creek habitats, wet season volume was the only significant predictor of diversity, where lower diversity was observed in years with high-volume wet seasons compared to those with low or medium-volume wet seasons (Figure 3). Species richness in creek habitats, on the other hand, was significantly higher during the late dry compared to early dry season (Figure 3), also showing interactions between time of day and wet season volume (Table 2). Faunal abundance in creek habitats was not influenced by any predictor variables (Table 2). In the main channel, diversity and species richness were higher at night than during the day, and abundance and species richness were higher in the late dry season compared to the early dry season. No factors were influenced by wet season volume in the main channel (Figure 3, Table 2).

Freshwater sawfish (*P. pristis*) were the only rare species identified in the data, caught on two out of 128 occasions, and were therefore removed prior to community composition analyses. All other species were present in >5% of samples and were retained. ANOSIM results (Table 3) indicated that habitat type was the most influential determinant of species assemblage structure overall (Figure 4). The two habitat categories supported both different types and different relative abundances of species (Figure 5). Creek habitats were dominated by fishes spending their full lifecycle in freshwater, with estuarine migrants rare in these habitats compared to main channel habitats, and the marine vagrants *G. filamentosus* and *S. multifasciata* exclusively found in main channel habitats (Figure 6). Conversely, two wet season spawning species were exclusively found in creek habitats: *Oxyeleotris selheimi* and *Porochilus rendahli*. Dry season spawning species were particularly abundant in creek habitats (Figures 5 and 6).

Time of year had the largest influence on assemblage composition in main channel habitats as well as substantial influence in creek habitats (Table 3). Preceding wet season volume was the most influential parameter associated with assemblage composition in creek habitats, but was not significant in main channel habitats (Table 3). Conversely, time of day did not influence our perception of assemblage composition in creek habitats, but was significant in main channel habitats (Table 3).

3.2 | Species-specific patterns in recruitment and growth

The magnitude of the preceding wet season significantly affected recruitment rates of most species examined; CPUE of recruits of *N. erebi*, *M. spinipes*, and *L. unicolor* (perennial and wet season spawners) increased positively with wet season magnitude, while recruitment CPUE of *C. lentiginosus* and *Ambassis* spp. (dry season spawners) decreased with increasing wet season magnitude (Figure 7). In most cases, several characteristics describing the preceding wet season magnitude had similar fit to the predictor in the best fit model (ΔAICc < 2), typically including early wet season discharge, late wet season discharge, total annual discharge, maximum discharge recorded, and the amount of time during the wet season where stage height exceeded 8 m (i.e. likely period of floodplain inundation), among others (see Table 4, Table S1). Recruitment CPUE of *G. aprion* (late dry season mouth brooder) was unaffected by wet season magnitude, with the null model showing a lower AICc than models with wet season descriptors included as a predictor (Table 4).

The preceding wet season magnitude was also significantly correlated with the size of recruits for *N. erebi*, *M. spinipes*, *L. unicolor*, and *G. aprion*, though not for the shorter-lived dry season spawning *Ambassis* spp. or *C. lentiginosus* (Table 4, Table S2). In all species where wet season magnitude influenced recruit size, smaller recruits were observed in years with larger wet seasons (Figure 7). Unlike recruitment CPUE, each species had a clear best predictor of recruit size, including the number of days since flow ceased for *M. spinipes*, and the number of days during the wet season where stage height was between 2–4, 4–6, or 6–8 m above the cease-to-flow stage height for *G. aprion*, *L. unicolor*, and *N. erebi*, respectively (Table 4), relating to the duration of moderate to high flow during the wet season.

Adult (age 1+) size of *N. erebi*, *L. unicolor*, and *G. aprion* was positively correlated with preceding wet season magnitude, while size

TABLE 1 Teleost, elasmobranch, and crustacean species caught in seine nets in the Fitzroy River between 2004 and 2021.

Scientific name **common name**	**Spawning guild**	**% Caught in creek**	**% Caught in channel**	**Median length (max.) (mm)**	**Number caught (% of total catch)**	**% Of creek catch**	**% Of channel catch**
Porochilus rendahli Rendahl's catfish	Wet season	100%	0%	114 (152)	290 (0.6%)	0.67%	0%
Oxyeleotris selheimi Blackbanded gudgeon	Wet season	100%	0%	66 (88)	10 (0.02%)	0.02%	0%
Pristis pristis Freshwater sawfish	Wet season (diadromous)	100%	0%	1118 (1140)	2 (0.004%)	0.005%	0%
Melanotaenia australis Western rainbowfish	Perennial	98.8%	1.2%	41 (97)	4315 (8.7%)	9.92%	0.78%
Glossamia aprion Mouth almighty	Late dry season	98.7%	1.3%	27 (186)	3952 (7.9%)	9.07%	0.80%
Neosilurus hyrtlii Hyrtl's tandan	Wet season	97.7%	2.3%	108 (186)	768 (1.5%)	1.74%	0.27%
Ambassis sp. 1[a] Fitzroy River glassfish *Ambassis* sp. 2[a] Northwest glassfish	Late dry season	97.6%	2.4%	34 (67)	7454 (15.0%)	16.92%	2.67%
Lates calcarifer Barramundi	Wet season (catadromous)	95.3%	4.7%	285 (762)	64 (0.1%)	0.14%	0.05%
Leiopotherapon unicolor Spangled perch	Wet season	94.5%	5.5%	75 (193)	4151 (8.4%)	9.12%	3.44%
Toxotes kimberleyensis Kimberley archerfish	Wet season	93.4%	6.6%	70 (175)	457 (0.9%)	0.99%	0.45%
Neosilurus ater Black catfish	Wet season	93.1%	6.9%	187 (413)	102 (0.2%)		
Nematolosa erebi Bony Bream	Perennial	90.9%	9.1%	53 (479)	12,271 (24.7%)	25.93%	16.84%
Hannia greenwayi Greenway's grunter	Wet season	90.3%	9.7%	83 (97)	31 (0.06%)	0.07%	0.05%
Stronglyura krefftii Freshwater longtom	Late dry season	89.8%	10.2%	128 (560)	88 (0.2%)	0.18%	0.14%
Megalops cyprinoides Oxeye herring	Estuarine migrant	84.3%	15.7%	175 (335)	51 (0.1%)	0.10%	0.12%
Macrobrachium australiense Common river prawn	Wet season	83.4%	16.6%	NA	169 (0.3%)	0.33%	0.42%
Craterocephalus lentiginosus Prince Regent hardyhead	Dry season	83.1%	16.9%	30 (78)	7100 (14.3%)	13.72%	18.01%

TABLE 1 (Continued)

Scientific name common name	Spawning guild	% Caught in creek	% Caught in channel	Median length (max.) (mm)	Number caught (% of total catch)	% Of creek catch	% Of channel catch
Macrobrachium spinipes Cherabin	Wet season (amphidromous)	76.2%	23.8%	15 (80)	3962 (6.9%)	7.02%	14.15%
Neoarius graeffei Blue catfish	Wet season	49.2%	50.8%	126 (495)	181 (0.4%)	0.21%	1.38%
Glossogobius giuris Flathead goby	Late dry	44.9%	55.1%	26 (196)	2293 (4.6%)	2.39%	18.97%
Anodontiglanis dahli Toothless catfish	Wet season	38.9%	61.1%	161 (298)	18 (0.04%)	0.02%	0.17%
Amniataba percoides Barred grunter	Late wet-early dry season	31.0%	69.0%	25 (115)	1634 (3.3%)	1.18%	16.93%
Hephaestus jenkinsi Western sooty grunter	Wet season	30.4%	69.6%	112 (166)	23 (0.05%)	0.02%	0.24%
Planiliza ordensis Diamond mullet	Estuarine migrant	20.0%	80.0%	183 (211)	15 (0.03%)	0.01%	0.18%
Gerres filamentosus Threadfin silverbiddy	Marine vagrant	0%	100%	110 (161)	95 (0.2%)	0%	1.43%
Selenotoca multifasciata Striped scat	Marine vagrant	0%	100%	91 (117)	162 (0.3%)	0%	2.43%

Note: Each species was assigned to a guild based on spawning time and origin, as either: Perennial spawners, dry season spawners, late dry season spawners, wet season spawners, estuarine migrants, or marine vagrants. Spawning guilds were assigned based on information published by Shelley et al. (2018). Species are listed in order of dominance in floodplain creek habitats vs channel habitats. Length reports total length for fish species, and orbital carapace length for crustaceans (*Macrobrachium spinipes*).

aThe two *Ambassis* species (sp. 1 and sp. 2 in Morgan and Hammer (2018) and Morgan et al. (2004)) were combined for analyses due to unreliable species-level identification in the early years of the study and the Fitzroy River glassfish species being as yet undescribed.

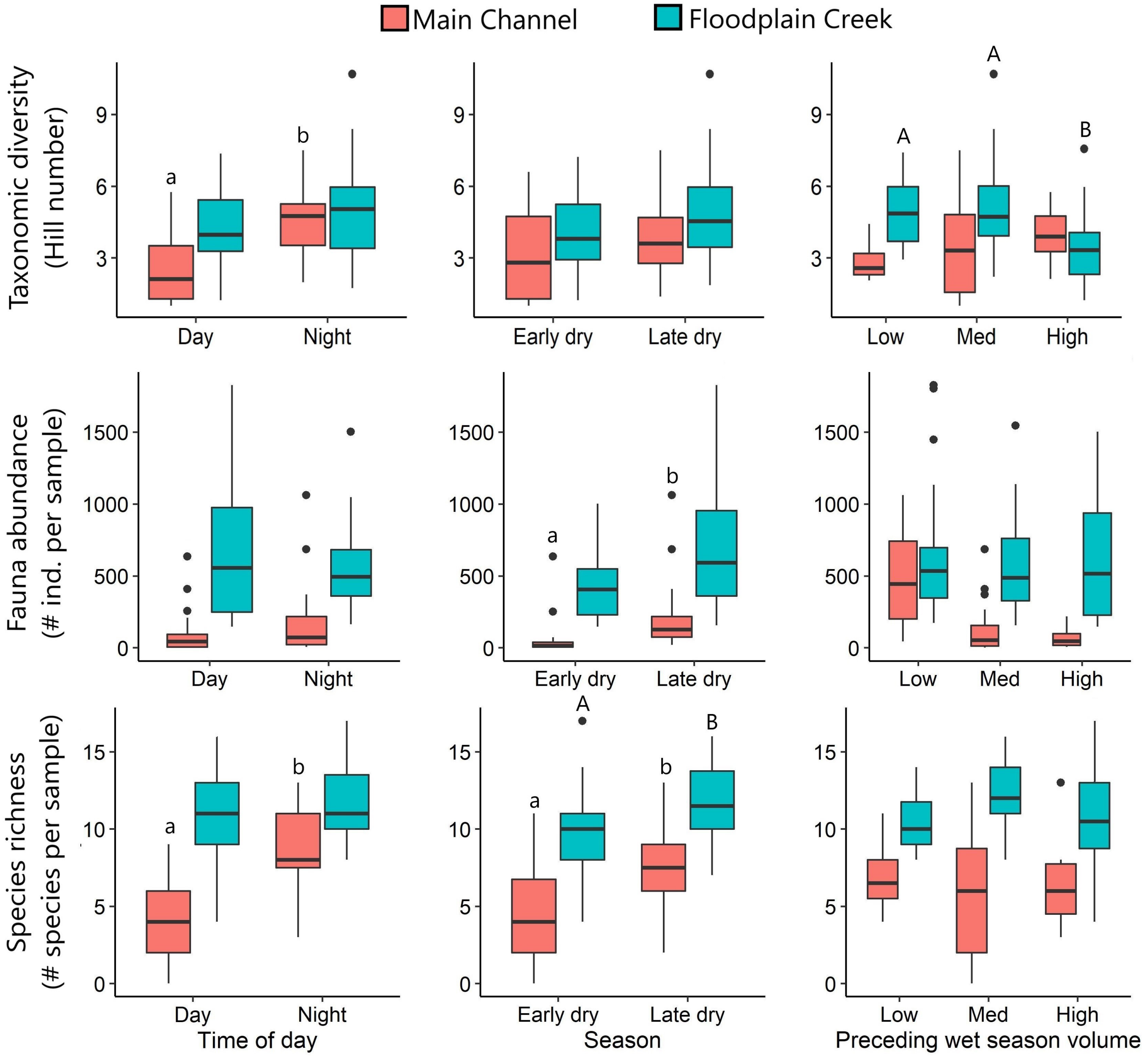


FIGURE 3 Assemblage diversity (Hill number), faunal abundance, and species richness of main channel (green) and floodplain creek (orange) aquatic communities, according to time of day, time of year, and preceding wet season volume. Boxes surround the interquartile range, with central bars showing the median value, whiskers the largest and smallest values within 1.5 interquartile ranges of the median, and points any outliers that exist. Significant differences ($p < .01$) between groups determined through PERMANOVA analyses (see Table 2) are denoted with lowercase letters in main channel habitats and uppercase letters in floodplain creek habitats. Note that several interactions between time of day and other parameters were significant (Table 2) but are not visualised here.

of *C. lentiginosus* adults was negatively correlated with wet season magnitude (Figure 7). The size of adult *Ambassis* spp. and *M. spinipes* was not significantly associated with any wet season descriptors (Table 4, Table S3). Adult size was best described by total wet season discharge for *G. aprion*, the period of low-moderate wet season flow for *N. erebi*, various descriptors relating to the time since flow or period of low-moderate flow for *L. unicolor*, and late wet season discharge and duration of high flow periods for *C. lentiginosus* (Table 4).

4 | DISCUSSION

This study has demonstrated that environmental factors, particularly those related to macrohabitat type and river flow, have substantial effects on the composition and size of fish assemblages in dryland river systems. This is one of few studies to examine how environmental variables affect dryland river communities over extended temporal scales (see Gido et al. (2013)), and our results highlight the value, and in many cases necessity, of observing the

TABLE 2 Permutational analyses of variance (PERMANOVA) model results, showing factors with significant influence on each assemblage descriptor ($p < .01$). Factors are arranged in the order of decreasing significance. A full list of significance of all factors is included in Table S1.

Model data	Assemblage descriptor	Significant fixed predictors	PERMANOVA *p*-value	*F*	df
Main channel and creek data; only years where both sampled	Diversity	Time of day	.001	16.1	1
		Habitat type × time of day	.010	7.2	1
	Abundance	Season	.001	105.9	1
		Habitat type	.001	33.3	1
		Habitat type × season	.001	18.4	1
		Wet season volume	.003	6.6	2
	Species richness	Season	.001	36.3	1
		Time of day	.001	26.8	1
		Habitat type	.001	19.9	1
		Habitat type × time of day	.001	15.3	1
Main channel	Diversity	Time of day	.001	30.8	1
		Time of day × wet season volume	.010	4.3	2
	Abundance	Season	.001	38.3	1
	Species richness	Time of day	.001	31.8	1
		Season	.001	13.8	1
Floodplain creek	Diversity	Wet season volume	.004	8.4	2
	Abundance	NA			
	Species richness	Season	.001	11.6	1
		Time of day × wet season volume	.002	6.4	2

TABLE 3 Analysis of similarity (ANOSIM) results.

Model data	Factor	*p*-value	$\overline{R}$
Main channel and creek, only years where both habitat types were sampled	***Habitat (channel or creek)***	**.0001**	***.53***
	Season (early or late dry)	**.0001**	**.29**
	Time (day or night)	**.003**	**0.04**
	Wet season volume (low, medium, or high)	.31	0.02
Main channel	***Season***	***.0004***	***0.35***
	Time of day	***.0018***	***0.12***
	Wet season volume	.37	0.02
Floodplain creek	***Wet season volume***	***.0001***	***0.33***
	Season	**.0001**	**0.25**
	Time of day	.07	0.03

Note: Significance of factors was assessed using the ANOSIM *p*-values (significant at $p < .01$, significant factors noted in bold), and the relative contribution of factors to community differentiation evaluated with the ANOSIM $\overline{R}$ statistic (0 is no contribution, 1 is high contribution), with the most influential factor for each group noted in italics. The separation in community assemblage associated with each factor is visualised in Figure 3.

influence of environmental factors on biotic communities over long time periods. The data collected here over an 18-year period have captured the variation in faunal assemblages driven by an over 30-fold variation in wet season river flow between years during the study, and presents an understanding of the composition and variation in these assemblages that would be very different to that gained if sampling occurred in only a few years. The degree of inter-annual variation in flow experienced in the Fitzroy River is relatively common in dryland river systems (Puckridge et al., 1998) and is one of the main components making these systems so vulnerable to impacts from changing climate or water resource developments.

4.1 | Effect of habitat type on faunal assemblage composition

Habitat was the most consistent and dominant driver that underpinned our catches in terms of abundance, species richness, and composition of the assemblages throughout two decades (Figure 8). Higher abundance and richness were recorded in floodplain creek habitats compared to the main channel regardless of all other temporal or environmental considerations, and habitat

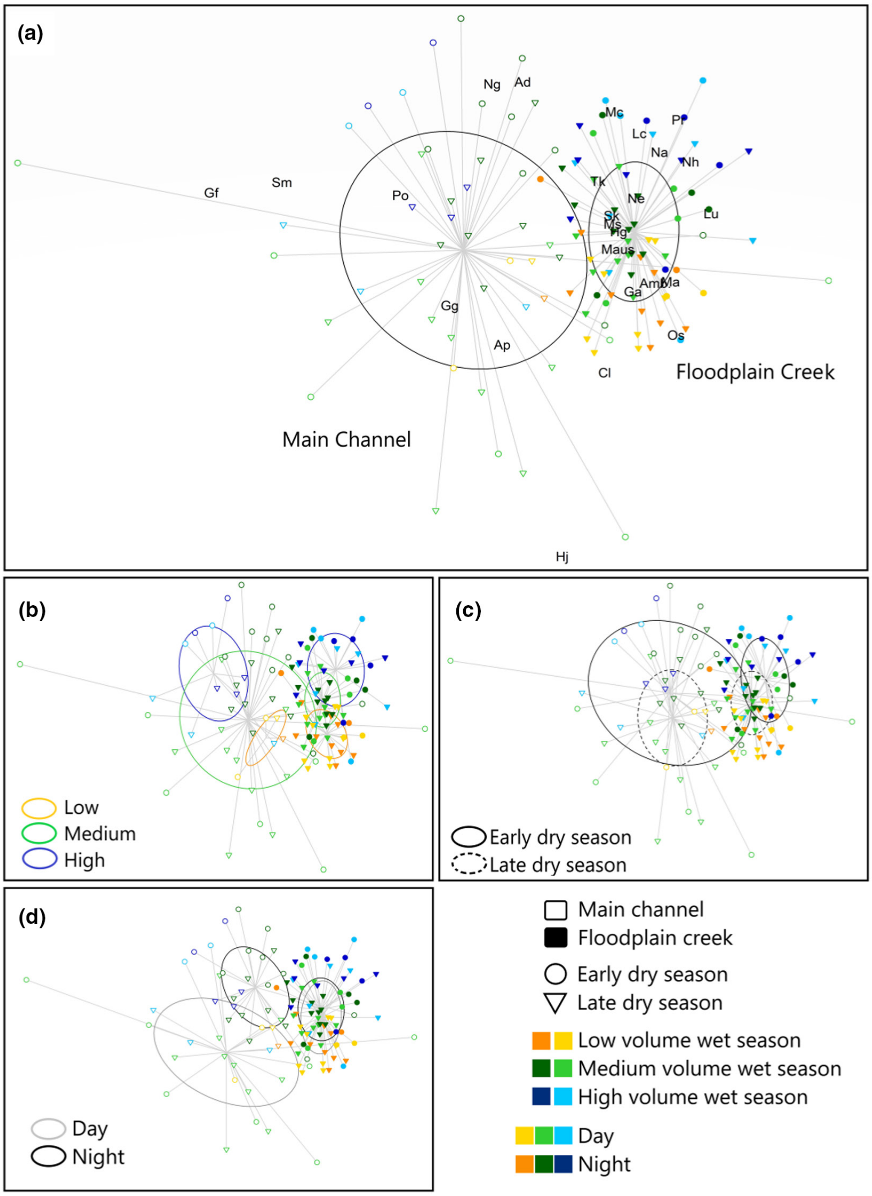


FIGURE 4 Nonmetric multidimensional scaling (NMDS) ordination plots, showing the similarity in community composition of all seine net sampling sets, created from Bray–Curtis dissimilarity matrices. Stress for all plots is 0.24. Ellipses show separation (or lack thereof) in community composition between (a) sampling location (main channel or floodplain creek system), which was the most influential determinant of community composition overall, (b) wet season volume, the most influential determinant of community composition in creek habitats, (c) time of year, and (d) time of day, the most influential determinant of community composition in main channel habitats. In all plots, the left-hand set of ellipses represent main channel communities and the right-hand set creek communities. The placement of abbreviated species names in panel a shows which species were most influential in differentiating or defining nearby communities. Species name abbreviations are as follows: Ad = *Anodontiglanis dahli*; Ap = *Amniataba percoides*; Amb = *Ambassis* spp. (includes *Ambassis* sp. 1 and *Ambassis* sp. 2 in Morgan and Hammer (2018); Cl = *Craterocephalus lentiginosus*; Ga = *Glossamia aprion*; gf = *G. filamentosus*; Hg = *H. greenwayi*; Hj = *H. jenkinsi*; Po = *P. ordensis*; Lc = *L. calcarifer*; Lu = *Leiopotherapon unicolor*; Ma = *Melanotaenia australis*; Maus = *Macrobrachium australiense*; Mc = *Megalops cyprinoides*; Ms = *Macrobrachium spinipes*; Na = *Neosilurus ater*; Ne = *Nematalosa erebi*; Ng = *Neoarius graeffei*; Nh = *Neosilurus hyrtlii*; Os = *Oxyeleotris selheimi*; Pr = *Porochilus rendahli*; Sk = *Strongylura krefftii*; Sm = *Selenotoca multifasciata*; Tk = *Toxotes kimberleyensis*.

exerted the strongest influence on assemblage composition out of all predictive factors. The differences in community composition and abundance between the main channel and floodplain creek are likely driven by several contributing mechanisms. High abundance of fishes in the floodplain creek compared to the main channel can be partially attributed to differences in productivity between habitats; nonchannel floodplain habitats receive high terrestrial nutrient loads from the nearby floodplains during flooding events, and consequently often support higher primary productivity than associated channel habitats (Bunn, Balcombe, et al., 2006; Kobayashi

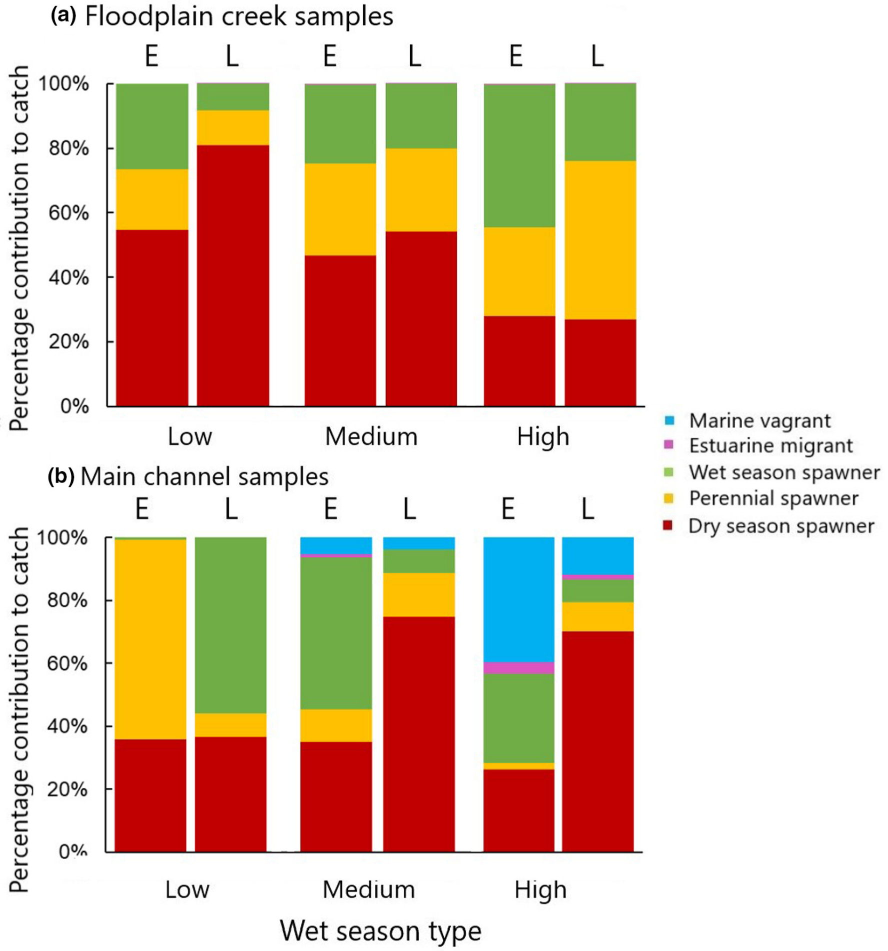


FIGURE 5 Percentage contributions of each guild of fish caught in seine net samples to community assemblages in (a) Uralla Creek and (b) the main channel of the Fitzroy River. Species included in each guild are noted in Table 1. Letters above columns indicate whether samples are from the early (E) or late (L) dry season, and wet season volume is noted on the *x*-axis.

et al., 2013; Molinari et al., 2021; Sheldon et al., 2010), leading to differences in the quantity and types of food available. For example, previous work has estimated that the amount of algal carbon produced in a dryland floodplain habitat in a single day was more than that produced in an equivalent main-channel habitat in 80 years (Bunn, Balcombe, et al., 2006). The proximity of fishes to highly productive resources can be a critical component of fish life history strategy, with fish using ephemeral wet season refuges or breeding areas more likely to emigrate to floodplain-associated habitats as the wet season recedes (Arthington et al., 2005; Balcombe et al., 2012).

On the other hand, the distinct differences in the composition of our catches in creek versus main channel habitats are likely driven by factors additional to basal productivity, including distinct differences in habitat characteristics (e.g. in available structure, visibility, and the presence and capability of top predators; Figure 8; see also Whitty et al., 2017). For example, aquatic macrophytes are a major feature of the floodplain creeks in the lowlands of the Fitzroy catchment but are not as abundant in the main channel (likely due to nutrient and alluvium availability, but also reduced flow-related scouring). Therefore, it follows that macrophyte-associated species would be more successful in the floodplain creek. For example, *Ambassis* spp. and *M. australis* associate with submerged macrophytes for courtship displays, spawning, and shelter, and *G. aprion* use this structure for shelter throughout all life stages and as ambush hunting arenas (Hammer & Gomon, 2018; D.L. Morgan and B.C. Ebner, pers. obs.), which likely explains their abundance in the floodplain creek habitats in the current study but relative rarity in main channel habitats (Figure 8). Previous work has also shown that *L. unicolor* and *Ambassis* spp. are excellent colonisers of ephemeral waterways and can be prolific in floodplain creeks and wetlands, particularly in the absence of some of the larger aquatic predators more typical of main channel habitats (e.g. Kerezsy et al., 2013; Pusey et al., 2004).

In contrast, the main channel typically has a sandy bottom and contains less macrophytes but substantial large woody debris and complex root systems from eucalypts, paperbarks, and notably pandanus trees (*Pandanus* spp.) (Freestone et al., 2021). These structures are also commonly associated with steep banks which incorporate undercuts on the outer bend of pools (and which are far less prevalent in the floodplain wetlands) (Whitty et al., 2017). Additionally, the main channel typically has much higher visibility than the floodplain creek (~1–3 m vs <0.5 m, respectively) and hosts visually centric large-bodied predators including bull sharks and large barramundi, which are much less common in floodplain creeks. These habitat characteristics would lend success to highly mobile and visually acute species adept at avoiding predators, such as *Gerres filamentosus* and *Selenotoca multifasciata* (Ebner & Morgan, 2013; D.L. Morgan and B.C. Ebner, pers. obs.), or species that refuge in complex structure and undercut banks during the day (e.g. catfishes). On the

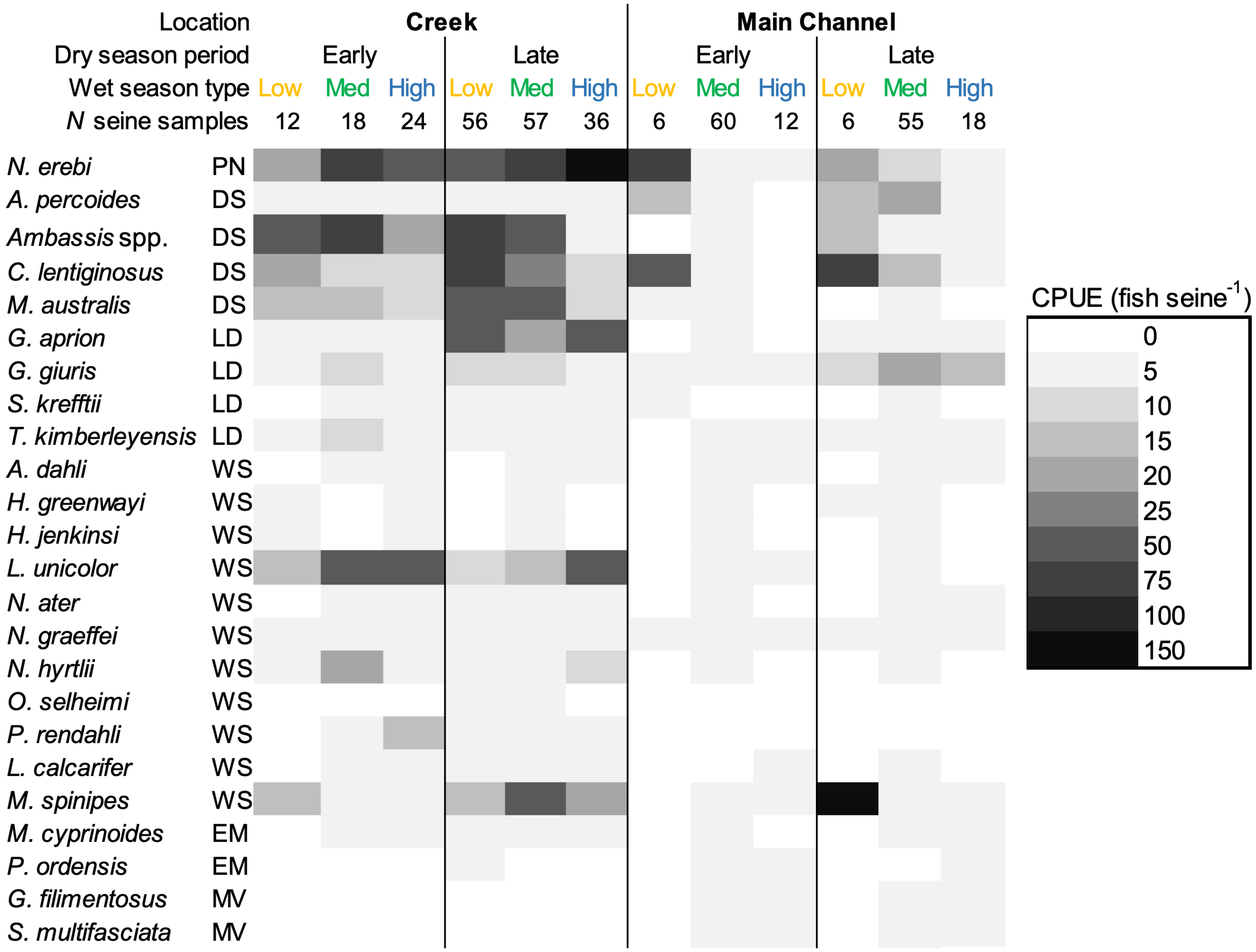


FIGURE 6 Shade plot indicating the catch rates (catch per unit effort, CPUE) of all fish species and cherabin caught in seine net samples, according to location, dry season period, and wet season volume. Darker shades indicate higher CPUE, but note that the shading scale is not linear (see legend), to account for the large difference in catch rates between species and samples. Spawning guilds are indicated to the right of the species name: PN = perennial spawner; DS = dry season spawners; LD = late dry season spawners; WS = wet season spawners; EM = estuarine migrants; MV = marine vagrants.

other hand, the dominant large-bodied predator in floodplain creek systems is the freshwater crocodile (*Crocodylus johnstoni*), which is substantially more abundant in creek systems compared to main channel systems (D. L. Morgan, unpublished data), and hunts at night by sensory ambush rather than visually (Webb et al., 1982).

For a subset of uncommon species, the long-term survey data provided confidence that particular species were more commonly associated with either main channel or floodplain creek habitat (Figure 8). For instance, *P. rendahli* and *O. selheimi* were seldom caught but exclusively associated with floodplain creek habitats. Similarly, two open-water estuarine migrants *G. filamentosus* and *S. multifasciata* specialised exclusively in main channel occupation (Figure 8). It is also notable that the main sampling technique in this study (seine netting) does not detect all species equally (e.g. Ebner & Morgan, 2013). In particular, large-bodied or highly structure-associated species are less likely to be caught in seine nets. As main channel habitats tend to be characterised by substantially more structure than floodplain creek habitats, have greater area and more deep habitats, and tend to host more large-bodied species (see Figure 8), it is possible that this method of survey-biased comparative results by underestimating species richness and abundance of fauna in the main channel. For example, large-bodied species (e.g. bull shark, sawfish, or adult barramundi and fork-tailed catfishes) and highly structure-associated species (e.g. western sooty grunter, *Hephaestus jenkinsi*) are also common in the main channel of the Fitzroy River (Beesley et al., 2020; Morgan et al., 2004; Thorburn et al., 2014) but are not readily detected by seine netting.

Connectivity to the marine environment could also play a role in species distribution, as marine or estuarine-associated species were typically more common or exclusively found in channel habitats. However, given these species already travel over 200 km from the estuary to reach the main channel sampling sites in this study, the additional short trip into the floodplain sites would not be prohibitive, as evidenced by the higher abundance of the estuarine migrant

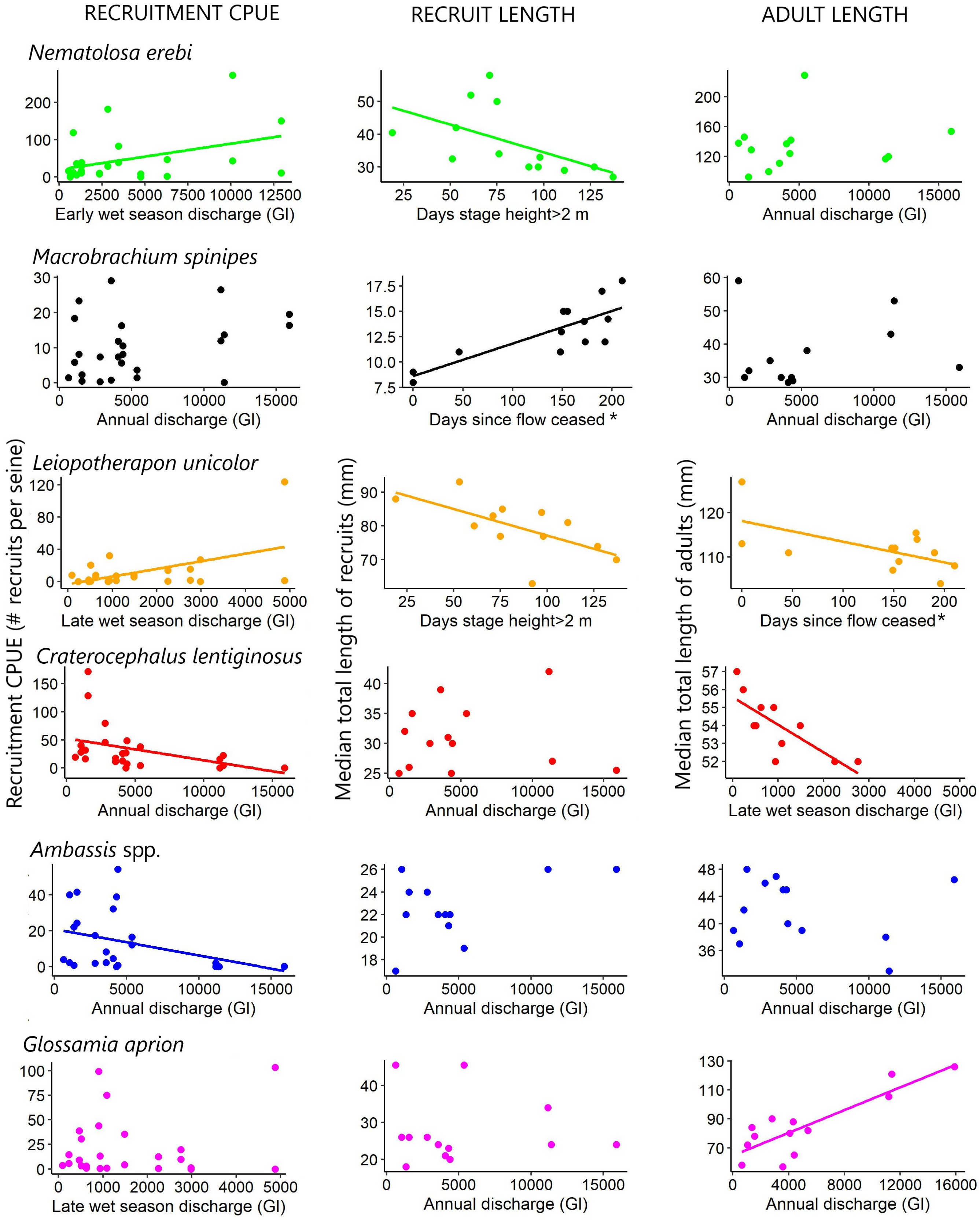


FIGURE 7 Patterns in recruitment rates, size of recruits, and size of adults compared to wet season descriptors for several species of different spawning guilds including *Nematalosa erebi* (perennial spawner), *Macrobrachium spinipes* (amphidromous wet season spawner), *Leiopotherapon unicolor* (wet season spawner), *Craterocephalus lentiginosus* (dry season spawner), *Ambassis* spp. (late dry season spawner), and *Glossamia aprion* (late dry season mouth brooder). Each parameter and species is plotted against the descriptor of the preceding wet season that best described the relationship, with regression lines shown for species where significant relationships were determined. *Note that for most metrics wet season magnitude increases on the *x*-axis from left to right, but in plots where "Days since flow ceased" is the selected metric, wet season magnitude increases from right to left.

TABLE 4 Model selection table for linear models investigating wet season drivers of the recruitment and size of recruits and adults of selected example species.

Response	Species	Wet season characteristic	AICc	df	Log-likelihood	R^2
Recruitment rates	*N. erebi**	Early wet discharge	282.82	3	−137.8	.16
	*M. spinipes**	Early wet discharge	167.45	3	−80.2	.26
	*L. unicolor**	Late wet discharge	230.37	3	−111.6	.26
	*C. lentiginosus**	Total wet discharge	256.81	3	−124.8	.19
	Ambassis spp.*	Maximum discharge	211.50	3	−102.2	.19
	G. aprion	Null	235.02	2	−115.2	.0
Recruit length	*N. erebi**	Days stage height 4–6 m	98.41	3	−44.9	.38
	*M. spinipes**	Days since flow ceased	59.06	3	−25.2	.64
	*L. unicolor**	Days stage height 6–8 m	85.55	3	−39.4	.31
	C. lentiginosus	Null	85.38	2	−40.1	.0
	Ambassis spp.	Null	63.14	2	−28.9	.0
	*G. aprion**	Days stage height 2–4 m	91.36	3	−41.3	.53
Adult length	*N. erebi**	Days stage height 0.9–2 m	112.47	3	−51.9	.44
	M. spinipes	Null	93.65	2	−44.2	.0
	*L. unicolor**	Days since flow ceased	78.22	3	−34.6	.37
	*C. lentiginosus**	Late wet discharge	41.19	3	−15.9	.59
	Ambassis spp.*	Null	81.00	2	−37.9	.0
	G. aprion	Total wet discharge	107.31	3	−49.3	.73

Note: The top model for each species/response (selected by lowest corrected Akaike's information criterion, AICc) is listed, with full model selection tables included in supplementary information as Tables S2–S4. Asterisks show species where the null model was rejected and the relationship deemed significant.

Megalops cyprinoides and high abundance of amphidromous *M. spinipes* in floodplain habitats. It is also notable that the characteristics of off-channel and main channel habitats can change substantially in the downstream dimension relative to the headwaters. For example, Greenway's grunter (*Hannia greenwayi*), which is endemic to the south-west Kimberley, is a headwater specialist that is dominant in tributaries in upstream areas (Morgan et al., 2004; Shelley et al., 2018), but in the lowland pools sampled in this study was more commonly found in floodplain habitats.

4.2 | Effects of flow on community composition, recruitment, and growth

In addition to habitat factors, flow period and wet season volume also substantially influenced aquatic community composition as well as growth and recruitment of different species, trends that were particularly evident within the productive floodplain creek systems. In years with higher magnitude wet seasons, the catches were dominated by *N. erebi* and wet season spawning species, whereas dry season spawning species were more common in drier years. In similar fashion, recruitment of *N. erebi* and wet season spawning species in the floodplain was highest in years with large wet seasons, while recruitment of dry season spawning species showed the opposite pattern. These trends are logical, as in high-volume wet seasons there is greater or prolonged access to floodplain habitats and flowing habitats that wet season spawners rely on for reproduction, resulting in higher recruitment and dominance of these species in assemblages. Conversely, in low-volume wet seasons there is greater access to the still, shallow habitats that most dry season spawners rely on for reproduction, enhancing success of these species. It is interesting that wet season flow did not affect recruitment rates of the dry season mouth brooder *G. aprion*. It is possible that this species is able to spawn and rear eggs under a greater diversity of hydrological conditions, as eggs are protected in the mouth rather than attached to various benthic strata, and therefore spawning or recruitment success in this species may not be as dependent on wet or dry season flow rates.

Flow-related patterns in faunal assemblage characteristics were not as obvious in main channel habitats, which tend to support more consistent habitat characteristics between years. Previous work has similarly shown that dynamics of biotic communities in floodplain-associated habitats are more strongly tied to changes in flow than other types of habitats (e.g. Pander et al., 2019). Rather than changes in the dominant spawning guild of main channel fishes, the major change in faunal assemblages driven by wet season volume in main channel habitats was an increase in marine vagrants and estuarine migrants in years with larger wet seasons, where extended flows provide greater opportunity for these species to migrate from marine or estuarine waters.

In the floodplain creek, wet season magnitude also influenced growth rates of recruits and adults in most species, where regardless

FIGURE 8 Conceptualisation of the fish assemblage in the: (a) main channel and (b) floodplain creek in the Lower Fitzroy River catchment. Seine-net catches demonstrate abundant small-bodied species associated specifically with each of these habitats (1) (e.g. *Amniataba percoides*, *Leiopotherapon unicolor*, *Melanotaenia australis*, *Ambassis* spp., *Glossamia aprion*) or in (2) both habitats (e.g. *Nematalosa erebi*, *Macrobrachium spinipes*). There are also species rarely detected by seine net, but which are more frequently detected in one of the habitats relative to the other (3) (e.g. *Selenotoca multifasciata*, *Gerres filamentosus*, *Porochilus rendahli*, *Oxyeleotris selheimi*, *Hannia greenwayi*) or detected in both habitats to a similar degree (4) (e.g. *A. dahli*). Note: The main channel pools are deep and outside bends comprise large-complex-undercut-banks, including root masses (e.g. *Pandanus* sp.), which provide diurnal shelter for small- and medium-bodied fishes and prawns. Submerged macrophytes are an important structure in the floodplain creek habitat, including for phytophilic spawners (e.g. *M. australis*), as shelter (e.g. *Ambassis* spp.) and/or ambush vantage points (e.g. *G. aprion*). Large-bodied aquatic predators including juvenile bull sharks, barramundi and freshwater crocodiles inhabit the main channel, the floodplain creek habitat contains barramundi and exceptionally high densities of freshwater crocodiles. Illustrated by B. C. Ebner.

of spawning guild, recruit size generally decreased with wet season magnitude while adult size increased, with a few exceptions. The decreased size of recruits observed in years with larger wet seasons may be due to a combination of factors. The most likely of these is that spawning begins and ceases according to levels of flow or pool depth. In years with larger wet season volumes, the wet season flow period typically lasts longer, and as a result recruitment of wet season spawners may extend further into the year and recruitment of dry season spawners may initiate later in the year. The smaller recruits measured in these years may therefore be younger, having been spawned later in the year. It is also possible that in years with larger wet seasons, the productivity booms within the river system (see Bunn, Thoms, et al., 2006) trigger females to produce greater numbers of smaller young (Olofsson et al., 2009), as the survival rates of small larvae or fry could improve under high productivity conditions. Finally, it is also possible that the productivity booms and the larger size of available aquatic habitat or protected shallow floodplain habitats increase survival rates of small recruits, resulting in more small recruits caught and measured in these years compared to drier years.

The higher productivity in years with larger wet season floods may also account for the larger size of adults observed in wetter years for most species. The high productivity booms from large floods are likely to increase food availability and quality, allowing for higher growth rates of fish during the wet season as well as the early dry season. Similar trends have been observed in previous studies which have found larger individuals or better body condition of individuals following larger floods in dryland rivers (Balcombe et al., 2012; Beesley et al., 2021; Lear et al., 2021). It is interesting that the opposite pattern was distinctly observed in *C. lentiginosus*; it is possible that this dry season specialist does not forage well under conditions typically observed in years with larger wet seasons, including higher flow rates and deeper pools, and therefore has reduced growth rates or reduced survival of large individuals during wetter years. It is also notable that there are greater numbers of predators in years with large wet seasons due to high recruitment of freshwater sawfish (Lear et al., 2019) and barramundi (Halliday et al., 2010; Staunton-Smith et al., 2004) in years with high wet season flows, and the greater abundance of estuarine migrant predators including *M. cyprinoides*. These predators are expected to mainly prey upon small freshwater fishes, particularly including *N. erebi* and *C. lentiginosus* (Thorburn et al., 2014). These high rates of predation in wet years may partially account for the low numbers of larger *C. lentiginosus* and the relatively low abundance of *N. erebi* found in the main channel in wet years.

4.3 | Temporal effects on dry season communities

Seasonal timing also influenced the community composition of floodplain creek habitats, and was a major driver of the abundance, richness, and diversity of dry season communities, likely through both temporal relationships to spawning periods and habitat changes tied to seasonality. For example, there is much greater habitat compression in the late dry season compared to the early dry season, which forces all fauna into a much smaller area. This habitat compression could partially account for the higher abundance and richness of communities sampled in the late dry season compared to the early dry season, as all fauna within the pools will be more densely confined to a smaller area in the late dry season, and therefore capture rates are likely to be higher for a given amount of sampling effort. Additionally, the change in habitat characteristics from flowing water to still, shallow pools as the dry season progresses means that by the late dry season, species of all spawning guilds typically have had the opportunity to spawn and replenish populations. This is also likely why season had a pronounced effect on community composition in both the main channel and floodplain habitats. As demonstrated by ANOSIM results, in the early dry season when minor to moderate flow is still present or has just recently ceased, wet season spawners may be expected to be more abundant, while dry season spawners would start to dominate assemblages as the dry season progresses and the water stills. The high abundance and diversity of fish in the late dry season emphasises the importance of maintaining sufficient habitat and water quality as the dry season progresses to ensure survival of the high density of species found in these area-limited habitats.

Time of day did not influence the composition of the faunal assemblages in the floodplain creek, however, it did in the main channel. The increased diversity and species richness estimates derived from night compared to day sampling in the main channel indicates that nocturnal rather than diurnal activity typifies a significant proportion of the small- to medium-bodied fishes in the main channel of the Fitzroy River (e.g. eel-tail catfishes). Notably, some of the highly abundant small- and medium-bodied fishes and *M. spinipes* are most frequently detected at night on the shallow sand flats (see also Whitty et al., 2017), possibly due to increased foraging activity of these species at night in shallow areas, while many of these species are thought to refuge in more structured or deeper habitats during the day. The heightened presence of large visual top predators in the main channel is undoubtedly an important agent shaping the density and diel activity of the small- to medium-bodied fishes and crustaceans. Furthermore, the increased habitat diversity in the main channel compared to the floodplain creek likely facilitates more habitat differentiation between refuging and foraging activity and therefore the greater diel shifts in habitat use observed in the main channel. However, much of the relevant food web literature focusses on day-time sampling or stable isotope-based food web studies, enabling limited comparison with our findings, though similar trends were identified in a North American dryland river (Roach & Winemiller, 2011).

4.4 | Implications for dryland river conservation

The floodplain habitats in this study hosted much greater faunal abundance and species richness than the main channel habitats and are therefore habitats of conservation priority for dryland ecosystems. However, floodplain systems including creeks and wetlands are often at higher risk than channel habitats from water resource developments (Ward et al., 1999), and drying through prolonged drought, water removal, or climate change (Sheldon et al., 2010), and most water monitoring stations and other ecological work have focused on main channel pools because of their more permanent nature (e.g. DWER, 2013, 2019). This introduces a disconnect where floodplain habitats support highly abundant and diverse fish communities in fragile systems, but our understanding of conservation and management needs is more often driven by main channel hydrology.

Additionally, our results have demonstrated that key changes in fish community structure, recruitment rates of certain species, and size of recruits and adults in the Fitzroy River are in many cases directly tied to flow characteristics. These results, in combination with similar findings in previous work supporting the importance of aspects of flow for reproduction, recruitment, and growth (e.g. Balcombe et al., 2006; Bunn & Arthington, 2002; Bunn, Balcombe, et al., 2006; Bunn, Thoms, et al., 2006; King et al., 2019; King et al., 2003; Tyler et al., 2021), produce clear qualitative guidelines for conserving biodiversity in dryland systems: maintaining high biodiversity of freshwater fauna requires maintaining flows of reliable timing on an annual basis (including periods of both high and low or no flow), and variable magnitude on an inter-annual basis to allow “booms” or restoration of populations of different species depending on the year, and therefore persistence of a diverse array of species across years (Saintilan & Overton, 2010).

The Fitzroy River supports extremely high aquatic diversity compared to most other river systems in Western Australia (Morgan et al., 2004), while also hosting several threatened fishes (Morgan et al., 2011). Many of these aquatic species also have considerable cultural significance to Traditional Custodians in the region including the Bunuba, Gooniyandi, Ngarinyin, Nyikina, and Walmajarri people of the Fitzroy River Valley (Morgan et al., 2004). Preserving the biodiversity and ecosystem functioning of this system is therefore of extremely high priority both regionally and globally. The understanding of how habitat, flow, and temporal characteristics affect aquatic communities can inform effective conservation of the unique and productive Fitzroy River ecosystem in the near future, as well as in other dryland ecosystems worldwide facing similar threats from water resource developments and climate change.

AUTHOR CONTRIBUTION

Study management: DM. Data collection: DM, KL, TF, JW, BE. Data analysis and interpretation: KL. Writing: KL, BE, DM, JW.

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CONFLICT OF INTEREST

The authors declare no conflict of interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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