

Will fencing floodplain and riverine wetlands from feral pig damage conserve fish community values?

N. J. Waltham*, J. Schaffer

Centre for Tropical Water and Aquatic Ecosystem Research (TropWATER), College of
Science and Engineering, James Cook University, Queensland, 4811, Australia

*Corresponding Author Tel + 61 7 4781 4191; fax + 61 7 4781 5589

E-mail address: nathan.waltham@jcu.edu.au

Keywords: tropical wetlands; restoration; feral pigs; exclusion fences; floodplains; connectivity

Running Head: Feral pig fencing floodplain wetlands for fish conservation

ABSTRACT: Installation of feral pig (*Sus scrofa*) exclusion fences to conserve and rehabilitate coastal floodplain habitat for fish production and water quality services remains untested. Twenty-one floodplain and riverine wetlands in the Archer River catchment (north Queensland) were surveyed during post-wet (June-August) and late-dry season (November-December) in 2016, 2017 and 2018, using a fyke net soaked overnight (~14-15hrs) to test: 1) whether the fish assemblage are similar in wetlands with and without fences; and 2) whether specific environmental conditions influence fish composition between fenced and unfenced wetlands. A total of 6,353 fish representing twenty-six species from 15 families were captured. There were no wetland differences in fish assemblages across seasons, years and for fenced and unfenced (PERMANOVA, Pseudo-F <0.589, $P < 0.84$). Interestingly the late-dry season fish were far smaller compared to post-wet season fish: a strategy presumably in place to maximise rapid disposal following rain and floodplain connectivity. In each wetland a calibrated Hydrolab was deployed (between 2-4 days, with 20min logging) in the epilimnion (0.2m) and revealed distinct diel water quality cycling of temperature, dissolved oxygen and pH (conductivity represented freshwater wetlands), which was more obvious in the late-dry season survey because of extreme summer conditions. Water quality varied among wetlands in terms of the daily amplitude and extent of daily photosynthesis recovery, which highlights the need to consider local conditions and that applying general assumptions around water quality conditions for these types of wetlands is problematic for managers. Though many fish access wetlands during wet season connection, the seasonal effect of reduced water level conditions seems more over-improvised when compared to whether fences are installed, as all wetlands supported few, juvenile, or no fish species because they had dried completely regardless of the presence of fences.

1. Introduction

43 Wetlands (palustrine and lacustrine) that are located on floodplains away from riverine
44 channels support rich aquatic plant and fauna communities (Ambrose & Meffert, 1999; Jiang et
45 al., 2015; Brandolin and Blendinger, 2016). However, after peak flood connection, aquatic
46 organisms occupying these wetlands face a moving land-water margin until connection is
47 broken, at which point wetlands have been shown to support a non-random assortment of
48 aquatic species, including fish (Arrington & Winemiller, 2006; Pander et al., 2018). The
49 duration, timing and frequency that off channel wetlands maintain lateral pulse connection with
50 primary rivers is an important determining factor in broader contribution to coastal fisheries
51 production – higher floodplain connection results in more fish production is the overwhelming
52 conclusion (Bennett & Kozak, 2016; Górski et al., 2016; Hurd et al., 2016; Galib et al., 2018).
53 In addition to connection, environmental conditions become important on floodplains,
54 including water quality (Waltham & Schaffer, 2018), but also access to shelter to escape
55 predation and available food resources (Jardine et al., 2012; Blanchette et al., 2014). Although
56 optimism about coastal floodplain restoration is building (Waltham et al., 2020), efforts by
57 managers to restore wetland services and values is increasing, though data delineating success
58 are limited. This lack of data becomes important when attempting to quantify biodiversity
59 returns for the funding investment made by government or private investor organisations
60 (Elliott et al., 2016; Weinstein & Litvin, 2016; Zedler, 2016; Waltham & Fixler, 2017).
61
62 At some point after floodplain connection, the waters begin receding and progressively
63 disconnect from the main river channel, forming smaller and shallower off channel
64 wetland/swamp refugia (McJannet et al., 2014; Pettit et al., 2012; Pusey & Arthington, 2003;
65 Abbott et al., 2020). In tropical north Australia, formation and persistence of seasonal off
66 channel wetland are more pronounced owing to high evaporation rates, loss to groundwater
67 (Petheram et al., 2008), and in many situations the water quickly retracts away from the banks
68 and riparian shade (Pusey & Arthington, 2003). After floodplain disconnection from primary

69 rivers, they become more prone to reduced water quality conditions - most notably reduced
70 water depth (Pettit et al., 2012), high water temperatures (Wallace et al., 2017), and suffer
71 extended low oxygen periods (Waltham & Schaffer, 2018). This reduced state of water quality
72 (or habitat) increases aquatic fauna exposure risks to acute and chronic thresholds (Burrows &
73 Butler, 2012; Wallace et al., 2015). In the late-dry season, fish confined to these isolated
74 wetlands on floodplains therefore have very limited avoidance choices (Waltham & Schaffer,
75 2018), and must exploit available habitat opportunities (Phelps et al., 2015; Love et al., 2017),
76 which are specific to each wetland depending on orientation and location (Schomaker &
77 Wolter, 2011), depth and vegetation cover (Wallace et al., 2017). Floodplain fish must deal
78 with these vagaries at least until the monsoonal rain again reconnects overbank coastal
79 floodplains.

80
81 Across northern Australia, feral pigs (*Sus scrofa*) have been shown to contribute wide-scale
82 negative impacts on wetland vegetation assemblages, water quality, biological communities
83 and wider ecological processes (Baber & Coblenz, 1986; Krull et al., 2013). Feral pigs utilise
84 an omnivorous diet supported by foraging or digging plant roots, bulbs and other below ground
85 vegetation material over terrestrial or wetland areas (Ballari & Barrios-García, 2014). This
86 feeding strategy has a massive impact on wetland aquatic vegetation communities (Doupé et
87 al., 2010), giving rise to soil erosion and benthic sediment re-suspension, reduced water clarity
88 and eutrophication which becomes particularly critical late-dry season. The fact that limited
89 data exists on the impact that feral pigs contribute to wetlands (Mitchell & Mayer, 1997; Doupe
90 et al., 2010; Steward et al., 2018; Waltham & Schaffer, 2018), places a strain on the ability for
91 land managers to quantify the consequences of pig destruction (Commonwealth of Australia,
92 2017). Conversely, a lack of baseline data means quantifying success following expensive
93 mitigation efforts is problematic.

Strategies focused on reducing or removing feral pigs from the floodplain landscape have been employed since their introduction to Australia (Fordham et al., 2006). Control strategies have included poison baiting, aerial shooting, and trapping using specially constructed mesh cages (that are baited sometimes) (Ross et al., 2017). Attempts have also included installing exclusion fencing that border the wetland of interest. While advantages of installing fencing around wetlands has been examined only recently in Australia (Doupe et al., 2010), those authors claim fencing might well be less effective particularly in situations where wetlands would normally dry before the next wet season rainfall and reconnection. Fencing is expensive to construct and maintain (Ross et al., 2017), but at the same time prevents other non-target terrestrial fauna from accessing wetlands, which becomes imperative late-dry season where wetlands become regional water points for many mobile fauna (Commonwealth of Australia, 2017).

The aims here were twofold: 1) what is the spatial and temporal variability of fish assemblages in waterbodies with and without feral pig fencing, and 2) does this pattern correlate to water quality variables?. These data are important and necessary given increasing government funding investment planned in northern Australia for restoration of wetlands impacted by feral animals (including pigs) (Waltham & Schaffer, 2018).

2. Methods

2.1 Description of Study System

The Archer River catchment is located on Cape York Peninsula, north Queensland (Fig 1). The head waters of the river rise in the McIlwraith range on the eastern side Cape York, where it flows and then enters Archer Bay on the western side of the Gulf of Carpentaria; along with the Watson and Ward Rivers. The catchment area is 13,820 km², which includes

120 approximately 4% (510 km²) of wetland habitats
121 (<https://wetlandinfo.des.qld.gov.au/wetlands/facts-maps/basin-archer/>), such as estuarine
122 mangroves, salt flats and saltmarshes, wet heath swamps, floodplain grass sedge, herb and tree
123 *Melaleuca* spp. swamps and riverine habitat. The lower region of the catchment includes part
124 of the Directory of Internationally Important Wetland network (i.e. nationally recognised status
125 for conservation and cultural value) that extends along much of the eastern Gulf of Carpentaria,
126 including the Archer Bay Aggregation, Northeast Karumba Plain Aggregation and Northern
127 Holroyd Plain Aggregation. Two national parks are located in the catchment (KULLA
128 (McIlwraith Range) National Park, and Oyala Thumotang National Park). Land use is
129 predominately grazing with some mining activities planned in the next few years on the
130 northern bank of the river (not within the area of this study).

131

132 Rainfall is tropical monsoonal, strongly seasonal, with between 60% and 90% of total annual
133 rain occurring between November and February. Rainfall records for the catchment reveal
134 highest wet season rainfall occurred in 1989/1999 (2515 mm), while lowest was 1960/1961
135 (563.5 mm) (Waltham & Schaffer, 2017). Total antecedent rainfall for the wet season prior
136 (Nov 2014 to Feb 2015) to this survey was 1081 mm, which is below the 10th percentile for
137 historical records. The wet seasons experienced through the years prior to this study (2010 to
138 2015) were among the wettest on record, within the 95th percentile of the long-term data
139 records. The low rainfall during this study may have contributed to a short flood duration, and
140 thereby connection between wetlands and the main Archer River, when compared to average or
141 above average rainfall years where connection is presumed to be far longer (Fig 2).

142

143 Twenty-one wetlands were sampled including both floodplain and riverine wetlands that were
144 not on the main flow channels, but on anabranches and flood channels that connect to the main

channels only during high flow conditions. All wetlands have been historically damaged by pigs (and cattle to a lesser extent) for up to 160 years (Gongora et al., 2004; Lopez et al., 2014), and there is no background data on the wetland condition before introduction of feral pigs in the region. In response to the obvious and widespread impact in the region, a small number were fenced to prevent feral pig and cattle from accessing wetlands, in accordance with the feral animal research and management program (to meet the objectives of traditional owners in the region) of both Kalan enterprises and Aak Puul Ngangtam, and their partners.

The characteristics of each wetland are summarised in Table S1. Here, sampling focused on two periods: 1) immediately following the wet season after disconnection between the river and wetlands (hereafter referred to as post wet season); and 2) late-dry season (hereafter late-dry) in 2016, 2017 and 2018. Each sampling campaign was completed over 14 days with six total campaigns (post-wet and late-dry season in 2016, 2017 and 2018).

2.2 Field Methods

In each wetland, a calibrated high frequency Hydrolab multi-parameter logger (OTT Hydromet USA) was deployed (0.2m depth) for between 2 and 4 days to record epilimnion (0.2m) water temperature, dissolved oxygen (%), electrical conductivity and pH every 20mins - logging at this frequency provides explicit insight into diel changes in environmental water processes (Wallace et al., 2015; Wallace et al., 2017). Weather conditions were fine with all surveys occurring on the falling limb of the hydrograph.

Fish were collected in wetlands using a fyke net (0.8m opening, double 4m wing panels, 1mm stretch mesh) that was soaked overnight (approximately 14:00 to 09:00). Wetlands substantially impacted by feral pigs; secchi disk depth < 0.1m, no submerged or floating aquatic plants exist, while the fenced wetlands were generally deeper (up to 1.5m), and had

submerged aquatic vegetation (Fig. 1). Fish were placed in a tub (~150L) temporarily, identified, measured (standard length, mm) and returned to the wetland alive in accordance with Australian laws (except for a small number that were kept for food web studies, data not shown here).

2.3 Data Analysis

There are two main biases in the sampling method here: 1) that the technique will capture large numbers of schooling fish along the wetland margins; and 2) the fact that predatory aquatic fauna including fish, snakes (macleays watersnakes, *Pseudoferania polylepis*), file snakes (*Acrochordus arafurae*) and freshwater turtles (*Chelodina oblonga*, *Chelodina canni* and *Emydura s. worrelli*) were periodically trapped for hours means that they could consume fish caught in nets. To overcome these uncertainties, analyses were based on presence/absence of species. Presence/absence provide robust data when relative abundance are of doubtful validity because it deals with species with a diversity of behaviours, trophic functions, and spatial distribute in a more equivalent way than fully quantitative techniques (Quinn & Keough, 2002).

Multivariate differences were examined using PERMANOVA using the Bray-Curtis similarities measure (Clarke, 1993) with significance determined from 10,000 permutations of presence/absence transformation. Multivariate dispersion were tested using PERMDISP, however, homogeneity of variance could not be stabilised with transformation, and therefore untransformed data were used. Three factors were included: years (fixed), season (fixed); and fenced/unfenced (random). These factors were determined *a-prior* during study design – in addition, the 2016 late dry season only had a single fenced wetland site; this data point was removed in the PERMANOVA. Spatial patterns in multivariate fish assemblage structure and the importance of explanatory data sets were analysed using a multivariate classification and

regression tree (mCARTs) (De'Ath, 2002) package in R (version 3.4.4). Analysis was conducted using presence/absence transformed fish data for the 10 species that occurred in >20% of wetland sites (to remove rare species). Selection of the final tree model was conducted using 10-fold cross validation, with a 1-SE tree; the smallest tree with cross validation error within 1 SE of the tree with the minimum cross validation error (Sheaves & Johnston, 2009). The relative importance of the explanatory variables were assessed to determine those with a high overall contribution to tree node split, with the best overall classifier being given a relative importance of 100%.

Kolmogorov-Smirnov (K-S) two-sample tests determined differences in the overall shape of fish body size distribution using a Bonferroni correction for multiple comparisons. K-S tests take into account differences between the location, skew, and kurtosis of frequency distributions; but do not identify which of these parameters are driving distributional differences. Therefore, we report the following characteristics of each body size distribution to further describe any differences found: mean, standard deviation (sd), minimum value (min), maximum value (max), the range of values, skewness, and kurtosis.

3. Results

3.1 Hydrology and wetland water quality

Wet season rainfall totals in the Archer River catchment were low during the study period compared to the preceding years (Fig. 2), with rainfall within the 10th percentile for historical recordings held by the Australian Bureau of Meteorology. This means that some caution is necessary with interpretation of these data; namely that floodplain connectivity under higher rainfall years is likely to have a longer duration when compared to lower connection duration under the current rainfall conditions.

222

223 A full summary of water quality data are provided in Supplementary files (S1). In summary,
224 water temperatures during the study period were generally about 26°C (Table 1). Minimum
225 water temperature recordings as low as 18°C, while maximum temperatures occurred in
226 November 2016 survey reached above 40°C for several hours of the day in some instances.
227 The water column exhibited pronounced diel temperature periodicity; one or two hours after
228 sunrise each day. Near-surface water temperatures began to rise at an almost linear rate for a
229 period of 8.0 ± 0.5 hours, generally reaching daily maxima during the middle of the afternoon.
230 The mean daily temperature amplitude was 6.2°C (highest daily amplitude 9.6°C, lowest
231 4.4°C). For the remaining 16 hours of each day, near-surface water temperatures gradually
232 declined reaching minimum conditions shortly after sunset.

233

234 The electrical conductivity (EC) was very low (Table S1) during the post wet season surveys,
235 while the late-dry season conductivity was higher, a consequence of evapo-concentration. The
236 lowest wetland in the catchment (AR08 located on the coastal floodplain) recorded the highest
237 conductivity, suggesting connection with tidal water from the nearby estuary at some stage.

238

239 There was evidence of cyclical daily DO fluctuations supporting the contention that biological
240 diel periodicity processes were probably not significantly inhibited in all wetlands (Fig. 3).
241 Daily minimum DO concentrations were low enough to suggest there was enough respiratory
242 oxygen consumption to measurably affect water quality, particularly so at the pig impacted
243 wetlands, but also during the late-dry season survey in November 2016. Dissolved oxygen
244 (DO) seemed to reach daily minima conditions, well below the asphyxiation thresholds of
245 sensitive fish species, in the early morning hours during all surveys. In the examples shown,
246 after the morning low DO (following overnight respiration processes), conditions generally

recovered to approximately 50%, but reaching a high of 100-160% in the late afternoon (before sunset).

pH is also potentially subject to the same kinds of biogenic fluctuations as DO, due to consumption of carbon dioxide (i.e., carbonic acid) by aquatic plants and algae during the day (through photosynthesis), and net production of carbon dioxide at night. If respiratory oxygen consumption is predominant, DO concentrations are low and pH values are generally moderately acidic to neutral, which was the case for wetlands examined here. All photosynthetically active organisms utilise carbon dioxide as a preferred carbon source. Some species (including most green algae) are unable to photosynthesise if carbon dioxide is unavailable, but there are other species (including most cyanobacteria and submerged macrophytes) which can utilise bicarbonate as an alternative carbon source. Carbon dioxide consumption causes pH to rise to values in the order of 8.6 to 8.7 (but that was not the case here during this survey period).

3.2 Fish community

A total of 6,353 fish were captured, representing twenty-six species from 15 families (Table 1). The most common species was the freshwater glassfish (*Ambassis sp.*, 51% total catch), delicate blue-eyes (*Pseudomugil tenellus*, 11%), and northern purple-spot gudgeon (*Morgunda morgunda*, 9%). A greater number of fish species were caught in the post wet season survey, with a lower number captured during the late-dry season, including the northern purple-spot gudgeon (*Morgunda mogunda*), chequered rainbow fish (*Melanotaenia s. inornata*), and the empire gudgeon (*Hypselostris compressa*). In addition to fish, we captured a freshwater crayfish (*Cherax sp.*), macleays watersnakes (*Pseudoferania polylepis*) and freshwater turtles (*Chelodina oblonga* and *Emydura s. worrelli*) in most wetlands, notably during post wet

season. Overall, there was no significant difference among seasons, fenced/unfenced wetlands and years (PERMANOVA, Pseudo-F <0.589, $P < 0.84$).

With a reduced list confined to dominant species, occurrence profiles for groups in the terminal branches of the mCART analysis (Fig. 4) show two initial wetland groups based on a split supported by region, with wetlands in the Coen (mid-catchment) region separating from those wetlands in the coastal plains. Following the left branch there is inter-annual variation among wetlands, and a second terminal node based on whether wetlands were fenced in 2016, but not so in 2017 and 2018 data. Following the right branch (APN, coastal plains), the first node separates seasons, and following late-dry season wetlands further separate based on mean dissolved oxygen (~3.0%), and then mean temperature (~28.5°C). The post-wet season branch appears to have more separation among data, with a separation based on mean water temperature (~26.5°C), years, and then finally dissolved oxygen (~4%).

Mean fish body size distributions differed between the three sample years (with fish for each wetland and survey pooled) (KS, $P < 0.001$, Table S2 – S5), with larger fish measured in 2017 (50.5mm) compared to 2016 (38.7mm) and 2018 (31.6mm), despite the assemblages having similar size ranges. When comparing the overall fish size distribution by pooling years, post wet season fish were larger (44.9mm) when compared to the late-dry season (39.7mm) (KS, $P < 0.01$). For some fish species such as the chequered rainbow fish (*Melanotaenia s. inornata*), the post wet season (32.5mm) was similar when compared to late-dry season (38.4mm) (KS, $P = 0.06$, S3). In contrast, the northern purple-spot gudgeon (*Mogurnda mogurnda*) was larger post-wet season (52.8mm) compared to late-dry season (37.1mm) (KS, $P < 0.01$, Table S4).

4. Discussion

297 While installation of fences can protect terrestrial ecosystem services from feral impacts
298 (Bariyanga et al., 2016), in the case here fences appear to offer little over-improvised fish
299 additional value compared to those that are not fenced – overall the fish assemblage remained
300 similar across years, seasons, and with and without fencing. While this is the case, importantly
301 what this means is that many fish indeed access both fenced and unfenced wetlands during wet
302 season connection, however, the seasonal effects of reduced water level conditions and the loss
303 of fish assemblage as the dry season progresses is a pattern that remains regardless of fencing.
304 To this end, installation of expensive exclusion fences might not offer additional protection to
305 fish species habitat on this tropical floodplain. The same conclusion was reported by Doupe et
306 al., (2010) where those authors surveyed strongly seasonal wetlands (similar to the wetlands
307 here) elsewhere in northern Australia, and concluded that the seasonal dry down of wetlands
308 ultimately prohibits the wetland contribution to future year successful fish recruitment. In
309 contrast, where floodplain wetlands remain more permanently connected, fish can take more
310 advantage of rich food and nutrient rich floodplains (Hurd et al., 2016; Love et al., 2017).
311
312 The low species richness in wetlands relative to the main Archer River channel might be a
313 consequence of the frequency and duration of connection between wetlands and the main
314 Archer River. The wet season rainfall immediately prior, and during this survey, was within
315 the 10th percentile for historical records. In research elsewhere, a longer connection duration
316 was shown to result in more fish present post wet season, and conceivably more species present
317 late-dry season (Arthington et al., 2015; Hurd et al., 2016). Examples exist where longer
318 connection between main river channels and wetlands contributes positively to fish growth
319 rates, and higher abundance and diversity of fish (Barko et al., 2006; Schomaker & Wolter,
320 2011; Love et al., 2017). It is also possible that the field methods used here confound our
321 ability to determine the full species composition in wetlands – this could be overcome by using
322 additional survey techniques, including multi-panel gill nets, traps or electrofishing (though we

attempted to electrofish these wetlands, however, the conductivity was too low to effectively use that method), in addition to the presence of crocodiles in these wetlands present a real challenge to sampling. Future research might consider riparian vegetation condition, benthic and floating aquatic plant extent and pig impact pressure as potential correlating variables describing the fish assemblage in fenced and unfenced wetlands.

An obvious characteristic of the fish assemblage here were larger, presumably adult, individuals in the wetlands after the wet season compared to small individuals present in the late-dry season. This suggests that the wetlands serve as important refugia for successful recruitment of freshwater fish, that adult fish remaining in the wetlands after disconnection are able to complete imperative life cycle stages. The fact that we did not catch large fish in the late-dry season suggests that adult fish might be lost as the dry season progresses, consumed either by predators such as estuarine crocodiles (*Crocodylus porosus*). Wetlands are also popular feeding and roosting locations for water birds (Chacin et al., 2015; Brandolin & Blendinger, 2016); we observed a large number of species at most wetlands in the late-dry season. The value of wetlands to wader birds is limited by the condition (Žmihorski et al., 2016; Robertson et al., 2017), but are thought to provide an important nutrient subsidy more broadly on seasonal floodplains (Ma et al., 2010; Buelow et al., 2018). Hurd et al., (2017) postulates that differences in fish communities between main channel and off channel waters is more influenced by the presence of piscivorous predators, or even via a function of competitive exclusion within fish guilds as resources diminish as the late-dry season takes hold. Examining this point could be achieved by investigating the species niche width (Jackson et al., 2011; Swanson et al., 2015) in drying waters by constructing food webs in individual waters to determine species ranges and changes with fencing treatment, and comparing post wet season and late-dry season conditions.

349 In the late-dry season for the few fish species present, juveniles dominated the catch regardless
350 whether wetlands were fenced. Having small recruits in the late dry period might be an
351 important strategy in maximising dispersal after connectivity with the commencement of the
352 wet season (Pusey et al., 2018). Moreover, late season conditions with no flow and warm
353 conditions might favour larval development (King et al., 2003; Godfrey et al., 2016).
354 *Melanotaeniid* rainbowfish, for example, have a flexible reproductive behaviour that is well
355 adapt to deal with the vagaries of temporal variation in habitat conditions (Pusey et al., 2001).
356 The same is true for both *Eleotrid* gudgeon species here with smaller recruits presumably ready
357 for wide-scape distribution with the pending wet season flow. Pusey et al., (2018) provides a
358 case that the reproduction success of freshwater fish in northern Australia could in fact hinge
359 on antecedent flow patterns across the landscape, and that this flexibility ensures population
360 level success (Stewart-Koster et al., 2011). This strategy might be particularly appropriate
361 given the below average summer rainfall totals seen during this survey, particularly when
362 compared to previous years.

363

364 As the dry season takes hold, water quality conditions progressively deteriorate mostly because
365 of increasing impact from rooting pigs as they access the wetland vegetation. Generally,
366 fenced wetlands change little in terms of water conditions (Fig. 5). However, it is the late-dry
367 season when water conditions are poorest and therefore most critical to fish. Unfenced
368 wetlands tended to be shallower, highly turbid, and suffer water temperatures that exceed acute
369 thermal effects thresholds for fish – which does provide good justification for fencing
370 wetlands, particularly those that are more permanent, such as those spring feed, compared to
371 wetlands that will dry because they are so distant from the primary water course (Waltham &
372 Schaffer, 2018). The most critical water quality condition for fish survival is dissolved
373 oxygen, and the solubility of dissolved oxygen in water is strongly affected by temperature
374 (i.e., high temperature reduces dissolved oxygen solubility (Diaz & Breitburg,

2009). Data on hypoxia tolerances of local freshwater fish species in northern Queensland is available (Butler & Burrows, 2007), and while tolerances vary between species and life stages, there were obvious periods in wetlands when these threshold limits are exceeded. During critical periods, fish must regulate breathing either via increasing ventilation rates (Collins et al., 2013), or by rising to the surface to utilise aquatic surface respiration and/or air gulping (e.g. tarpon, *Megalops cyprinoides*). In any case, the capacity for fish to do that safely depends on the timing of the oxygen sag and antecedent conditions, though notably it appears that most hypoxia-induced fish kills originate from thermal stress and sunburn resulting from the animals' need to remain at the surface during the heat of the day in order to access available oxygen for respiration. Increasing these risks to fish can have important chronic effects including reducing physical fitness to successfully contribute to future populations (Flint et al., 2018; Gilmore et al., 2018).

387

388

389

390

391

392

393

M.

A.

G.

australis

percoides

aureus

394

395

396

397

398

399

400

401

402

403

404

405

406

407

408

409

410

411

412

413

414

415

416

417

418

419

420

421

422

423

424

425

426

427

428

429

430

431

432

433

434

435

436

437

438

439

440

441

442

443

444

445

446

447

448

449

450

451

452

—

453

454

455

456

457

458

—

459

460

461

462

463

464

465

466

467

468

469

470

471

472

473

474

475

476

477

478

479

480

481

482

483

484

485

486

487

—

488

489

490

491

492

493

494

495

496

497

498

499

500

501

502

503

504

505

506

507

508

509

510

511

512

513

514

515

516

517

518

519

520

521

522

M.

523

australis

A.

524

percoides

G.

525

aureus

526

527

528

529

530

531

532

533

534

535

536

537

538

539

540

541

542

543

544

545

546

547

548

549

550

551

552

553

554

555

556

557

558

559

560

561

562

563

564

565

566

567

568

569

570

571

572

573

574

575

576

577

578

579

580

581

582

583

584

—

585

586

587

588

589

590

—

591

592

593

594

595

596

597

598

599

600

601

602

603

604

605

606

607

608

609

610

611

612

613

614

615

616

617

618

619

—

620

621

622

623

624

625

626

627

628

629

630

631

632

633

634

635

636

637

638

639

640

641

642

643

644

645

646

647

648

649

650

651

652

653

654

M.

655

australis

A.

656

percoides

G.

657

aureus

658

659

660

661

662

663

664

665

666

667

668

669

670

671

672

673

674

675

676

677

678

679

680

681

682

683

684

685

686

687

688

689

690

691

692

693

694

695

696

697

698

699

700

701

702

703

704

705

706

707

708

709

710

711

712

713

714

715

716

—

717

718

719

720

721

722

—

723

724

725

726

727

728

729

730

731

732

733

734

735

736

737

738

739

740

741

742

743

744

745

746

747

748

749

750

751

—

752

753

754

755

756

757

758

759

760

761

762

763

764

765

766

767

768

769

770

771

772

773

774

775

776

777

778

779

5. Summary and Conclusions

The cultural and ecological value of coastal wetlands means that management intervention is increasingly necessary to ensure they remain productive and viable habitat (Creighton et al., 2015; Canning & Waltham 2021). Overall, these data support a model that damage to wetlands from pig activities not only contributes to reduced aquatic habitat, through loss of aquatic vegetation communities, but also probably has secondary impacts including water temperature and asphyxiation risks for many hours each day, that are higher than when compared to fenced wetlands (Fig. 5). However, fish occupying fenced and unfenced wetlands here were similar, particularly in the late-dry season where those remaining few species were small and presumably juveniles ready for wet season re-distribution. On this basis, installing fences to both floodplain and riverine wetlands that were not on the main flow channels, but rather were on anabranches and flood channels that connect to the main channels only during high flow conditions, seems to offer little additional habitat value for fish from the treat of feral pig impact. Where wetlands are largely ephemeral and will dry anyway, or where wetlands remain until the next seasons rain connection; species abundance and/or diversity is not improved by restricting feral pig access – the exception is that unfenced wetlands tend to be hotter and experience lower available oxygen for fish which may support fencing wetlands

most distant from primary water courses if they are like to remain until the next wet season.

Further research is necessary to examine climate change resilience on permanent wetlands (and managed wetlands) particularly whether they provide a similar level of refugia as future climate warming in the region is likely to result in more variable wet season rainfall and flow patterns (James et al., 2017). Under this scenario, it is possible that even the more persistent wetlands might suffer similar dry out fate to the ephemeral wetlands examine here.

References

- Abbott, B. N., Wallace, J., Nicholas, D. M., Karim, F., Waltham, N. J., 2020. Bund removal to re-establish tidal flow, remove aquatic weeds and restore coastal wetland services—North Queensland, Australia. *PloSone* **15**:e0217531. doi.org/10.1371/journal.pone.0217531
- Ambrose, R.F., Meffert, D. J. (1999). Fish-assemblage dynamics in Malibu lagoon, a small, hydrologically altered estuary in southern California. *Wetlands* **19**, 327-340.
- Arrington, D.A., Winemiller, K. O. (2006). Habitat affinity, the seasonal flood pulse, and community assembly in the littoral zone of a Neotropical floodplain river. *Journal of the North American Benthological Society* **25**, 126-141. [doi.org/10.1899/0887-3593\(2006\)25\[126:HATSFJ\]2.0.CO;2](https://doi.org/10.1899/0887-3593(2006)25[126:HATSFJ]2.0.CO;2)
- Arthington, A.H., Godfrey, P. C., Pearson, R. G., Karim, F., Wallace, J. (2015). Biodiversity values of remnant freshwater floodplain lagoons in agricultural catchments: evidence for fish of the Wet Tropics bioregion, northern Australia. *Aquatic Conservation: Marine and Freshwater Ecosystems* **25**, 336-352. doi.org/10.1002/aqc.2489
- Commonwealth of Australia (2017). Threat abatement plan for predation, habitat degradation, competition and disease transmission by feral pigs (*Sus scrofa*) (2017) — Background Document. Canberra: Department of Environment and Energy, 54 p.
- Baber, D.W., Coblentz, B. E. (1986). Density, home range, habitat use, and reproduction in feral pigs on Santa Catalina Island. *Journal of Mammalogy* **67**, 512-525. doi.org/10.2307/1381283
- Ballari, S.A., Barrios-García, M. N. (2014). A review of wild boar *Sus scrofa* diet and factors affecting food selection in native and introduced ranges. *Mammal Review* **44**, 124-134. doi.org/10.1111/mam.12015
- Bariyanga, J.D., Wronski, T., Plath, M., Apio, A. (2016). Effectiveness of electro-fencing for restricting the ranging behaviour of wildlife: a case study in the degazetted parts of Akagera National Park. *African Zoology* **51**, 183-191. doi.org/10.1080/15627020.2016.1249954
- Barko, V.A., Herzog, D. P., O'Connell, M. T. (2006). Response of fishes to floodplain connectivity during and following a 500-year flood event in the unimpounded upper Mississippi River. *Wetlands* **26**, 244-257. [doi.org/10.1672/0277-5212\(2006\)26\[244:ROFTFC\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2006)26[244:ROFTFC]2.0.CO;2)
- Bennett, M.G., Kozak, J. P. (2016). Spatial and temporal patterns in fish community structure and abundance in the largest US river swamp, the Atchafalaya River floodplain, Louisiana. *Ecology of Freshwater Fish* **25**, 577-589. doi.org/10.1111/eff.12235

- Blanchette, M.L., Davis, A. M., Jardine, T. D., Pearson, R. G. (2014). Omnivory and opportunism characterize food webs in a large dry-tropics river system. *Freshwater Science* **33**, 142-158. doi.org/10.1086/674632
- Brandolin, P.G., Blendinger, P. G. (2016). Effect of habitat and landscape structure on waterbird abundance in wetlands of central Argentina. *Wetlands Ecology and Management* **24**, 93-105. doi.org/10.1007/s11273-015-9454-y
- Buelow, C.A., Baker, R., Reside, A. E., Sheaves, M. (2018). Nutrient subsidy indicators predict the presence of an avian mobile-link species. *Ecological Indicators* **89**, 507-515. doi.org/10.1016/j.ecolind.2018.02.029
- Burrows, D., Butler, B. (2012). Primary studies of temperature regimes and temperature tolerance of aquatic fauna in freshwater habitats of northern Australia. Australian Centre of Tropical Freshwater Research (12/01), James Cook University, Townsville, Australia.
- Butler, B., Burrows, D. W. (2007). Dissolved oxygen guidelines for freshwater habitats of northern Australia. Australian Centre for Tropical Freshwater Research (07/31), James Cook University, Townsville, Australia.
- Canning, A.D., Waltham, N.J., (2021). Ecological impact assessment of climate change and habitat loss on wetland vertebrate assemblages of the Great Barrier Reef catchment and the influence of survey bias. *Ecology and Evolution*. <https://doi.org/10.1002/ece3.741>
- Chacin, D.H., Giery, S. T., Yeager, L. A., Layman, C. A., Langerhans, R. B. (2015). Does hydrological fragmentation affect coastal bird communities? A study from Abaco Island, The Bahamas. *Wetlands Ecology and Management* **23**, 551-557. doi.org/10.1007/s11273-014-9389-8
- Clarke, K.R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**, 117-143. doi.org/10.1111/j.1442-9993.1993.tb00438.x
- Collins, G.M., Clark, T. D., Rummer, J. L., Carton, A. G. (2013). Hypoxia tolerance is conserved across genetically distinct sub-populations of an iconic, tropical Australian teleost (*Lates calcarifer*). *Conservation Physiology* **1**, cot029. doi.org/10.1093/conphys/cot029
- De'Ath, G. (2002). Multivariate regression trees: a new technique for modeling species–environment relationships. *Ecology* **83**, 1105-1117. [doi.org/10.1890/0012-9658\(2002\)083\[1105:MRTANT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[1105:MRTANT]2.0.CO;2)
- Diaz, R.J., Breitburg, D. L. (2009). The hypoxic environment. *Fish Physiology* **27**, 1-23.
- Doupe, R.G., Mitchell, J., Knott, M. J., Davis, A. M., Lymbery, A. J. (2010). Efficacy of exclusion fencing to protect ephemeral floodplain lagoon habitats from feral pigs (*Sus scrofa*). *Wetlands Ecology and Management* **18**, 69-78. DOI 10.1007/s11273-009-9149-3
- Elliott, M., Mander, L., Mazik, K., Simenstad, C., Valesini, F., Whitfield, A., Wolanski, E. (2016). Ecoengineering with Ecohydrology: Successes and failures in estuarine restoration. *Estuarine, Coastal and Shelf Science* **176**, 12-35. doi.org/10.1016/j.ecss.2016.04.003
- Flint, N., Pearson, R. G., Crossland, M. R. (2018). Reproduction and embryo viability of a range-limited tropical freshwater fish exposed to fluctuating hypoxia. *Marine and Freshwater Research* **69**, 267-276. doi.org/10.1071/MF16388
- Fordham, D., Georges, A., Corey, B., Brook, B. W. (2006). Feral pig predation threatens the indigenous harvest and local persistence of snake-necked turtles in northern Australia. *Biological Conservation* **133**, 379-388. doi.org/10.1016/j.biocon.2006.07.001
- Galib, S.M., Lucas, M. C., Chaki, N., Fahad, F. H., Mohsin, A (2018). Is current floodplain management a cause for concern for fish and bird conservation in Bangladesh's largest

- wetland? *Aquatic Conservation: Marine and Freshwater Ecosystems*. **28**, 98-114.
doi.org/10.1002/aqc.2865
- Gilmore, K.L., Doubleday, Z. A., Gillanders, B. M. (2018). Testing hypoxia: physiological effects of long-term exposure in two freshwater fishes. *Oecologia* **186**, 37-47.
doi.org/10.1007/s00442-017-3992-3
- Godfrey, P.C., Arthington, A. H., Pearson, R. G., Karim, F, Wallace, J. (2016). Fish larvae and recruitment patterns in floodplain lagoons of the Australian Wet Tropics. *Marine and Freshwater Research* **68**, 954-979. doi.org/10.1071/MF15421
- Gongora, J., Fleming, P., Spencer, P. B., Mason, R., Garkavenko, O., Meyer, J. N., Droegemueller, C., Lee, J. H., Moran, C. (2004). Phylogenetic relationships of Australian and New Zealand feral pigs assessed by mitochondrial control region sequence and nuclear GPIP genotype. *Molecular Phylogenetics and Evolution* **33**, 339-348. doi.org/10.1016/j.ympev.2004.06.004
- Górski, K., De Leeuw, J., Winter, H., Khoruzhaya, V., Boldyrev, V., Vekhov, D., Nagelkerke, L. (2016). The importance of flooded terrestrial habitats for larval fish in a semi-natural large floodplain (Volga, Russian Federation). *Inland Waters* **6**, 105-110. DOI: [10.5268/IW-6.1.914](https://doi.org/10.5268/IW-6.1.914)
- Hurd, L.E., Sousa, R. G., Siqueira-Souza, F. K., Cooper, G. J., Kahn, J. R., Freitas, C. E. (2016). Amazon floodplain fish communities: Habitat connectivity and conservation in a rapidly deteriorating environment. *Biological Conservation* **195**, 118-127.
doi.org/10.1016/j.biocon.2016.01.005
- Jackson, A.L., Inger, R., Parnell, A. C., Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER—Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology* **80**, 595-602.
- James, C.S., Reside, A. E., VanDerWal, J., Pearson, R. G., Burrows, D. W., Capon, S. J., Harwood, T. D., Hodgson, L., Waltham, N. J. (2017). Sink or swim? Potential for high faunal turnover in Australian rivers under climate change. *Journal of Biogeography*. **44**, 489-501. doi.org/10.1111/jbi.12926
- Jardine, T.D., Pettit, N. E., Warfe, D. M., Pusey, B. J., Ward, D. P., Douglas, M. M., Davies, P. M., Bunn, S. E. (2012). Consumer-resource coupling in wet-dry tropical rivers. *Journal of Animal Ecology* **81**, 310-322. doi.org/10.1111/j.1365-2656.2011.01925.x
- Jiang, T.-t., Pan, J. F., Pu, X. M., Wang, B., Pan, J. J. (2015). Current status of coastal wetlands in China: degradation, restoration, and future management. *Estuarine, Coastal and Shelf Science* **164**, 265-275. doi.org/10.1016/j.ecss.2015.07.046
- King, A., Humphries, P., Lake, P. (2003). Fish recruitment on floodplains: the roles of patterns of flooding and life history characteristics. *Canadian Journal of Fisheries and Aquatic Sciences* **60**, 773-786. doi.org/10.1139/f03-057
- Krull, C.R., Choquenot, D., Burns, B. R., Stanley, M. C. (2013). Feral pigs in a temperate rainforest ecosystem: disturbance and ecological impacts. *Biological Invasions* **15**, 2193-2204. doi.org/10.1007/s10530-013-0444-9
- Lopez, J., Hurwood, D., Dryden, B., Fuller, S. (2014). Feral pig populations are structured at fine spatial scales in tropical Queensland, Australia. *PloS one* **9**, e91657. □
doi.org/10.1371/journal.pone.0091657
- Love, S., Phelps, Q., Tripp, S., Herzog, D. (2017). The importance of shallow–low velocity habitats to juvenile fish in the middle Mississippi River. *River Research and Applications* **33**, 321-327. doi.org/10.1002/rra.3075
- Ma, Z., Cai, Y., Li, B., Chen, J. (2010). Managing wetland habitats for waterbirds: an international perspective. *Wetlands* **30**, 15-27. DOI [10.1007/s13157-009-0001-6](https://doi.org/10.1007/s13157-009-0001-6)
- McJannet, D., Marvanek, S., Kinsey-Henderson, A., Petheram, C., Wallace, J. (2014). Persistence of in-stream waterholes in ephemeral rivers of tropical northern Australia

- and potential impacts of climate change. *Marine and Freshwater Research* **12**, 1131-1144. doi.org/10.1071/MF14035
- Mitchell, J., Mayer, R. (1997). Diggings by feral pigs within the Wet Tropics World Heritage Area of north Queensland. *Wildlife Research* **24**, 591-601. doi.org/10.1071/WR96041
- Pander, J., Mueller, M., Geist, J. (2018). Habitat diversity and connectivity govern the conservation value of restored aquatic floodplain habitats. *Biological Conservation* **217**, 1-10. doi.org/10.1016/j.biocon.2017.10.024
- Petheram, C., McMahon, T. A., Peel, M. C. (2008). Flow characteristics of rivers in northern Australia: implications for development. *Journal of Hydrology* **357**, 93-111. doi.org/10.1016/j.jhydrol.2008.05.008
- Pettit, N., Jardine, T., Hamilton, S., Sinnamon, V., Valdez, D., Davies, P., Douglas, M., Bunn, S. E. (2012). Seasonal changes in water quality and macrophytes and the impact of cattle on tropical floodplain waterholes. *Marine and Freshwater Research* **63**, 788-800. doi.org/10.1071/MF12114
- Phelps, Q.E., Tripp, S. J., Herzog, D. P., Garvey, J. E. (2015). Temporary connectivity: the relative benefits of large river floodplain inundation in the lower Mississippi River. *Restoration Ecology* **23**, 53-56. doi.org/10.1111/rec.12119
- Pusey, B.J., Arthington, A. H. (2003). Importance of the riparian zone to the conservation and management of freshwater fish: a review. *Marine and Freshwater Research* **54**, 1-16. doi.org/10.1071/MF02041
- Pusey, B.J., Bird, J. R., Close, A. H., Arthington, A. H. (2001). Reproduction in three species of rainbowfish (Melanotaeniidae) in rainforest streams of north-eastern Queensland. *Ecology of Freshwater Fish* **10**, 75-87. doi.org/10.1034/j.1600-0633.2001.100202.x
- Pusey, B.J., Kennard, M. J., Douglas, M., Allsop, Q. (2018). Fish assemblage dynamics in an intermittent river of the northern Australian wet-dry tropics. *Ecology of Freshwater Fish* **27**, 78-88. doi.org/10.1111/eff.12325
- Quinn, G.P., Keough, M. J. (2002). *Experimental design and data analysis for biologists*. Cambridge University Press
- Robertson, E.P., Fletcher, R. J., Austin, J. D. (2017). The causes of dispersal and the cost of carryover effects for an endangered bird in a dynamic wetland landscape. *Journal of Animal Ecology*. **86**, 857-865 doi.org/10.1111/1365-2656.12676
- Ross, B., Waltham, N. J., Schaffer, J., Jaffer, T., Whyte, S., Perry, J., Vanderduys, E., Macdonald, S., Morgan, M., Walsh, T., Huerlimann, R., LePort, A., Burrows, D., Jerry, D. (2017). *Improving biodiversity outcomes and carbon reduction through feral pig abatement*. Cairns: Balkanu Cape York Development Corporation Ltd Pty, 172 p.
- Schomaker, C., Wolter, C. (2011). The contribution of long-term isolated water bodies to floodplain fish diversity. *Freshwater Biology* **56**, 1469-1480. doi.org/10.1111/j.1365-2427.2011.02583.x
- Sheaves, M., Johnston, R. (2009). Ecological drivers of spatial variability among fish fauna of 21 tropical Australian estuaries. *Marine Ecology Progress Series* **385**, 245-260. doi.org/10.3354/meps08040
- Steward, A.L., Negus, P., Marshall, J. C., Clifford, S. E., Dent, C. (2018). Assessing the ecological health of rivers when they are dry. *Ecological Indicators* **85**, 537-547. doi.org/10.1016/j.ecolind.2017.10.053
- Stewart-Koster, B., Olden, J., Kennard, M. J., Pusey, P., Boone, E., Douglas, M., Jackson, J. (2011). Fish response to the temporal hierarchy of the natural flow regime in the Daly River, northern Australia. *Journal of Fish Biology* **79**, 1525-1544. doi.org/10.1111/j.1095-8649.2011.03072.x
- Swanson, H.K., Lysy, M., Power, M., Stasko, A. D., Johnson, J. D., Reist, J. D. (2015). A new probabilistic method for quantifying n-dimensional ecological niches and niche overlap. *Ecology* **96**, 318-324. doi.org/10.1890/14-0235.1

- Wallace, J., Waltham, N. J., Burrows, D. (2017). A comparison of temperature regimes in dry-season waterholes in the Flinders and Gilbert catchments in northern Australia. *Marine and Freshwater Research* **68**, 650-667. doi.org/10.1071/MF15468
- Wallace, J., Waltham, N. J., Burrows, D. W., McJannet, D. (2015). The temperature regimes of dry-season waterholes in tropical northern Australia: potential effects on fish refugia. *Freshwater Science* **34**, 663-678. doi.org/10.1086/681278
- Waltham, N., Schaffer, J. (2017). Continuing aquatic assessment of wetlands with and without feral pig and cattle fence exclusion, Archer River catchment. Centre for Tropical Water and Aquatic Ecosystem Research (TropWATER), James Cook University, Townsville, Queensland, Australia.
- Waltham, N., Fixler, S. (2017). Aerial herbicide spray to control invasive water hyacinth (*Eichhornia crassipes*): Water quality concerns fronting fish occupying a tropical floodplain wetland. *Tropical Conservation Science* **10**, 1940082917741592. doi.org/10.1177/1940082917741592
- Waltham, N.J., Schaffer, J. R. (2018). Thermal and asphyxia exposure risk to freshwater fish in feral-pig-damaged tropical wetlands. *Journal of Fish Biology* **93**, 723-728. doi.org/10.1111/jfb.13742
- Waltham, N.J., Elliott, M., Lee, S.Y., Lovelock, C., Duarte, C.M., Buelow, C., Simenstad, C., Nagelkerken, I., Claassens, L., Wen, C.C.K., Barletta, M., Connolly, R.M., Gillies, C., Mitsch, W.J., Ogburn, M.B., Purandare, J., Possingham, H., Sheaves, M. (2020). UN Decade on Ecosystem Restoration 2021-2030: what chance for success in restoring coastal ecosystems? *Frontiers in Marine Science* **7**:71 doi.org/10.3389/fmars.2020.00071
- Weinstein, M.P., Litvin, S.Y. (2016). Macro-restoration of tidal wetlands: A whole estuary approach. *Ecological Restoration* **34**, 27-38. doi: 10.3368/er.34.1.27
- Zedler, J.B. (2016). What's New in Adaptive Management and Restoration of Coasts and Estuaries? *Estuaries and Coasts* **40**, 1-21. DOI 10.1007/s12237-016-0162-5
- Žmihorski, M., Pärt, T., Gustafson, T., Berg, A. (2016). Effects of water level and grassland management on alpha and beta diversity of birds in restored wetlands. *Journal of Applied Ecology* **53**, 587-595. doi./10.1111/1365-2664.12588

Declaration of competing interest. The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Data Accessibility Statement. All data associated with this publication (sample sites, coordinates, environmental data and fish catch) can be accessed on Dryad

CRedit authorship contribution statement. Nathan Waltham: Data curation, Formal analysis, Conceptualisation, Writing - original draft, Writing - review & editing. Jason Schaffer: Conceptualisation, Writing - review & editing.

1034

1035 **Acknowledgements**

1036 This project builds on a long-term feral animal management and monitoring program
1037 developed by Kalan enterprises and Aak Puul Ngangtam (APN) and their partners. Kalan and
1038 APN have developed their feral animal research and management agenda to meet the
1039 objectives of traditional owners in the region and have invited science organisations (CSIRO,
1040 James Cook University and the Department of Science and Environment) to contribute to the
1041 outcomes. APN and Kalan have conducted systematic feral pig control and monitoring in the
1042 Archer River basin for the past 6 years. This study was completed in accordance with the
1043 Queensland Animal Care and Protection Act 2001, and JCU animal ethics permit number
1044 A2178. We thank the reviewers who improved this manuscript considerably. This study
1045 (Project 2.5) is funded by the Australian Government National Environment Sciences Program
1046 (Northern Australian Hub).

1047