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RESEARCH ARTICLE

Long and lasting: spatial patterns and temporal trends in a fish community responding to landscape-scale hydrological restoration of a coastal freshwater wetland complex

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Abstract

Context Freshwater wetlands, including those in coastal regions, are among the most important, albeit threatened, environments worldwide. Beyond protection, restoration is urgently required to halt the trend of wetland loss. Restoring natural hydrology offers potential to achieve this by landscape-scale rehabilitation of wetland habitat and connectivity for aquatic biodiversity, including freshwater fishes.

Objectives This study assessed the response of a fish community, across pre-, during and post-restoration periods, to hydrological restoration works within an internationally significant coastal freshwater wetland complex with a history of flow diversion and drainage.

Methods Biannual sampling of the fish community occurred across five zones of the wetland complex over the pre-, during and post-restoration periods spanning an eight-year timeframe (2012–19).

Results The study revealed a coastal freshwater wetland harbouring an abundant (179,557 fish caught in this study) and regionally diverse (19 species) fish community, with the catch numerically dominated by native freshwater specialists and diadromous species. Fish community composition and abundance along with species diversity and total abundance responded significantly according to an interaction between zones and the three periods of restoration. Water quality and habitat parameters varied significantly in space and time over the study period, and helps to partially explain the responses of the fish community.

Conclusions This study provides a practical demonstration on the application of landscape-scale restoration of wetland hydrology and associated rehabilitation of aquatic habitat and connectivity to benefit freshwater fishes.

Keywords Coastal freshwater wetland · Coastal lagoon · Freshwater fish · Hydrological restoration · Functional groups · Ramsar

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Introduction

Wetlands are among the most important ecosystems in the world (Dudgeon et al. 2006; Vörösmarty et al. 2010; Batzer and Sharitz 2014) as they provide a myriad of benefits including critical ecological services such as carbon sequestration, filtration of water, nutrient cycling, and a variety of habitats and resources along with basin-wide hydrological services (Mitsch and Gosselink 2015; Wu et al. 2019). It has been estimated that, although only representing ≈3% of the world's surface area, wetlands account for almost half of the global monetary value of ecosystem services (Davidson et al. 2019). Further, wetlands occurring in coastal systems (i.e. at the transition between land and ocean: Kjerfve 1994) deliver 43.1% of the total global monetary value of all wetlands, despite representing less than 10% in terms of area (Davidson et al. 2019). Whilst certain types of coastal wetlands, such as mangroves and coral reefs, are well understood and studied, coastal freshwater wetlands (CFWs or freshwater lagoons sensu Ramsar) have received less attention (Boon 2012; Saintilan et al. 2018).

Coastal freshwater wetlands are distinguished as being transitional and complex ecosystems (Pérez-Ruzafa et al. 2011). They primarily receive freshwater inputs from rainfall, terrestrial runoff, streamflow and groundwater, although some may often experience periods when salinities are elevated (Pérez-Ruzafa et al. 2011, 2019; Herbert et al. 2015). Similarly, there is a continuum of connectivity with nearby ecosystems (i.e. rivers, estuaries and oceans), which can result in the hydrological isolation of CFWs. In this way, CFWs vary dynamically in space and time, and this variation influences habitat suitability for freshwater fishes for which CFWs, like other freshwater wetlands, afford cover, refuge, food resources, and spawning and nursery habitats (Copp 1997; Zeug and Winemiller 2008). Their proximity to marine ecosystems also ensures that CFWs often support critical life stages of diadromous species and, at times, estuarine and marine species. Indeed, CFWs can support a higher fish abundance and biomass compared to nearby riverine, estuarine and marine environments (Gray et al. 2011; de Andrade-Tubino et al. 2020).

Despite their importance to biodiversity and ecosystem services, wetlands are under critical threat (Strayer and Dudgeon 2010; Davidson 2014; Kingsford et al. 2016). It is estimated that 87% of global wetlands have been lost over the past three centuries (70% decline since the year 1900), with the trend in wetland extent and condition continuing to decline (Davidson 2014; Davidson et al. 2018). Coastal lagoons, including CFWs, are particularly at risk given the overlap with global human populations, with the most severe impacts being salinisation and sea-level rise, human development and pollution (cf. eutrophication), as well as hydrological alteration (Barbier et al. 2011; van Dijk et al. 2015; Kingsford et al. 2016). These multiple pressures on coastal lagoons threaten ecological integrity, with wetland-dependent species, including freshwater fishes, being detrimentally impacted. It is therefore unsurprising that one quarter of all wetland-dependent species (including those inhabiting coastal) have been assessed globally as threatened with extinction (Gardner and Finlayson 2018).

Although the consequences of impacts such as sea-level rise have been investigated (Carrasco et al. 2016; Runting et al. 2017), the influences of hydrological alteration in coastal wetlands are comparatively less studied. As with other wetland types, hydrological alterations, such as artificial drainage, diversion of flows, disconnection of tidal influence or detrimental changes in groundwater conditions will likely reduce or eliminate suitable habitat and resources thereby disrupting connectivity across the broader ecosystem. For this reason, hydrological restoration of coastal wetlands presents as an opportunity to reinstate landscape processes and connectivity to aid biodiversity recovery. Specific examples include the reinstatement of tidal influence with coupled benefits to vegetation, fish and waterbird communities in estuarine coastal lagoons (Howe et al. 2010; Boys and Pease 2017; Perillo et al. 2018) and the rehabilitation of CFWs through reinstatement of natural flowpaths and inundation regimes (Boon 2011; Raulings et al. 2011). Ensuring restoration of broader connectivity of CFWs to adjacent ecosystems such as estuaries or even other coastal wetlands is a key strategy in supporting the dispersal of species (especially those with limited dispersal capabilities) and therefore their regional recovery (Gimmi et al. 2011; Verheijen et al. 2018). In acknowledging the dynamism and complexity of CFWs, these landscape-scale restoration efforts must account for multiple influences on hydrology and the nature of hydrological impact (Hua et al. 2016; Zhao et al. 2016).

Hydrological restoration works have been recently implemented, triggering landscape-scale changes to inundation patterns and flows, across the Long Swamp Wetland Complex (hereafter, Long Swamp) – a large

(≈1100 ha) coastal freshwater wetland system situated within the internationally recognised Glenelg Estuary and Discovery Bay Ramsar site in southwest Victoria, Australia (Fig. 1; Bachmann 2020; DELWP 2017). Prior to this time, for a period of up to eight decades, the combined effects of the diversion of flows through drainage (via two artificial outlets), and the interception of groundwater recharge (through adjacent land-use change) led to a reduction in the duration, extent and frequency of wetland inundation and flows, in turn triggering a process of drying and terrestrialisation across the wetland complex (Bachmann et al. 2018; Bachmann 2020). Guided by the observed impacts of the natural earlier closure of one of the artificial outlets (at White Sands), trial structures were later constructed over 2014 to 2015 to regulate and ultimately block the other artificial outlet (at Nobles Rocks) (Fig. 1). As has been utilised elsewhere, applied historical ecology (e.g. Grossinger et al. 2007; Beller et al. 2016) provided historical context on the ecology and hydrology of Long Swamp to guide the restoration works and identify clear objectives (Bachmann 2020). This restoration work, motivated by the local community and driven by a not-for-profit organisation collaborating with a range of stakeholders (i.e. government agencies, Traditional Owners, local community), aimed to increase wetland inundation and facilitate flows across the wetland complex towards the natural outlet (Bachmann 2020). In spite of the impacts associated with past hydrological change, up until that time the wetland complex continued to maintain a range of freshwater habitats, which are known to support regionally important freshwater fishes (DELWP 2017). It was therefore critical to consider how freshwater fishes would respond to the restoration process and its impacts upon the hydrology of the wetland complex.

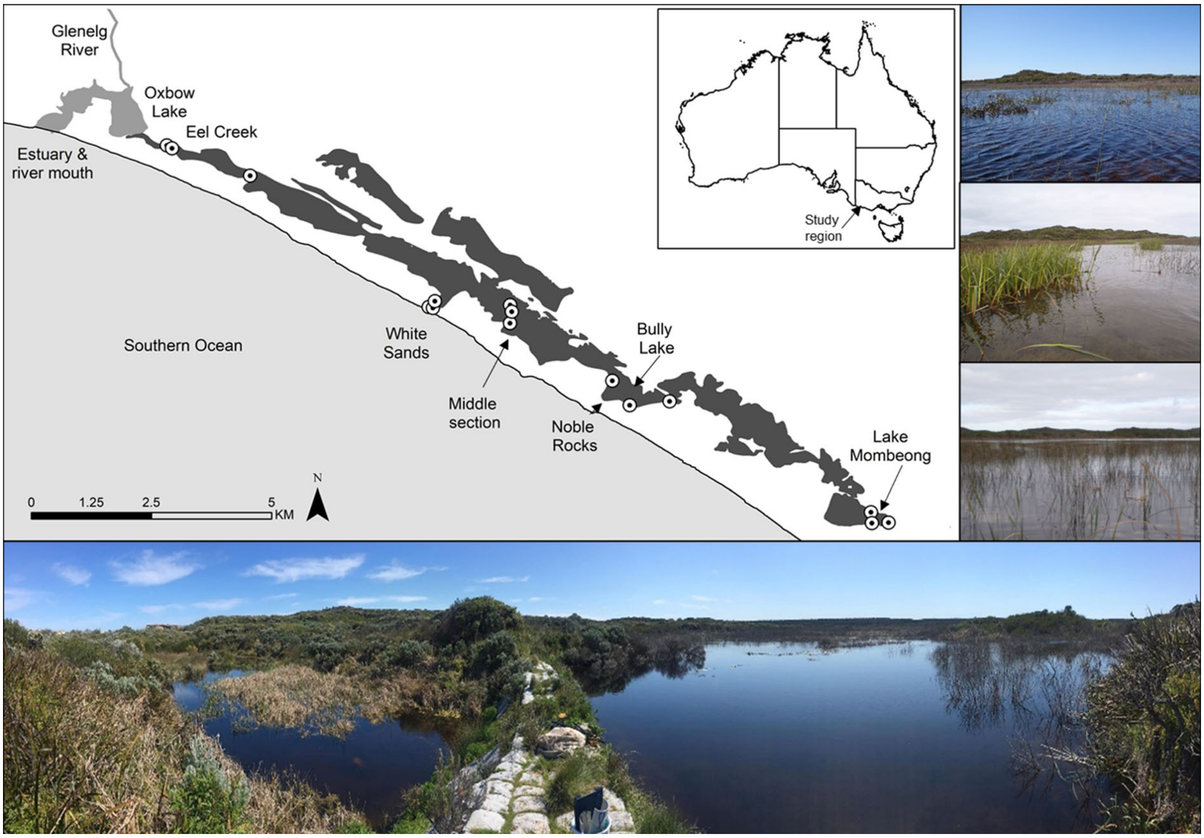

Fig. 1 Location of the 15 sampling sites (dots) across the Long Swamp Wetland Complex (dark grey) in the lower reaches of the Glenelg River Basin (light grey), southern Australia. Also shown is representative habitat (right three panels) and restored Bully Lake behind the final Nobles Rocks restoration structure (bottom panel)

This study aimed to assess changes in the fish community abundance and composition of Long Swamp in response to rehabilitation through large-scale restoration of hydrological drivers. This was explored through biannual sampling of the fish community across five zones during three periods defined as 'pre-', 'during' and 'post-'restoration. It was predicted that: (i) the freshwater fish composition would be diverse in the pre-restoration period, and (ii) substantial changes in the fish community would be experienced both during restoration, due to declines in diadromous species (resulting from the deliberate closure of the artificial outlet), and post-restoration, when greater connectivity and habitat availability would see a shift towards a more homogenous fish community. The outcomes of this study are expected to provide guidance for practitioners planning and implementing landscape-scale wetland rehabilitation projects in other regions.

Materials and methods

Study location and restoration summary

Long Swamp consists of an extended ($\approx$ 15 km) and generally narrow (but in some areas up to 2–3 km wide) series of freshwater wetlands, impounded by an adjacent coastal sand dune system, in the lower reaches of the Glenelg River Basin (Fig. 1). Combined archaeological and sedimentary data indicate that the wetland complex was mostly estuarine prior to the ocean stabilising nearer to its current elevation a few thousand years ago at which time it transitioned to a predominantly freshwater system (Head 1987, 1988). The wetland complex consists of the permanent, groundwater-fed freshwater Lake Momboeng in the east. Discharges from the lake slowly flow in a westerly direction along an ill-defined water course known as Eel Creek, which is interspersed by freshwater wetlands such as Bully Lake near Nobles Rocks, before reaching the defined lower section of Eel Creek and outflowing into Oxbow Lake and the Glenelg River estuary (Reynolds 2007). The groundwater spring discharges from Lake Momboeng are supplemented along the entire length of the wetland complex by localised rainfall and additional groundwater discharges from the shallow, unconfined tertiary limestone aquifer in the form of springs, seeps and direct groundwater expression (Bachmann 2020). The estuary, Oxbow Lake and (to some extent) Eel Creek are under tidal influence, but the river mouth intermittently closes through a combination of low flows from the Glenelg River, as well as sand accumulation driven by wind and ocean swells (Fig. 2).

Long Swamp has a complex history of hydrological alteration, as the two artificial outlets, present until recently, were established through the coastal dune at White Sands and Nobles Rocks during the 1930s and 1940s (Bachmann 2020). The White Sands artificial outlet naturally closed around 2004–05, whereas more recent regulation and closure of the Nobles Rocks outlet occurred sequentially from 2014 (across three stages) as the focal location for planned hydrological restoration works. The restoration process was informed by a detailed analysis of site history, elevation data (based on Light Detection and Ranging: LiDAR), biological records and predictive inundation modelling, as well as detailed communication and negotiation with Gunditjmara Traditional Owners, the local community and relevant government agencies. Initially, over autumn and winter 2014, temporary geo-fabric sandbag weirs were installed to commence the process of regulating outflows, with the third stage of restoration involving the construction of a more substantial geo-fabric sandbag trial structure during autumn and spring 2015, to effect complete closure of the outlet (Bachmann 2020).

By mid-2015, increases in water level behind the restoration structure resulted in Bully Lake being reinstated as a permanently inundated wetland (Fig. 2). The associated expansion of wetland habitats surrounding Bully Lake led to vegetation shifts up the elevation gradient in response to the change in hydrological regime, and all surface flows have since been re-directed along the original westerly flow path towards the Glenelg River. This has increased the trend in water availability (e.g. greater maximum water level, reduced periods of drying) across wetlands throughout Long Swamp proper, although ephemerality remains a feature in some zones with lower groundwater contributions (e.g. White Sands: Fig. 2). The shallow groundwater aquifer in the vicinity of Nobles Rocks is now being buffered (i.e. the local water table has risen permanently) because of the restoration works to close the outlet, and this change is directly linked to the ongoing retention of

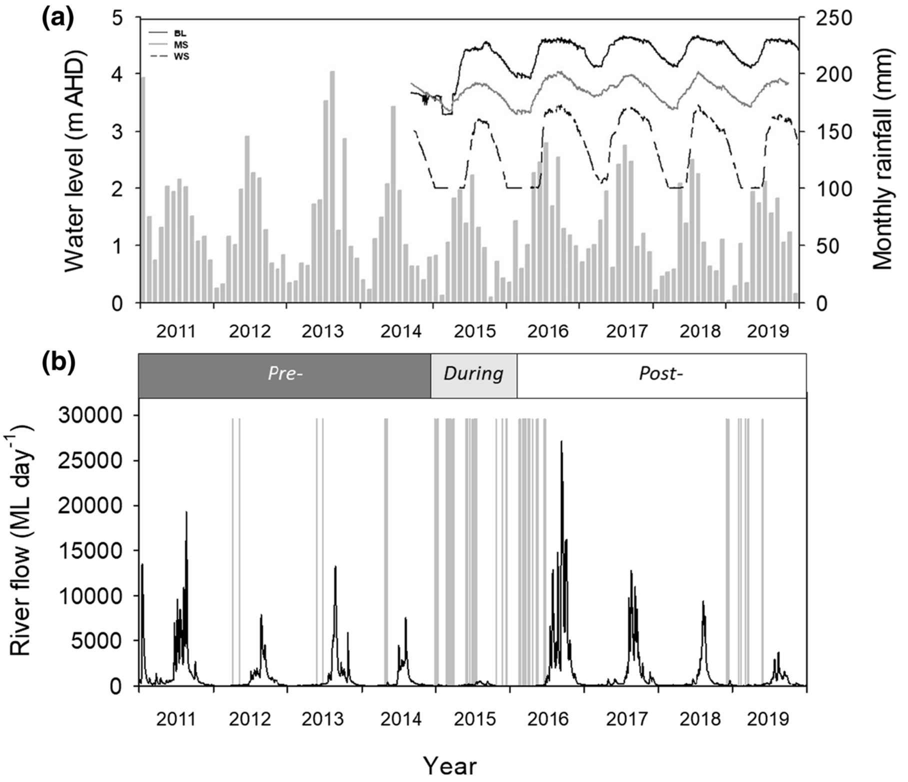

Fig. 2 Relevant hydrological data across the study area: **a** water level (m, Australian Height Datum: AHD) in Long Swamp and mean monthly rainfall (Nelson, station number 090059), and **b** mean daily river flow (ML day^{-1}, black line) and status of river mouth (closed = grey bars) for the lower reaches of the Glenelg River Basin. Water level data provided by in situ loggers (HOBO U20); mean monthly rainfall (Nelson, station number 090059) obtained from the Australian Bureau of Meteorology; mean daily river flow (Glenelg River at Dartmoor, station number 238206) provided by the Victorian Department of Environment, Land, Water and Planning; mouth opening status courtesy of the Estuary Entrance Management Support System, Glenelg Hopkins Catchment Management Authority

freshwater in Bully Lake (Bachmann et al. 2018 and Fig. 2).

Based on when restoration structures were demonstrated to be influencing the hydrology of Bully Lake and the broader movement of freshwater flows within Long Swamp, the study period was temporally segregated into three phases: pre- (before summer 2014–15), during (summer 2014–15 to summer 2015–16) and post-restoration (summer 2015–16 onwards).

Sampling design and protocol

Sampling focused on five zones across Long Swamp: Eel Creek (EC), White Sands (WS), the Middle Section (MS), Bully Lake (BL) behind Nobles Rocks structure, and Lake Momboeng (LM) (the last four zones being part of Long Swamp proper: Fig. 1). Sampling occurred biannually (autumn and spring) in the pre- (three occasions: spring 2012, autumn and spring 2014), during (twice: autumn and spring 2015), and post-restoration periods (eight occasions: autumn and spring 2016, autumn and spring 2017, autumn and spring 2018, autumn and spring 2019). In each zone, three sites were established, which were sampled using four single-wing (3 m long wing, 4 mm mesh, 0.6 m D-shaped entrance) fyke nets deployed overnight amongst all prevailing habitat on each occasion, except when water availability or depth limited the sites that could be sampled or the number of nets that could be deployed (Table 1).

All sampled fish were identified to species (McDowall 1996; Gomon et al. 2008), with native species returned alive to the water at the point of capture and alien species euthanased as per requirements of research permits. Each sampled fish species was then

Table 1 Spatial and temporal sampling for fish communities across the Long Swamp Wetland Complex in relation to years and over the three periods (Pre-, During, Post-) of hydrological restoration

Zone	Pre-			During		Post-							
	Spring 2012	Autumn 2014	Spring 2014	Autumn 2015	Spring 2015	Autumn 2016	Spring 2016	Autumn 2017	Spring 2017	Autumn 2018	Spring 2018	Autumn 2019	Spring 2019
Eel Creek	1	3	3	3	2	3	3	3	3	3	3	2	3
White Sands	3	3	3	Ns	3	3	3	1	3	ns	3	ns	3
Middle section	1	2	2	3	3	3	3	3	3	3	3	ns	3
Bully Lake	1	1	1	2	3	3	3	3	3	3	3	3	3
Lake Momboeng	3	3	3	3	3	3	3	3	3	3	3	3	3

The spatial component consists of the number of sites (or whether a site was dry) within each zone; the temporal component consists of the biannual sampling grouped according to restoration period

Sites that were dry or too shallow were not sampled (indicated as ‘ns’)

ascribed to the freshwater (generalist and specialist), diadromous, and estuarine and marine (i.e. solely estuarine, estuarine and marine, and estuarine-marine opportunist) functional groups (adapted from Potter et al. 2015; Whiterod et al. 2015).

At each site and during all sampling events, dissolved oxygen concentration (DO: $\mathrm{mgL^{-1}}$), electrical conductivity (EC: $\mu\mathrm{Scm^{-1}}$), pH, and water temperature (°C) were recorded as water quality parameters using a YSI 556 multiprobe (Yellow Springs Institute, Yellow Springs, Ohio, USA). Water depth (m) and aquatic habitat cover (estimated percentage of aquatic plants covering the site) were also recorded as habitat parameters.

Statistical analyses

Fish catch data were converted to catch-per-unit-effort (CPUE: fish $\mathrm{net^{-1}\ h^{-1}}$) abundance by dividing fyke net catch data by the soak time in each fyke net. This estimate of CPUE abundance was achieved for each species in each fyke net at each site during each sampling event and used in subsequent analyses. Total CPUE abundance (i.e. summed over all species) and species diversity were also computed.

Hypotheses relating to spatial and temporal variability were investigated using a nested-factorial design. Differences in total CPUE abundance and diversity were analysed by permutational ANOVA, whereas differences in water quality and habitat parameters (hereafter, ‘environmental data’) and in CPUE abundance for functional groups and species were analysed by permutational MANOVA. The design consisted of the fixed factor Period (pre-, during, post-), the random factor Year (2012, 2014–2019) nested within Period, the random factor Season (Spring, Autumn) nested within Year and Period, and the fixed factor Zone (BL, EC, LM, MS, WS) crossed with the above three factors (noting that for the environmental data, BL was excluded from analysis due to that zone being dry in autumn 2014). Analyses were carried out in PRIMER v7, with CPUE abundance data $\sqrt{}$-transformed, diversity data normalised and EC (cf. environmental data) log-transformed, using a Bray–Curtis dissimilarity measure for CPUE abundance and a Euclidean dissimilarity measure for diversity and environmental data. Probability values were obtained with 9999 permutations of the residuals under a reduced model (because of the nested design: (Anderson and Robinson 2001)) with the significance level set at $\alpha = 0.05$, including that for a posteriori pairwise comparisons. Patterns of variation in multivariate composition and abundance revealed by PERMANOVA for environmental data, functional groups and species were visualised by canonical discriminant analysis of the principal coordinates (CAP) plots (Anderson and Willis 2003).

Spatial and temporal relationships between fish and environment were further analysed using STATICO (Thioulouse et al. 2004) – a multivariate statistical method for the analysis of series of paired ecological tables. For both the most abundant (hence, 'representative') functional groups and species ($\sqrt{}$-transformed), three tables were produced with the zones as replicates and grouped according to period. Similarly, three environmental tables were produced that included the four water quality and two habitat descriptors. Following the three-step STATICO strategy: (i) a PCA was performed on each pair of functional groups/species and environmental tables, (ii) each pair was linked through co-inertia analysis producing a cross-table, and (iii) partial triadic analysis was used to analyse the series of cross-tables.

Temporal trends in abundance for (the representative) functional groups and species were investigated by min–max autocorrelation factor analysis (MAFA: Zuur et al. 2007) and by dynamic factor analysis (DFA: Zuur et al. 2003a). Using MAFA, the main trends in the data are extracted by producing axes that have maximum autocorrelation with time lag k. The first MAF axis represents the main trend or underlying pattern in the data associated with the highest autocorrelation at lag 1, the second axis has the second highest autocorrelation at lag 2, and so forth. Cross-correlations (or canonical correlations) between variables and trends are then computed and tested for significance. DFA is another multivariate technique used to estimate underlying common trends and effects of explanatory variables in multiple time series. DFA applies a dimension reduction whereby multiple time series are modelled as a linear combination of common trends, explanatory variables, a constant, and a noise component. Differences between MAFA and DFA are: (i) in MAFA the trends are independent and the first MAF trend is the most important one, unlike DFA in which the order of the trends is irrelevant; (ii) explanatory variables can be incorporated into DFA models, whereas in MAFA only correlations between axes and explanatory variables can be calculated; and (iii) DFA allows for comparison of alternative models. Because of their complementary features, MAFA and DFA are often used in conjunction in ecological studies (e.g. Erzini et al. 2005; Ligas et al. 2011; Vilizzi 2012). With both MAFA and DFA, the number of time points (i.e. the seven years of sampling in this study) is constrained to be larger than the number of variables, so that the five fish guilds and the species that were recorded in the highest abundance were retained for analysis. Prior to analysis, CPUE abundance and environmental data were $\sqrt{}$-transformed and centred. For MAFA, the first two MAF axes were estimated and canonical correlations between the individual variables and the two MAF axes tested for significance ($\alpha = 0.05$). For DFA, a series of 18 models was fitted, ranging from the simplest (one common trend plus noise) to the most complex (one common trend, all six explanatory variables for the environmental data, plus noise) and with a diagonal covariance matrix (noting that no convergence was achieved with either two common trends or a symmetric positive-definite matrix: see Vilizzi 2012). Akaike's information criterion (AIC) was then used as a measure of goodness of fit to compare models and select the one providing the lowest AIC value (Zuur et al. 2003b). Analyses were carried out in Brodgar 2.7.5 statistical package (Highland Statistics Ltd, Newburgh, UK) following Woillez et al. (2009).

Results

Catch summary

In total, 179,557 fish across 19 species (17 native, two alien), representing seven functional groups, were caught across Long Swamp (Table 2). Based on raw abundance, the freshwater specialist southern pygmy perch *Nannoperca australis* was by far the most abundant, followed by diadromous common galaxias *Galaxias maculatus*, the alien freshwater generalist eastern gambusia *Gambusia holbrooki*, and the estuarine smallmouth hardyhead *Atherinosoma microstoma* and Yarra pygmy perch *Nannoperca obscura*, and with the remaining 14 species accounting for less than 2% of the total catch. Amongst the less commonly encountered species were the estuarine

Table 2 Fish species sampled across Long Swamp, with indication of abundance (n = absolute; % = relative) across five zones (EC = Eel Creek; WS = White Sands; MS = Middle Section; BL = Bully Lake; LM = Lake Momboeng: see Fig. 1) and three restoration periods (Pre-, During and Post-: see Table 1)

Species			IUCN status	Functional group	Abundance		Zone					Restoration period		
Scientific name	Common name	Code			*n*	%	EC	WS	MS	BL	LM	Pre-	During	Post-
Freshwater														
Carassius auratus	Goldfish	Car.aur	–	AFG	1	< 0.01	100.00	–	–	–	–	–	–	< 0.01
Gadopsis marmoratus	River blackfish	Gad.mar	LC	FS	240	0.13	–	–	–	–	100.00	0.12	0.12	0.15
Galaxiella toourtkoourt	Little galaxias	Gal.too	VU	FS	1488	0.83	0.47	53.70	0.27	45.50	0.07	2.53	0.04	0.88
Gambusia holbrooki	Eastern gambusia	Gam.hol	–	AFG	21,974	12.24	0.69	21.79	34.36	43.16	–	3.21	2.49	24.97
Nannoperca australis	Southern pygmy perch	Nan.aus	NT	FS	98,458	54.83	0.47	78.64	8.71	11.44	0.74	51.00	76.14	36.56
Nannoperca obscura	Yarra pygmy perch	Nan.obs	EN	FS	4684	2.61	0.23	14.84	58.30	3.69	22.93	2.59	1.30	3.84
Philypnodon grandiceps	Flathead gudgeon	Phi.gra	LC	FG	353	0.20	99.43	0.57	–	–	–	0.28	0.08	0.27
Retropinna semoni	Australian smelt	Ret.sem	LC	FG	950	0.48	–	–	–	–	100.00	0.16	0.28	0.91
Diadromous														
Anguilla australis	Southern shortfin eel	Ang.aus	NT	DI	65	0.04	50.77	–	12.31	1.54	35.38	0.06	0.01	0.05
Galaxias maculatus	Common galaxias	Gal.mac	LC	DI	31,348	17.46	4.76	1.23	3.44	3.79	86.79	27.70	10.46	19.82
Pseudaphritis urvillii	Tupong	Pse.urv	LC	DI	61	0.03	98.36	–	–	1.64	–	0.03	–	0.06
Estuarine and marine														
Acanthopagrus butcheri	Black bream	Aca.but	LC	SE	1	< 0.01	100.00	–	–	–	–	–	–	< 0.01
Afurcagobius tamarensis	Tamar River goby	Afu.tam	–	SE	10	< 0.01	30.00	–	–	–	70.00	0.03	–	
Aldrichetta forsteri	Yelloweye mullet	Ald.for	LC	EM	1	< 0.01	100.00	–	–	–	–	–	–	< 0.01
Ammotretis rostratus	Longsnout flounder	Amm.ros	–	EMO	1	< 0.01	100.00	–	–	–	–	–	–	< 0.01
Atherinosoma microstoma	Smallmouth hardyhead	Ath.mic	–	SE	19,815	11.04	0.18	0.03	69.32	–	30.47	12.27	9.06	12.37
Mugil cephalus	Sea mullet	Mug.cep	LC	EMO	4	< 0.01	100.00	–	–	–	–	< 0.01	–	< 0.01
Pseudogobius olorum	Bluespot goby	Pse.olo	–	SE	46	0.03	95.65	–	–	–	4.35	0.01	0.01	0.04

Table 2 continued

Species			IUCN status	Functional group	Abundance		Zone					Restoration period		
Scientific name	Common name	Code			*n*	%	EC	WS	MS	BL	LM	Pre-	During	Post-
Tasmanogobius lasti	Lagoon goby	Tas.las	–	SE	57	0.03	14.04	–	–	–	85.96	< 0.01	0.01	0.06

IUCN status: EN Endangered, *LC* Least Concern, *NT* Near Threatened, *VU* Vulnerable (based on IUCN Red List for Threatened Species: IUCN 2020)

Functional groups: *AFG* Alien freshwater generalist, *DI* Diadromous, *EM* Estuarine and marine, *EMO* Estuarine-marine opportunist, *FG* Freshwater generalist, *FS* Freshwater specialist, *SE* Solely estuarine (adapted from Potter et al. 2015; Whiterod et al. 2015)

and marine black bream *Acanthopagrus butcheri* and yelloweye mullet *Aldrichetta forsteri*, the estuarine-marine opportunist longsnout flounder *Ammotretis rostratus*, and the alien freshwater generalist goldfish *Carassius auratus* (all sampled as single individuals). Other species included the freshwater generalist flathead gudgeon *Philypnodon grandiceps*, the diadromous southern shortfin eel *Anguilla australis* and tupong *Pseudaphritis urvillii*, and the estuarine and marine Tamar River goby *Afurcagobius tamarensis*, western bluespot goby *Pseudogobius olorum* and lagoon goby *Tasmanogobius lasti*. Spatially, only four species (i.e. the freshwater specialists little galaxias *Galaxiella toourtkoourt, N. australis* and *N. obscura*, and *G. maculatus*) occurred across all zones, whereas seven species (i.e. the freshwater specialist river blackfish *Gadopsis marmoratus*, the freshwater generalists Australian smelt *Retropinna semoni* and *C. auratus*, and the four estuarine and marine species *A. butcheri*, *A. forsteri*, *A. rostratus* and sea mullet *Mugil cephalus*) were recorded in only one zone (Table 2). Temporally, most species were recorded across each restoration period with *N. australis* being the most abundant in each of the periods. At LM and MS, a higher number of species was consistently observed compared to the other zones.

Spatial and temporal variation

For total fish CPUE abundance, there were statistically significant differences among restoration periods depending on zone (Period × Zone interaction: Table 3, Fig. 3a). In the pre-restoration period, there was only a difference between EC and WS, where the lowest and highest fish abundances, respectively, amongst the zones were recorded. During the restoration period, WS was by far the zone with the highest fish abundance and differed significantly from all other zones. In the post-restoration period, fish abundance at EC was significantly lower compared to the other zones. Based on the seven most abundant species: pre-restoration, *N. australis* was especially abundant at WS and *G. maculatus* at LM (Fig. 3b); during restoration, *N. australis* was the most abundant at WS (Fig. 3c); post-restoration, *G. maculatus* was again the most abundant species at LM, whereas at EC most of the species were caught in lower abundance (Fig. 3d).

Table 3 Permutational ANOVA for spatial and temporal variability in total CPUE abundance (fish net^{-1} h^{-1}) of the fish sampled across the Long Swamp Wetland Complex

Source of variation	df	MS	$F^{\#}/t^{\#}$	$P^{\#}$
Period	2	125.34	3.77	0.110
Zone	4	241.89	35.34	**< 0.001**
Period × Zone	8	62.69	8.94	**0.004**
Pre-				
BL *vs* EC	1		1.44	0.388
BL *vs* LM	1		3.90	0.160
BL *vs* MS	1		1.14	0.463
BL *vs* WS	1		2.55	0.236
EC *vs* LM	1		2.08	0.283
EC *vs* MS	1		1.28	0.426
EC *vs* WS	1		30.87	**0.019**
LM *vs* MS	1		0.01	0.994
LM *vs* WS	1		1.02	0.490
MS *vs* WS	1		0.65	0.634
During				
BL *vs* EC	1		6.55	0.093
BL *vs* LM	1		6.24	0.102
BL *vs* MS	1		2.71	0.226
BL *vs* WS	1		4.45	**< 0.001**
EC *vs* LM	1		6.35	0.107
EC *vs* MS	1		3.34	0.177
EC *vs* WS	1		4.55	**< 0.001**
LM *vs* MS	1		0.58	0.667
LM *vs* WS	1		3.57	**0.002**
MS *vs* WS	1		3.07	**0.005**
Post				
BL *vs* EC	1		4.70	**0.018**
BL *vs* LM	1		0.23	0.838
BL *vs* MS	1		0.66	0.564
BL *vs* WS	1		1.60	0.186
EC *vs* LM	1		3.45	**0.046**
EC *vs* MS	1		4.13	**0.022**
EC *vs* WS	1		3.12	**0.044**
LM *vs* MS	1		0.42	0.710
LM *vs* WS	1		0.78	0.482
MS *vs* WS	1		1.51	0.200
Year(Period)	4	36.19	1.99	0.220
Season(Year(Period))	6	19.23	6.71	**< 0.001**
Year(Period) × Zone	16	7.41	1.129	0.376
Season(Year(Period)) × Zone	20	6.72	2.346	**0.003**
Residual	593	2.86		

Statistically significant effects, including a posteriori pairwise comparisons, in bold ($\alpha = 0.05$)

$^{\#}$ = permutational value. Zone abbreviations as per Table 2

Year (within Period): 2012, 2014–2019; Season (within Year and Period) = Spring, Autumn. See also Fig. 3a

For water quality and habitat, there were significant differences among periods and among zones (Table 4). Temporally, DO was higher and pH was lower post-restoration relative to pre-restoration period (Fig. 4a). Spatially, the Eel Creek (EC) zone differed from LM and MS due to higher EC and lower DO (Fig. 4b). For

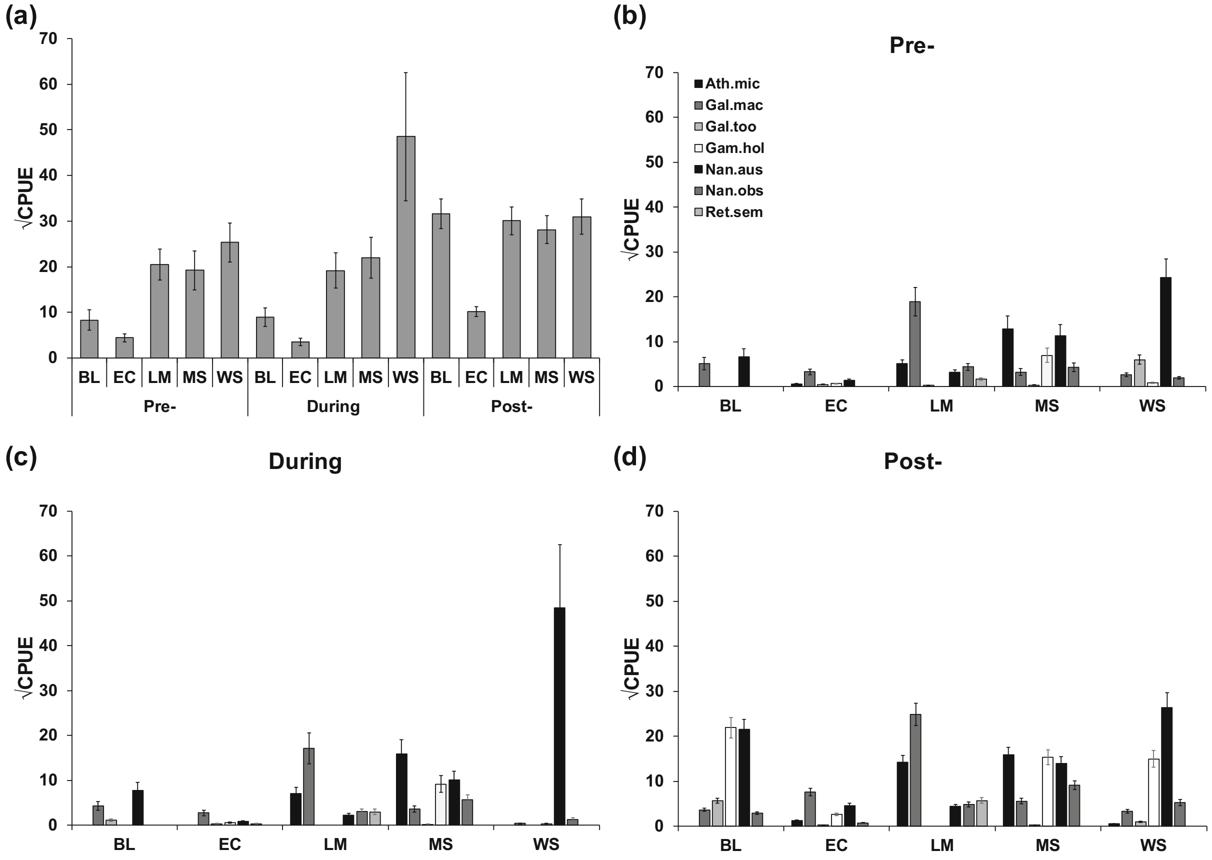

Fig. 3 **a** Differences in total CPUE abundance across the five study zones sampled pre-, during and post-restoration. **b** Differences in CPUE abundance for the most abundant species (codes as in Table 2) sampled across the five study zones in the pre-restoration period. **c** Same during the restoration period. **d** Same in the post-restoration period. BL = Bully Lake; EC = Eel Creek; LM = Lake Momboeng; MS = Middle Section; WS = White Sands. Errors bars are ± SE

both functional groups and species CPUE abundance, there were significant differences among zones (Table 5). At the functional group level (noting that estuarine and marine and estuarine-marine opportunists did not contribute significantly to the patterns), alien freshwater generalists (cf. *G. holbrooki*) were more abundant at BL, MS and WS, diadromous and freshwater generalists at LM, estuarine-marine and estuarine-marine opportunists at EC, freshwater specialists at WS, and solely estuarine at MS (Fig. 4c). At the species level, *A. microstoma* and *N. obscura* were more abundant at MS, *G. marmoratus* and *G. maculatus* at LM, and *P. grandiceps* at EC (Fig. 4d), with all other species not contributing significantly to the patterns.

For both functional groups and species (represented as for the above patterns), fish–environment associations varied according to restoration period. At the group level: pre-restoration, freshwater specialists were associated with higher pH and temperature, solely estuarine species with higher DO, and diadromous species with higher depth (Fig. 5a); during restoration, freshwater specialists were associated with higher EC, pH and temperature and with more cover, whereas diadromous and solely estuarine species with higher DO (Fig. 5c); post-restoration, alien freshwater generalists were associated mainly with higher depth and cover, whereas freshwater specialists and solely estuarine with higher DO (Fig. 5c). At the species level: pre-restoration, *G. maculatus* was associated with higher depth and *N. australis* with higher pH and temperature (Fig. 5d); during restoration, *N. australis* was again associated with higher pH and temperature, and *G. maculatus* and *A. microstoma* with higher depth (Fig. 5e); post-restoration, *G. maculatus* and *A. microstoma* were still

Table 4 Permutational MANOVA for spatial and temporal variability in water quality (DO, EC, pH, Temp) and habitat (Depth, Cover) parameters (see text for details) across the Long Swamp Wetland Complex (statistical details in Table 3)

Source of variation	df	MS	$F^{\#}/t^{\#}$	$P^{\#}$
Period	2	48.57	3.54	**0.012**
Pre- *vs* During	1		1.15	0.400
Pre- *vs* Post-	1		2.36	**0.005**
During *vs* Post-	1		1.46	0.095
Zone	3	32.96	4.87	**< 0.001**
EC *vs* LM	1		2.97	**0.006**
EC *vs* MS	1		2.67	**0.018**
EC *vs* WS	1		1.78	0.076
LM *vs* MS	1		1.92	**0.044**
LM *vs* WS	1		1.29	0.208
MS *vs* WS	1		1.09	0.335
Period × Zone	6	5.13	0.75	0.769
Year(Period)	4	13.75	0.87	0.597
Season(Year(Period))	6	16.50	7.38	**< 0.001**
Year(Period) × Zone	12	7.00	1.29	0.193
Season(Year(Period)) × Zone	14	5.48	2.45	**< 0.001**
Residual	90	2.23		

Statistically significant effects, including a posteriori pairwise comparisons, in bold ($\alpha = 0.05$)

See also Fig. 4a, b

associated with higher depth and *G. holbrooki* with more cover (Fig. 5f).

Profiles for the five representative functional groups indicated a sharp increase in freshwater specialists during restoration, a progressive increase of alien freshwater generalists (cf. *G. holbrooki*) throughout the study period (except for the last year of sampling), and an overall decrease in diadromous and solely estuarine species post-restoration following an increase pre-restoration (Fig. 6a). Based on MAFA, the first axis of variation (MAF1) indicated a downward trend from the beginning of the study through to the restoration period, except for the last year of sampling when an increase was present; the second axis (MAF2) indicated a peak during restoration and in the first-year post-restoration (Fig. 6b). The increase in the alien freshwater generalist group was highlighted by the significant negative correlation with MAF1 (Fig. 6c), whereas diadromous and estuarine species were significantly correlated with MAF2 (Fig. 6d). Based on DFA, the lowest AIC value was achieved with a model including the water quality parameters EC and temperature plus depth and cover. The DFA trend confirmed the peak during restoration (Fig. 6e) attributable to the freshwater specialists (Fig. 6f).

Profiles for the five representative species indicated a sharp increase in *N. australis* during restoration, a progressive increase throughout the study period (except for the last year of sampling) in *G. holbrooki*, and an overall decrease in *A. microstoma* and *G. maculatus* post-restoration following an increase pre-restoration (Fig. 7a). Based on MAFA, the first axis of variation (MAF1) indicated a downward trend from the beginning of the study through to restoration, except for the last year of sampling when an increase was present; the second axis (MAF2) indicated a peak during restoration and in the first-year post-restoration (Fig. 7b). The increase in *G. holbrooki* was highlighted by the significant negative correlation with MAF1 (Fig. 7c), whereas *A. microstoma* was significantly correlated with MAF2 (Fig. 7d). Based on DFA, the lowest AIC value was achieved with a model including the water quality parameters pH and temperature plus depth and cover. The DFA trend confirmed the peak during restoration (Fig. 7e) attributable to *N. australis* (Fig. 7f).

Discussion

The responses of a fish community to the landscape-scale hydrological restoration of an internationally significant coastal freshwater wetland were investigated in this study. Prior to restoration, the wetland complex already provided an important regional refuge for a diverse range of freshwater fishes but was experiencing a long-term drying trend as a result of past hydrological modifications. Despite the mosaic of permanent (and groundwater-fed) to ephemeral freshwater-dominated and densely vegetated habitats that prevailed, as well as the dynamic intermittent connectivity with the lower Glenelg River and estuary (and ocean), aquatic habitats in portions of the system had declined in extent and were slowly being displaced by terrestrial vegetation communities migrating downslope. Hence, while the newly listed Ramsar site of Long Swamp was found to support important populations of internationally and regionally threatened species, artificial drainage (which is

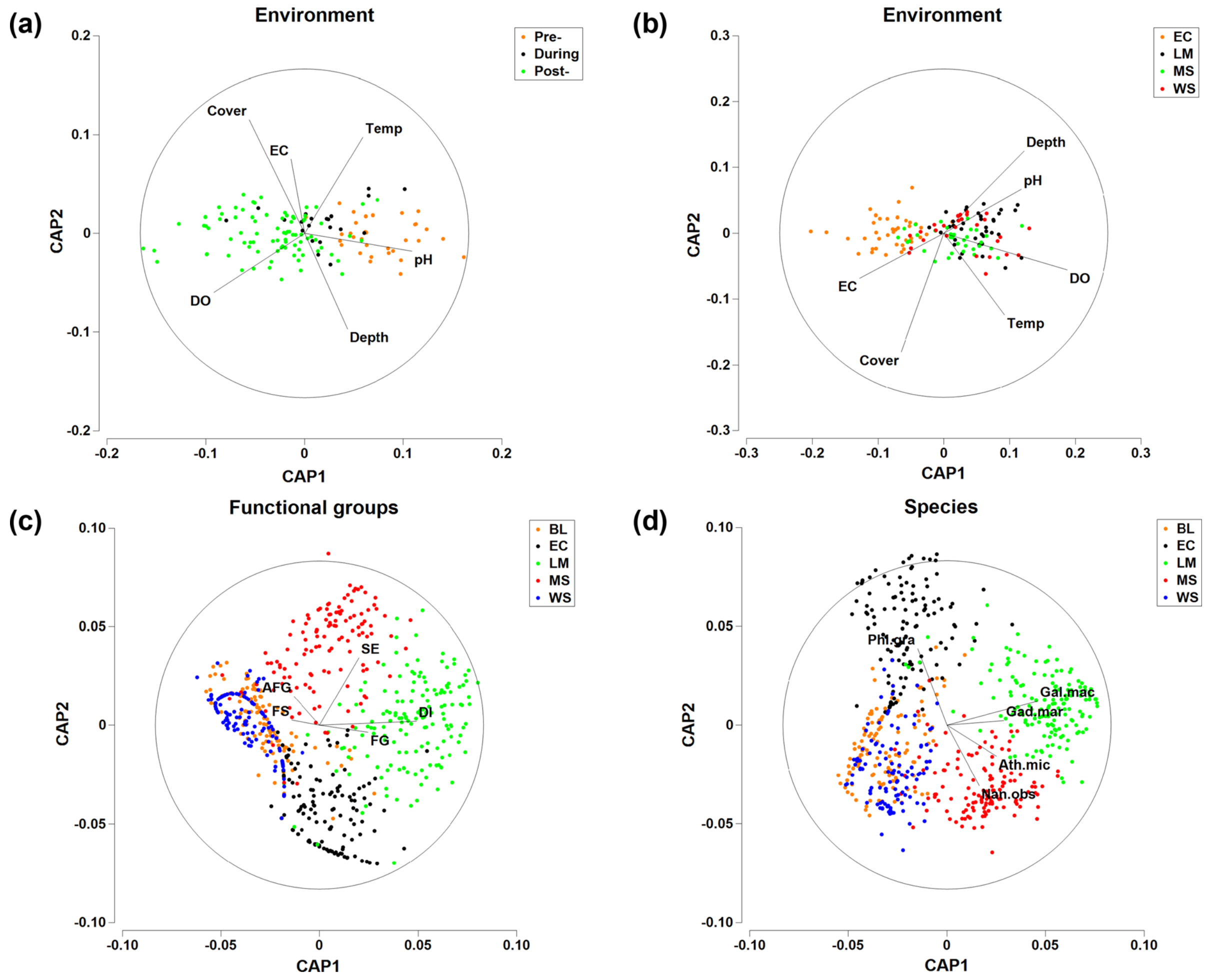

Fig. 4 Canonical discriminant analysis of the principal coordinates (CAP) plots for: **a** environmental variables according to restoration period; **b** environmental variables according to zone; **c** functional groups according to zone; **d** species according to zone. Zone abbreviations as in Fig. 3. See also Table 4

commonly encountered globally in coastal wetlands) and resultant reductions in both freshwater habitat availability and connectivity across the landscape was a key ongoing threat. Thus, as an existing public conservation reserve, it was considered an ideal site for restoration works to reverse the observed drying trend that threatened to undermine those residual aquatic habitat values, and support the expansion and regional recovery of native fish and other dependent wetland species.

It was predicted that temporal responses in freshwater fishes would be linked to pre-defined periods of restoration. Consistently, the total CPUE abundance varied significantly due to a Period × Zone interaction. However, in contrast to predictions, there was no decline in the fish community experienced during the restoration phase, but rather the highest total CPUE abundance was revealed and a post-restoration increasing trend was largely absent. It is evident that the temporal trends were strongly regulated by significant spatial structuring in freshwater fishes (revealed most strongly in terms of functional group and species CPUE abundance and species diversity). Whilst EC had the highest overall species diversity as anticipated given its more variable hydrology and closer proximity to the estuary and ocean ecosystems (Pérez-Ruzafa et al. 2007), the average species diversity (as well as total CPUE abundance) was consistently lower there than in other zones. At the other geographic extent of the wetland complex, the diverse fish community of

Table 5 Permutational MANOVA (functional groups and species) and permutational ANOVA (diversity) for spatial and temporal variability in CPUE abundance (fish net^{-1} h^{-1}) and number of species of fish sampled across the Long Swamp Wetland Complex (statistical details in Table 3)

Source of variation	df	Functional groups			Species			Diversity		
		MS	$F^{\#}/t^{\#}$	$P^{\#}$	MS	$F^{\#}/t^{\#}$	$P^{\#}$	MS	$F^{\#}/t^{\#}$	$P^{\#}$
Period	2	7620.8	0.96	0.491	7845.6	0.94	0.493	0.27	0.03	0.980
Zone	4	61,787.0	18.72	**< 0.001**	72,616.0	18.71	**< 0.001**	49.13	23.97	**< 0.001**
BL *vs* EC	1		3.01	**0.011**		2.84	**0.014**		1.04	0.347
BL *vs* LM	1		4.36	**0.003**		4.60	**0.002**		6.34	0.002
BL *vs* MS	1		3.13	**0.016**		3.45	**0.011**		9.73	**< 0.001**
BL *vs* WS	1		3.14	**0.007**		2.86	**0.009**		2.51	0.059
EC *vs* LM	1		5.28	**0.003**		5.59	**0.001**		6.81	**0.001**
EC *vs* MS	1		5.67	**0.003**		5.56	**0.002**		6.33	**0.002**
EC *vs* WS	1		4.45	**0.002**		3.99	**0.004**		0.01	0.989
LM *vs* MS	1		4.42	**0.005**		4.54	**0.005**		1.04	0.350
LM *vs* WS	1		4.69	**0.002**		4.75	**0.003**		5.50	**0.003**
MS *vs* WS	1		2.93	**0.016**		2.98	**0.016**		12.48	**< 0.001**
Period × Zone	8	4829.4	1.40	0.179	5833.0	1.44	0.123	3.35	1.59	0.199
Year(Period)	4	8589.8	1.67	0.180	9049.7	1.53	0.216	8.41	16.37	**0.004**
Season(Year(Period))	6	5466.8	11.62	**< 0.001**	6274.8	11.30	**< 0.001**	0.52	1.16	0.331
Year(Period) × Zone	16	3817.4	1.96	0.021	4478.6	1.88	0.015	2.25	1.08	0.435
Season(Year(Period)) × Zone	20	2012.5	4.28	**< 0.001**	2465.4	4.44	**< 0.001**	2.15	4.82	**< 0.001**
Residual	593	470.3			555.1			0.45		

Statistically significant effects, including a posteriori pairwise comparisons, in bold ($\alpha = 0.05$)

See also Fig. 4c, d

the permanent (groundwater-fed) lake of the LM zone was significantly differentiated. In Long Swamp proper (e.g. BL, MS, WS), zones were more similar (often due to the consistent presence of *G. holbrooki*), although the high abundance of *N. australis* recorded at WS contributed to some differences. Regardless, there was some evidence that spatial variability declined over time in Long Swamp proper supporting the prediction of a more homogenous fish community post-restoration, as a result of reduced direct oceanic connectivity for the upstream (eastern-most) sections of the wetland complex (via the former artificial ocean outlet at Nobles Rocks).

Significant changes in environmental parameters were observed between zones and over time. For instance, EC maintained significantly higher electrical conductivity (and lower dissolved oxygen: DO) than other permanently inundated freshwater zones which, coupled with the estuary connectivity, reflects the hydrological influence of the estuary. However this site was still characteristically 'fresh' (i.e. electrical conductivity below 2000μScm^{-1} during more than half of sampling events, and < 4000μScm^{-1} on all but one sampling occasion (autumn 2016: 10,540 and 11,800μScm^{-1} at two EC sites) across the study period, and is therefore less variable in terms of salinity than typical coastal wetlands (Pérez-Ruzafa et al. 2019; van Dijk et al. 2015). As hydrological restoration commenced, there were significant increases in DO across the wetland complex, presumably reflecting greater flow and turnover (i.e. mixing), water level (e.g. less deterioration of water quality), and aquatic plant growth (photosynthesis). Although habitat cover did not change significantly at specific sample points over time, the breakdown of inundated terrestrial vegetation and organic matter at the margins of the wetland areas likely resulted in the significant post-restoration decline in pH.

Whilst both wetted extent and duration of flows increased broadly following hydrological restoration, depth at the sampling sites did not change significantly, except for the BL site. Equally, the wetland area immediately behind the restoration structure (BL), and extending over an area within the zone of influence of the structure, transitioned rapidly from an invading vegetation community dominated by terrestrial (*Acacia longifolia*, *Olearia axillaris* and *Leucopogon parviflorus*) and wet (*Leptospermum lanigerum*) shrubland to an aquatic herbland (primarily *Cycnogeton procerum*) with an associated upslope expansion of sedgeland communities (primarily *Baumea arthrophylla* and *B. juncea*). These proximal and immediate physical changes to vegetation communities were not consistent across the landscape; but rather moderated gradually with increasing distance from the area of restoration works (Bachmann 2020). Remote sensing of vegetation dynamics associated with restoration (Taddeo and Dronova 2020), is a potential avenue for further exploration to determine changes in habitat availability that influence fish communities across the landscape.

The temporal trends in fish community observed across the study period are suggestive of a lag in the ecological response to hydrological changes caused by restoration works (cf. Thompson et al. 2018). These lagged responses were evident not only in the years post-restoration but also by the fact that the initial (during) impacts were not immediate (e.g. peak in CPUE abundance in 2015). These observed responses reflect a delay in broader water level and flow trends experienced across the wider wetland complex, which are heavily influenced in any given year by climate – because the system as a whole, including the shallow local groundwater aquifer that underpins it, is highly responsive to rainfall. Hence, water level increases and improved flows (i.e. connectivity) across the wetland complex following completion of the restoration structure have not been uniform in space and time. To illustrate this, whilst water levels increased rapidly at BL (behind the restoration structure), wider impacts associated with changes in surrounding groundwater and the rehabilitation of westerly flows from BL (including physical changes to vegetation and flow paths) are likely to take several years to emerge and stabilise, and these effects continue today. As a result, there appears to a landscape legacy in the flow 'signal' required for reliable fish movement, caused by a sustained shift in flow direction (and connectivity) across the bulk of Long Swamp toward the EC flowpath, is still developing. Whilst there were some significant changes in water quality and habitat cover in the areas of the wetland that experienced the most dramatic change in static inundation depth, it was also anticipated that there would be a lag in the conditions prevailing across the wetland complex for large areas where hydrological changes (such as flow duration) have been more subtle, and therefore causing a delayed influence on fish communities.

For freshwater coastal wetlands such as Long Swamp, inherent dynamism in wider regional climate and rainfall further influence landscape processes, relating to groundwater (and river) flows and connectivity and, to a lesser extent, the status of the Glenelg River mouth, that will influence fish responses. For example, rainfall was well below average during 2013, 2014 and 2015, before a period of above average rainfall in mid-late 2016, which coincided with the transition into the post-restoration period. Similarly, the river mouth was closed with greater frequency from early 2015 to mid-2016 relative to other times (e.g. open continuously from mid-2016 to late 2018) and thus impaired landscape connectivity is anticipated to have influenced migration into and dispersal within the wetland complex. Therefore, the maintenance of higher water levels and extended duration of flows and connectivity throughout the wetland seen in summer to autumn 2017, which inevitably influenced the observed shift in fish community composition, was the combined result of hydrological restoration and the corresponding natural end to a prolonged dry period – with each of these hydrological drivers likely enhancing the benefit of the other.

Unlike many freshwater systems nowadays (Darwall and Freyhof 2016), Long Swamp was dominated by native freshwater specialists (as opposed to freshwater generalists and alien species), which contributed strongly to the changes experienced over time. *Nannoperca australis* was widespread and abundant, with unexpected peaks in CPUE abundance experienced in the during-restoration period that were linked higher pH. This finding reflected a single sampling event (spring 2015) in one zone (WS), which was preceded by complete drying and refilling, indicating a capacity for dispersal, recolonisation and rapid population growth. This refilling also triggered the re-establishment of a thick growth of aquatic herbs which likely drove a marked increase in pH that is reflective of a spike in photosynthetic activity. The presence of

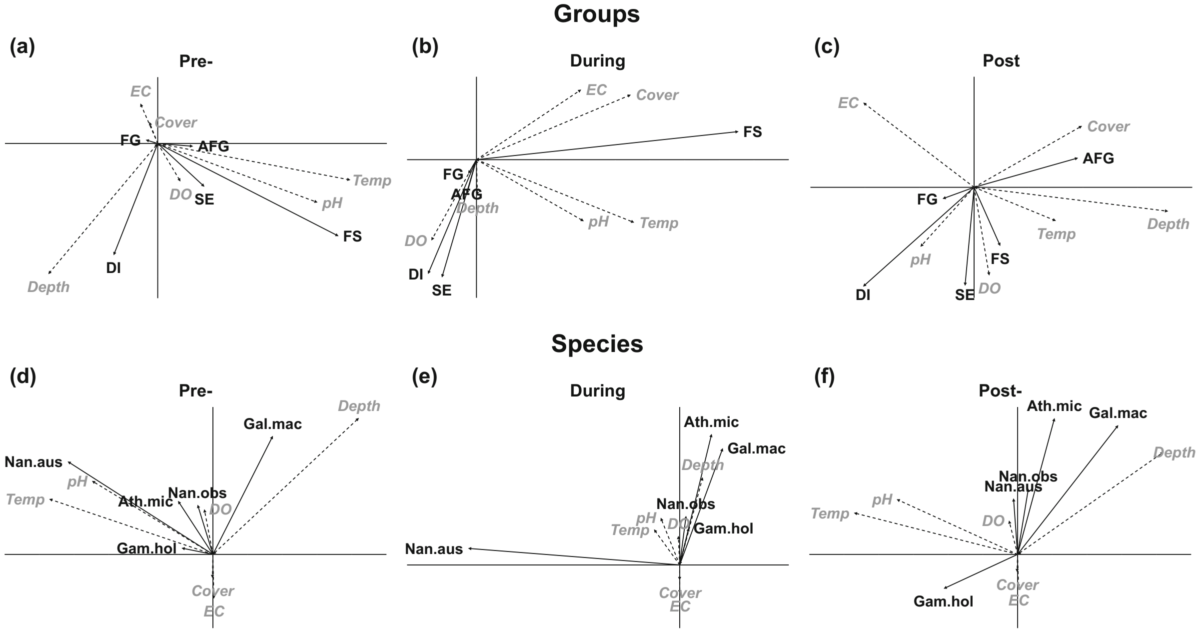

Fig. 5 Fish-environment association plots for: functional groups (**a** pre-restoration, **b** during restoration, and **c** post-restoration) and species (**d** pre-restoration, **e** during restoration, and **f** post-restoration). Functional group and species codes as in Table 2

the globally endangered *N. obscura* (Whiterod et al. 2019) is encouraging as it may serve as the future source for conservation translocations to re-establish locally extirpated populations in other parts of the species' range (Wedderburn et al. 2019). In contrast, the globally vulnerable *G. toourtkoourt* (Coleman et al. 2019), a small aestivating species reliant on ephemeral habitats (Coleman et al. 2017), has shown a decline in CPUE abundance in the wetland complex over all zones and over time. However, it also remains possible, indeed probable based on habitat preferences, that the species has expanded into newly created areas of ephemerality on the edge of the recovering permanent habitats (a zone that was not routinely sampled) and is now less detectable at the standard sampling locations. Hence, this trend remains unclear and targeted future surveys are required to better understand and verify this pattern. The CPUE abundance of the large-bodied *G. marmoratus*, found only in the LM zone, has remained relatively stable over time, possibly reflecting sustained groundwater inputs and specific deep-water habitats provided almost exclusively in this zone. In the context of this finding, it is also worth noting that the LM zone has experienced no direct hydrological change as a result of being sufficiently distant from, as well as being both at a higher elevation and upstream of, restoration works.

The deliberate closure of the artificial outlet at Nobles Rocks was predicted to disrupt migration into the wetland complex, leading to a decline in diadromous species during restoration before increasing again with enhanced connectivity across the landscape (e.g. broader wetland, Glenelg River estuary, ocean) over time. However, the opposite trend was observed for *G. maculatus* (e.g. in 2015 and 2016, CPUE abundance remained stable but post-restoration declined subsequently with time). Consistent with the lagged responses mentioned above, the relatively stable *G. maculatus* CPUE abundance in the years during restoration largely reflected a greater proportion of adults (which persisted in the LM zone) as opposed to migrating juveniles, as the migration flowpath through EC was restricted. Over time, the limited migration and recruitment into the wetland complex by this largely annual species (cf. Egan et al. 2019) eventually led to the predicted declines in *G. maculatus* CPUE abundance, which were realised in the years post-restoration. In the last year of the study, the number of juveniles contributing to increases in the CPUE abundance of *G. maculatus* is in line with the shift in flow direction now under way, suggesting that

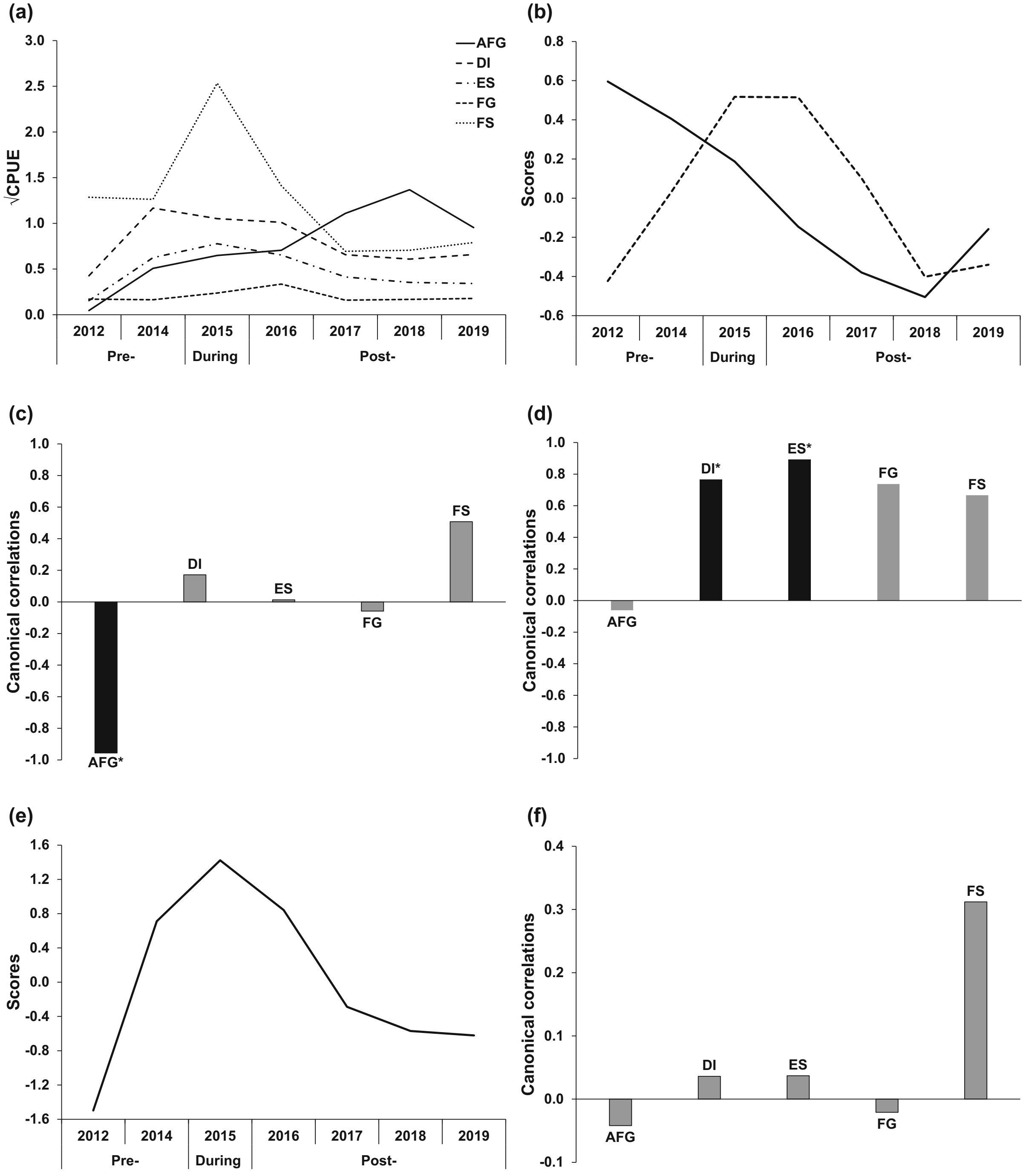

Fig. 6 **a** CPUE abundance profiles for the functional groups sampled in the study zone. **b** Min–max autocorrelation factor (MAF) trends (solid line for Axis 1, dashed line for Axis 2) in functional group abundance during the study period. **c** Canonical correlations with MAF axis 1. **d** Canonical correlations with MAF axis 2. Trends associated with significant (α = 0.05) canonical correlations with MAF axis 1 or 2 in black with corresponding functional group marked with an asterisk. Functional group abbreviations as in Table 2

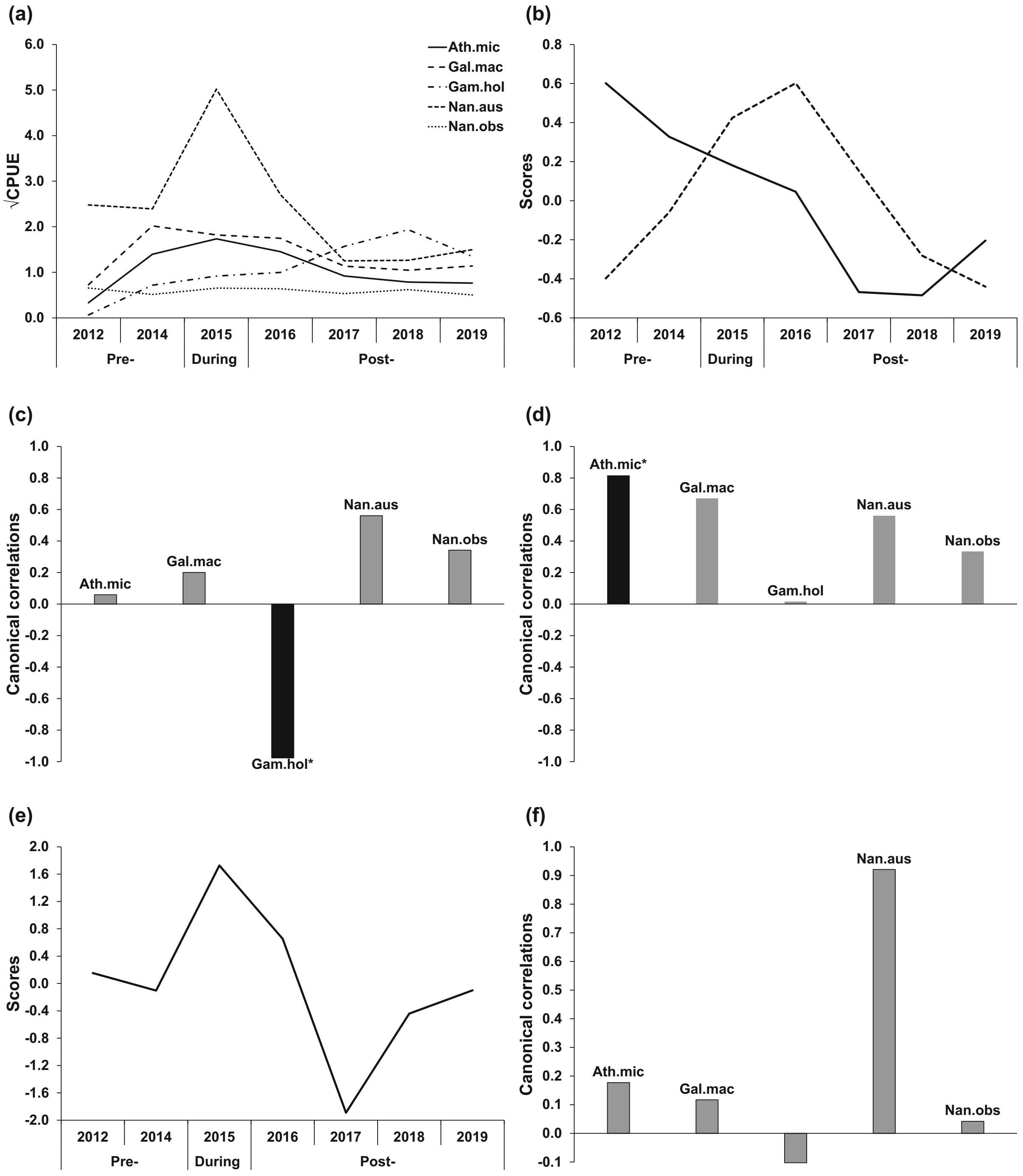

Fig. 7 **a** CPUE abundance profiles for the representative species sampled in the study zone. **b** Min–max autocorrelation factor (MAF) trends (solid line for Axis 1, dashed line for Axis 2) in species abundance during the study period. **c** Canonical correlations with MAF axis 1. **d** Canonical correlations with MAF axis 2. Trends associated with significant (α = 0.05) canonical correlations with MAF axis 1 or 2 in black with corresponding species marked with an asterisk. Species codes as in Table 2

newly sustained flows through Long Swamp and to the ocean via the Glenelg River estuary is beginning to have a post-restoration influence on fish movement and populations.

Consistent with the above finding, other diadromous species including *P. urvilli* were detected at BL for the first time towards the end of the study period. Equally, four estuarine and marine species made incursions, albeit as single individuals, into the lower reaches of EC during the post-restoration period. It is possible that rarer species that are either present in the Glenelg River estuary (such as pouched lamprey *Geotria australis* and shorthead lamprey *Mordacia mordax*) or regionally (e.g. the globally vulnerable Australian mudfish *Neochanna cleaveri* and climbing galaxias *Galaxias brevipinnis*) will eventually migrate into the wetland complex as landscape connectivity develops. However, barriers do remain, namely the intermittent closures of the river mouth and culvert structures in the lower reaches of the EC zone (at Beach Road, Nelson), which may constrain the benefits of the landscape hydrological restoration works being fully realised.

The period of hydrological restoration coincided with an increase in alien *G. holbrooki* at the BL and MS zones. First recorded in the wetland complex in 2012, the species represented a relatively minor component of the fish community prior to restoration. The expansion in rehabilitated wetland habitat (specifically, the persistence of additional shallow waters over the summer and autumn months) is anticipated to have created favourable conditions for the species. Yet, the wetter climatic phase experienced during 2016 and 2017, also naturally and concurrently improved seasonal habitat availability and connectivity across the wetland complex. Hence, as *G. holbrooki* is an aggressive invader that can achieve rapid population growth in newly established areas (cf. Pyke 2008), it likely would have proliferated over the study period regardless of hydrological restoration. *Gambusia holbrooki* is capable of significantly impacting small-bodied freshwater fishes such as the pygmy perches (Macdonald et al. 2012; Nicol et al. 2015), but it is unclear how the species is impacting fish communities across the restored wetland complex (in this respect, it is worth noting that *N. obscura* has shown a parallel expansion in response to restoration, especially at BL). Whilst its removal or control is not feasible in Long Swamp, it has been demonstrated that aggressive interactions between *G. holbrooki* and native species can be minimised by maintaining or enhancing thick aquatic vegetation (Pyke 2008) and minimising low water events (Macdonald et al. 2012), both of which have been positively influenced and sustained by the restoration process at a landscape-scale throughout Long Swamp.

Conclusions

The restoration of hydrological drivers to rehabilitate freshwater wetlands, including those in coastal regions, occur against a backdrop of dynamic conditions in these highly changeable environments, and responses therefore cannot always be accurately anticipated (Moreno-Mateos et al. 2015). In many ways, each restoration project is a unique experience and needs to be approached as such, although some key commonalities worth considering have been revealed by this study. Firstly, uncertainty regarding the original character of wetlands can hamper restoration efforts: in this instance, deep exploration of historical reference material and extensive stakeholder engagement was necessary to help define original hydrological conditions and inform the restoration strategy (Bachmann 2020). Secondly, many, often unmanageable, drivers such as the interplay of surface and groundwater inputs, the degree and extent of terrestrialisation of wetland habitats, broader connectivity of flows (e.g. river mouth openings) and the regional climate will characterise and considerably influence the trajectory and nature of restoration.

In acknowledging these complex landscape-scale dynamics and context, realistic expectations of the timeframe (and scope) for restoration are required, as is the commitment to a monitoring regime of sufficient scale (e.g. from years to decades, across the whole system) to understand the state of the system as that trajectory of change unfolds (Simenstad et al. 2006). In the case of Long Swamp and of note, the process of ecological change within the fish community, in response to the wetland complex being rehabilitated through the restoration of hydrological processes and migration patterns five years ago (at the time of writing), appears to be still under way, but it is anticipated that this landscape legacy will be overcome in the future. Finally, short-term detrimental impacts during restoration and the possibility of contributing to unintended consequences should not discourage restoration efforts which (when carefully researched and planned) are almost always universally positive and impart much greater long-term resilience into the ecosystem. The Long Swamp example supports this perspective and demonstrates that with the best available knowledge and planning, and an acceptance of the unknown, landscape-scale restoration of hydrology can provide effective redress for the global loss and degradation of wetlands and biodiversity.

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