Independent analysis of lungfish monitoring data at Paradise Dam

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Report for analysis of lungfish monitoring data at Paradise dam

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Summary

Background

The Queensland Lungfish (*Neoceratodus forsteri*) is a nationally threatened fish that is native to the Mary and Burnett river systems. As part of the Commonwealth environmental approval for the construction and operation of Paradise Dam, Burnett Water (owned by SunWater) was required to implement a lungfish monitoring programme. The approval required Burnett Water to undertake aquatic ecosystem monitoring at points on the Burnett River in the vicinity of Paradise Dam. This 10-year monitoring program included the measurement of the condition of lungfish. Between 2006 and 2016, lungfish were sampled every 6 months (summer and winter) at seven sites: two downstream sites (Sites 1 and 2), two sites in the dam impoundment (Sites 4 and 5), and three upstream sites (Sites 6, 7 and 8). Fish were sampled using electrofishing methods and collected fish were tagged and measured.

Purpose

In 2016, an initial analysis of this monitoring program was completed and the report was submitted to the Commonwealth for review. Comments from the Commonwealth led to the commissioning of additional analyses. Specifically, a re-analysis of the catch-per-unit effort (CPUE) and mark-recapture data was requested. This report presents the results from this re-analysis.

CPUE results

For each sampling event at each site, CPUE was calculated. Since comparison between CPUE estimates assumes similar catchability, CPUE were statistically standardised by several environmental covariates: water flow, water temperature, conductivity, and season (when applicable to the site). Overall, CPUE was found to be decreasing at the downstream sites [Site 4 (Kalliwa) and 5 (Mingo)] and the upstream Site 7 (Claude Wharton). No significant temporal patterns were found for Site 1 (Isis) or Site 8 (Mundubbera).

For Site 2 (Figtree) , no statistically significant temporal trend was found when environmental covariates were included. However, the correlation between time and water flow (i.e. later years had higher water flows) led to the confounding of time and water flow. Therefore, the model was rerun with no environmental covariates and showed a significant decline in summer CPUEs, but not in winter CPUEs. Summer surveys were associated with high water flows, whereas winter surveys had much lower fluctuations in water flow. Therefore, the lack of significant decline during winter adds additional support that water flow explains declines during the summer.

Similarly, no statistically significant temporal trend in CPUE was found for Site 6 (Gray's waterhole) when environmental covariates were included. When the environmental covariates are removed, a significant decline was found. Again, the confounding of the covariates and time complicates interpretation.

Mark-recapture results

For upstream and downstream sites, a Jolly-Seber model with a POPAN (superpopulation) formulation was created. This model allows for the estimation of population size, recruitment, catchability and apparent survival [i.e. the probability that a fish remains in the population (does not migrate or die)].

Mark-recapture models for the downstream Sites 1 and 2 (Isis and Figtree) had very similar patterns. Lungfish populations increased at both sites over time, though the pattern was more evident at Site 2

(Figtree). Apparent survival was high at both sites at ~95%, although this is not surprising for such a long lived species as the lungfish. Catchability was low (~1-5%), similar to other freshwater fish (i.e. golden perch), and decreased with increased water flow.

For upstream sites Site 6 and 7, models found that lungfish abundances decreased over time. Apparent survival was lower for these sites than the downstream sites. In contrast, model results for Site 8 showed increasing lungfish abundance, due to higher apparent survival rates.

Conclusions

The main results of this report can be used to supplement the analysis in the initial monitoring report. The main results were the following:

1. For downstream sites (Isis and Figtree), standardised CPUE results suggested no decline. Mark-recapture analyses indicated high apparent survival and stable or increasing population sizes.
2. For dam sites (Kalliwa and Mingo), standardised CPUE declined to low levels. Whether this is due to reduced catchability with the current methods or lungfish emigrating or dying cannot be determined. Movement data did suggest a possible efflux of lungfish from dam sites, with large proportion of those fish emigrating to the Figtree site.
3. For upstream sites 6 (Gray's waterhole) and 7 (Claude Wharton), standardised CPUE patterns were not conclusive, but results were suggestive of declining CPUE at sites 6 and 7. Supportingly, the mark-recapture data estimated lower apparent survivorship for sites 6 and 7 compared to downstream sites and found decreasing population sizes.
4. For upstream sites 8 (Mundubbera), standardised CPUE suggested no decline and mark-recapture analysis estimated a high survivorship and increasing population sizes.

1 Introduction

In 2005, the construction of the Paradise Dam along the Burnett River (131 km AMTD) was completed. As part of the Commonwealth environmental approval for the construction and operation of this dam, Burnett Water (owned by SunWater) was required to implement a lungfish monitoring program. A main objective of this program was to assess population trends over time of lungfish at different sites along the river. Consequently, a 10-year monitoring project (2006-2016) was initiated in which lungfish were regularly sampled (every winter and summer) at seven sites, located upstream (x3 sites), within (x2), and downstream (x2) of Paradise Dam. In 2016, a draft monitoring report was submitted to the Commonwealth presenting the initial findings of this monitoring program.

In this draft monitoring report, the analysis of population trends was assessed mainly through two methods: catch-per-unit effort (CPUE) and a mark-recapture analysis. CPUE is a common used method in fisheries and provides a proxy for population size (Walters and Martell, 2004). In this study, lungfish were sampled using electrofishing and the captured fish were measured and tagged. With electrofishing, CPUE is calculated as the number of fish per unit time of electrofishing (e.g. number of fish per minute) and comparing CPUE across time can provide insights into population trends (Hangsleben et al., 2013). Though commonly used, this method relies on the assumption that fish catchability remains constant over time. However, this assumption is likely violated in aquatic systems. Riparian systems often have changing water conditions due to seasonal and yearly rainfall variations. These variations can affect the effectiveness of electrofishing by altering water conductivity, turbidity, and water depth; all conditions known to affect electrofishing effectiveness and hence catchability of fish (Lyon et al., 2014). For instance, increasing turbidity reduces the researcher's ability to spot fish, leading to lower CPUE.

The second population assessment method used in this draft monitoring report was calculating population size with the mark-recapture data. Mark-recapture methods are a very useful method for estimating population size and assessing population temporal trends. Mark-recapture allows for the estimation of catchability (i.e. the probability an individual present is captured), which can then lead to an actual estimate of population size, instead of just being a proxy like CPUE. Furthermore, mark-recapture data can be used to estimate important population parameters, such as survival and recruitment rates. Mark-recapture methods are well-developed and diverse, ranging from models estimating population size in closed populations (no births, migration, deaths) to integrated population models that estimate birth, deaths, and migration rates (Cooch and White, 2006). As with any estimation method, many of these models rely on various assumptions (e.g. no mortality, no migration, no loss of tag) and violations of these assumptions can lead to biased estimates.

After submitting the initial report, the Commonwealth responded with brief feedback, with two main comments about the initial analyses (and hence the conclusions from these analyses). The first main comment was in regards to the CPUE analysis. The report's CPUE analysis indicated that CPUE changed over years and concluded that there was an overall decline. The report then stated that "the overall decline was almost certainly influenced by declining catches at the two locations within the dam". The Commonwealth reviewer correctly noted (and showed) that there were declines in other sites, with Figtree (a downstream site) being most evident. However, neither the report's nor the reviewer's analysis explicitly incorporated the potential effects of changing catchability. Catchability likely varied during the study period as 2007-2009 represented drought years and 2010-2016 had major flood events, which greatly affected water conditions.

The second main comment regarded the mark-recapture analysis. In the report, the mark-recapture data were analysed using the Lincoln-Petersen method. This method assumes a closed population; in other words, there is no migration, births, or deaths. Consequently, the Lincoln-Petersen approach is often used with mark-recapture data that are collected over a short time frame (days, weeks). The reviewer notes that this assumption is highly unlikely given that the study lasted 10-years. Though lungfish are best described as k-selected species (i.e. low mortality and birth rates), there would still be non-ignorable mortality over 10 years (e.g. if a 99% annual survival rate is assumed, 10% of the population would have died over 10 years). As with the CPUE analysis, varying fish catchability over time is problematic in comparing the Lincoln-Petersen population estimates.

To address these criticisms, SunWater commissioned further analyses to be performed. Consequently, temporal trends in CPUE were re-analysed using standardized CPUE. Standardized CPUE were created by including environmental variables (e.g. flow rate, water temperature, conductivity) in the model to statistically control for their effects on catchability. Next, the mark-recapture data were re-analysed either using an open-population model (Jolly-Seber using POPAN formulation in JAGS) if sufficient data existed or using an Cormack-Jolly-Seber to estimate apparent survivor rates. This report presents the findings from these analyses.

2 Experimental design and site covariates

Before commencing the analyses, an initial exploration of the data was conducted to elucidate the experimental design, as well as describe the correlation between environmental covariates at each sites. Describing these correlations provides insights in which variable may be confounded (i.e. strongly correlated with each other).

2.1 Sampling design

Overall, 6353 individual fish were tagged, with 839 fish recaptured at least once across seven sites.

Figure 1 shows an overview of when the sampling event occurred. There was a shift in summer sampling in 2013 and a slight shift in winter 2014, but otherwise the sampling was fairly consistent.
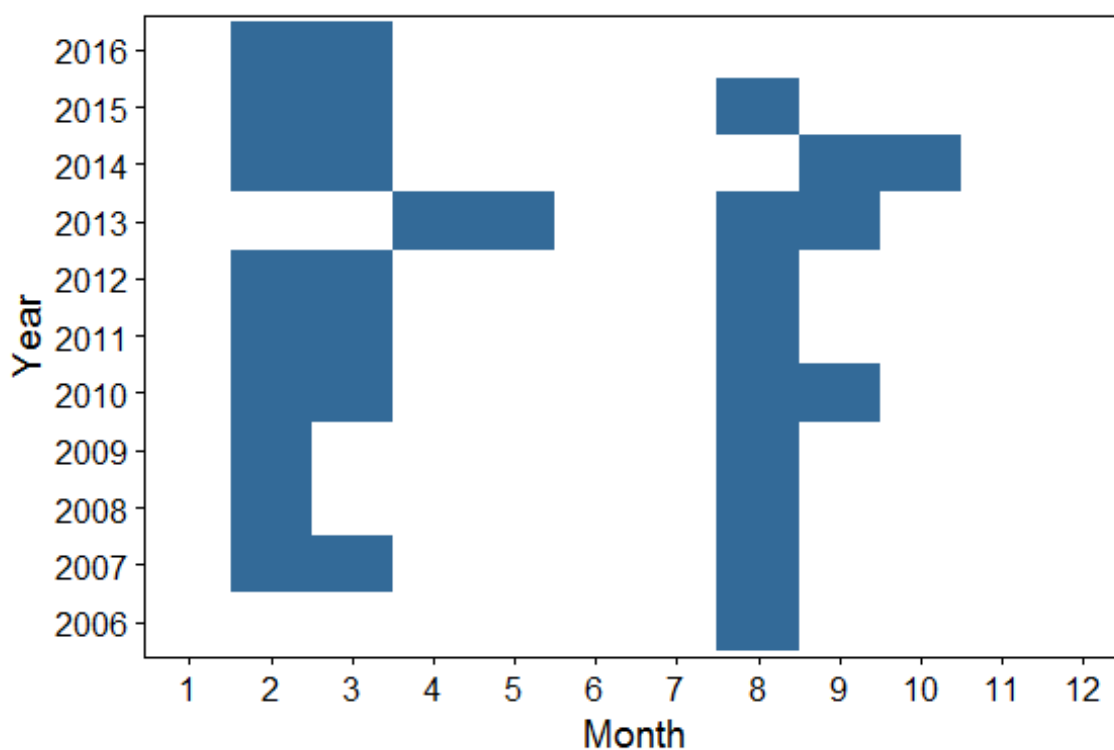
Figure 1. Sampling periods between 2006 and 2016. Blue rectangles indicate sampling periods.

Conclusion: If there are oddities in summer 2013 or winter 2014 estimates, it could reflect this temporal shift in sampling.

2.2 Site covariates

Next, the environmental covariates were explored. The environmental variables were water temperature, water flow, season, and water conductivity. The purpose of this section is to assess how correlated the covariates were as well as assess the distribution of the covariates to determine if transformations are needed to prevent excess influence of large values in the analyses. Correlations

were also examined between each environmental variable and date, as this will indicate if any of the environmental variables changed systemically over time, possibly confounding time effects with that variable.

As seen in Figure 2, there are a several key findings that will shape the analysis and complicate interpretation of the results.

1. Water temperature will be confounded with season (i.e. if there is a season effect, it may be due to colder water), but it may be possible to examine how water temperature within a season affects counts. Another insight is that water temperature is fairly similar across sites. Note - water temperature data were missing for sites 7 and 8.

2. As for water conductivity, there is large variation in the data, with points ranging up to three-fold higher than the median and leading to a skewed distribution. Consequently, a log-transformation will be needed. Site 6 appears to have higher conductivity. Note - water conductivity data were missing for sites 7 and 8.

3. Finally, for water flow (ML/day), the vast majority of the variance is in summer, with winter having much lower flow and variation. The lack of flow at Site 4 and 8, and the near lack of flow at Site 5, is readily apparent. Thus, flow rate and sites are strongly confounded. Also, for sites 1, 2, 6, and 7 flow rate is confounded with season.

Figure 2. Boxplots of each covariate (water temperature, conductivity and flow) by site and season. Each panel shows a boxplot of the covariates by site, grouped by season (summer=red, winter=blue). The horizontal bar in the middle of each box shows the median value of the data. The lower and upper ends of the box show the 25th and 75th percentiles of the data (in other words, 50% of the data lie between the ends of the box). The whiskers (the vertical bars) show the minimum and maxi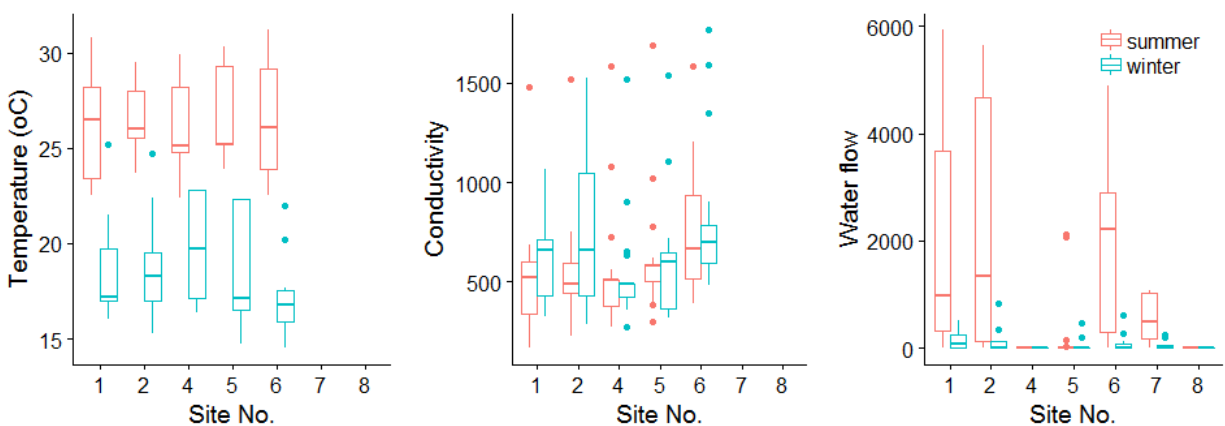mum values within 1.5 times of the interquantile range. Dots are values above or below 1.5 times the interquantile range.

Additionally, pairwise correlations between the environmental variables were calculated, as well as the correlation with date. These correlations will help determine which variables are confounded and help in interpretation of model results.

1. For sites 1, 2, and 6 (the open stream sites), a positive correlation between water temperature and water flow was evident, as well as date with all variables.

2. Date and conductivity are positively correlated for all sites with conductivity data.

Table 1. Pearson correlations between covariates for each site. Last three columns show the correlation between the third column covariate and the column covariate. For instance, the correlation between conductivity and flow rate is -0.16 for Isis site. Bold values show the correlations between date and flow rate.

Site No.	Site Name	Covariate	Conductivity	Flow rate	Date
1	Isis	Temperature	-0.01	0.59	0.44
		Conductivity		-0.16	0.35
		Flow rate			**0.58**
2	Figtree	Temperature	0.02	0.54	0.28
		Conductivity		-0.22	0.38
		Flow rate			**0.46**
4	Kalliwa	Temperature	0.11		0.22
		Conductivity			0.64
		Flow rate			
5	Mingo	Temperature	0.09	0.14	0.06
		Conductivity		0.04	0.42
		Flow rate			**0.29**
6	Gray's Waterhole	Temperature	-0.16	0.49	0.25
		Conductivity		-0.27	0.35
		Flow rate			**0.26**
7	Claude Wharton	Temperature			
		Conductivity			
		Flow rate			**0.48**
8	Mundubbera	Temperature			
		Conductivity			
		Flow rate			

Conclusion: The above findings suggest that there is some confounding of date and the other variables. Therefore, for sites with complete environmental data, it may be preferred to run two models: 1) model with just date and 2) a model with date and the environmental variables. Comparison of these results will indicate how robust the model conclusions are.

3 Temporal patterns in CPUE

3.1 Statistical methods

For CPUE data, each site was analysed separately for the following reasons: 1) flow covariates were not comparable between sites (e.g. actual streamflow vs. water released from upstream weir vs. no flow at pond sites) and hence covariates were confounded by site (i.e. stream sites differ from ponded sites by more than just flow rate); 2) inspection of exploratory graphs revealed that some sites had more

variation in counts that would not be remedied by transformation and the included predictors; and 3) the project brief supplied by the client asked specifically for a trend analysis of Site 2 (Figtree).

For each site, a generalized additive model (GAM) was run using the *gam()* function in *mgcv* package (Wood 2004) in R (R Core Team 2016). For each model, the number of fish caught was the response variable. Date was included as a thin-plate spline (*s(date)*), as well the following linear predictors (if applicable for the site): water temperature, water conductivity (log-transformed), and flow/storage depth (log-transformed + 1). It was assumed that the number of fish captured followed a negative binomial distribution. An offset of fish time was included to control for variable sampling effort. Smoothness of the splines were estimated using the REML approach (Wood 2006).

To determine if temporal patterns in CPUE differed between seasons (i.e. do winter CPUE patterns differ from summer CPUE patterns), the above models were compared to a model in which separate splines were fitted for each season [*s(date, by=season)*]. AIC was used to determine the best fitting model (Anderson and Burnham 2002). If the date spline had an estimated degree of freedom (EDF) of one, the model was refitted assuming a linear relationship between CPUE and date so that a slope estimate could be estimated.

Since season was confounded with water temperature and flow rate for some sites (as shown above in the covariate section), the above model was fitted and then a term for season was added and compared the two models using AIC to determine if season provided additional information. If the model with season did not improve the model by >2 AIC units, season was not included in the final model.

Next, another GAM was run in which only date (as a spline) and season were included in the model. This model was compared to the model with both date and the environmental covariates. If conclusions about the effect of date differed between the models, this would suggest that date and the environment may be explaining the same patterns and hence confounded.

For each model, a residual analysis were performed to assess model assumptions (e.g. no temporal correlation in residuals, no influential points, linear effect of covariates).

Note - As the fitted parameters for GAMs are not informative without the underlying basis formula, only the significance level and estimated degree of freedom (EDF) for the spline fit were presented, as well as a graphical representation of the spline. The number for the EDF indicates the shape of the curve. For reference, EDF near 1 is linear, and EDF near 2 is quadratic(-ish). For the environmental variables, results are presented as the slope estimate ± one standard error.

3.2 Results

Site 1: Isis

No statistically significant temporal pattern in CPUE was detected (Table 1; Figure 3). Furthermore, no environmental variables were significant either (Table 2). Running the model with only date and season, no statistically significant temporal pattern was found (EDF = 1.0, p = 0.07). The mean CPUE for the site was 1.69 (95%CI 1.44, 1.99).

Site 2: Figtree

No statistically significant temporal pattern in CPUE was detected (Table 2; Figure 3) when environmental variables were included. Flow rate was found to be significant, with decreased CPUE estimates with higher flow rates.

When the model was re-run with no environmental covariates, a significant temporal pattern is found (EDF = 2.6, p = 0.01), in which summer CPUE initially decrease between 2006 and 2012 and then levels off (see Figure 4). Winter CPUE did not significantly change over time (EDF = 1, p = 0.23). The mean CPUE for the site was 3.02 (95%CI 2.66, 3.42).

Site 4: Kalliwa Hut

Temporal patterns differed by season (Table 2; Figure 3). In summer, a significant decline in CPUE that eventually leveled off, but no change in winter CPUE was detected. The mean CPUE for the site was 0.11 (95%CI 0.07, 0.16).

Site 5: Mingo Gorge

CPUE significantly decreased over time (Table 2; Figure 3). Water temperature had a negative effect on CPUE, which could reflect a general seasonal effect. Re-running the model with just date and season resulted in the same pattern (EDF = 1, p < 0.001). The mean CPUE for the site was 0.32 (95%CI 0.19, 0.55).

Site 6: Gray's Waterhole

No statistical significant temporal pattern in CPUE was detected (Table 2; Figure 3). Furthermore, no environmental variables were significant (Table 2). Running the model with only date and season, the temporal pattern was significant, with decreasing CPUE until 2012 at which point CPUE levels off (EDF = 1.9, p = 0.02; see Figure 4). The mean CPUE for the site was 0.53 (95%CI 0.35, 0.79).

Site 7: Claude Wharton Weir

CPUE significantly decreased over time (Table 2; Figure 3). When the model was re-run excluding flow rate, the temporal pattern was very similar (linear decrease). The mean CPUE for the site was 1.56 (95%CI 1.2, 2.02).

Site 8: Mundubbera

No statistical significant temporal pattern in CPUE was detected (Table 2; Figure 3). Season also was not significant (Table 2). The mean CPUE for the site was 0.53 (95%CI 0.38, 0.75).
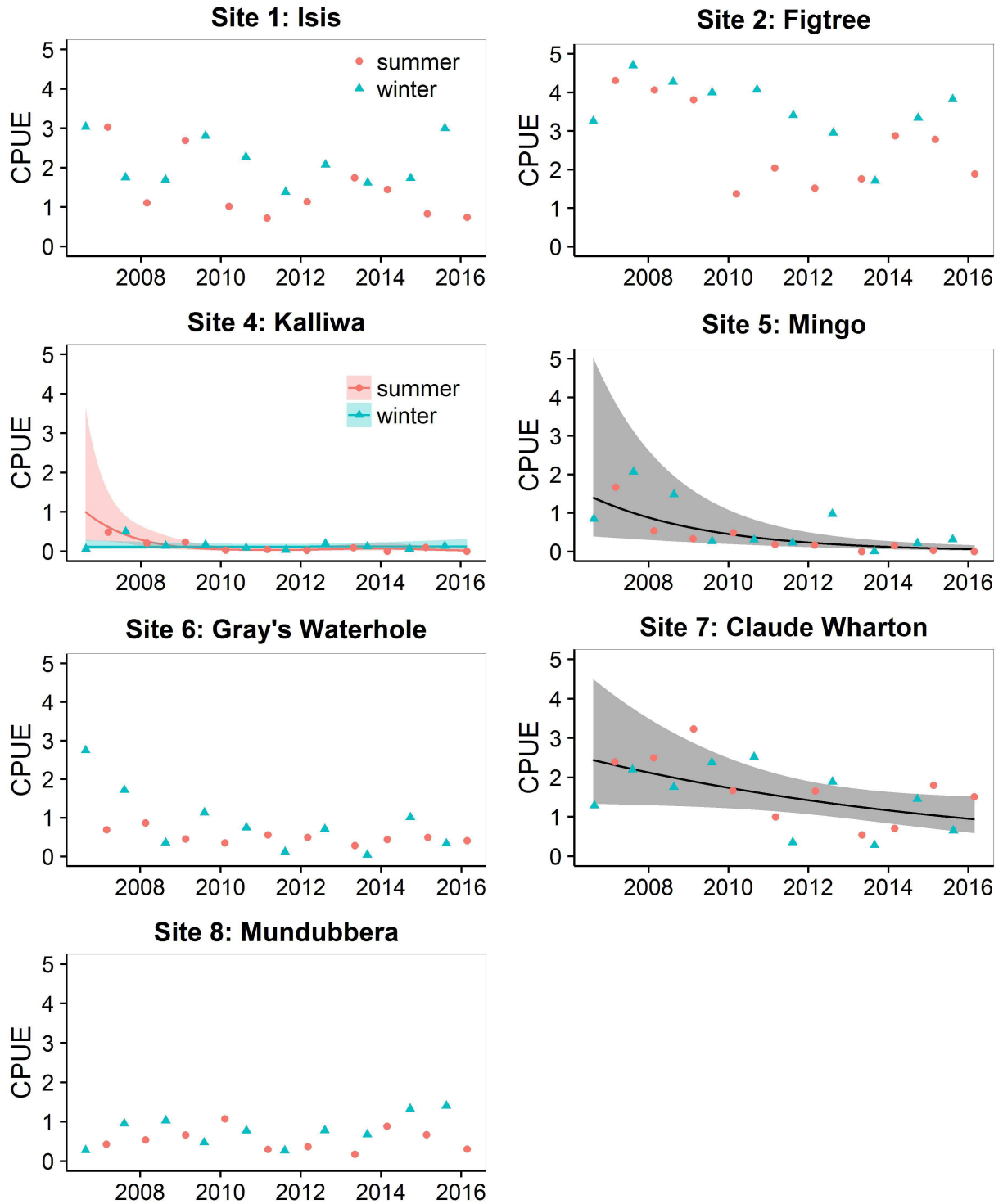
Figure 3. Temporal patterns in CPUE for each site from GAM model. Points show raw data, grouped by season. If a panel has not plotted curve, then there was no significant trend over time. Black curves indicate that there was the same temporal pattern across seasons. If there are two curves, temporal patterns differed significantly by season.
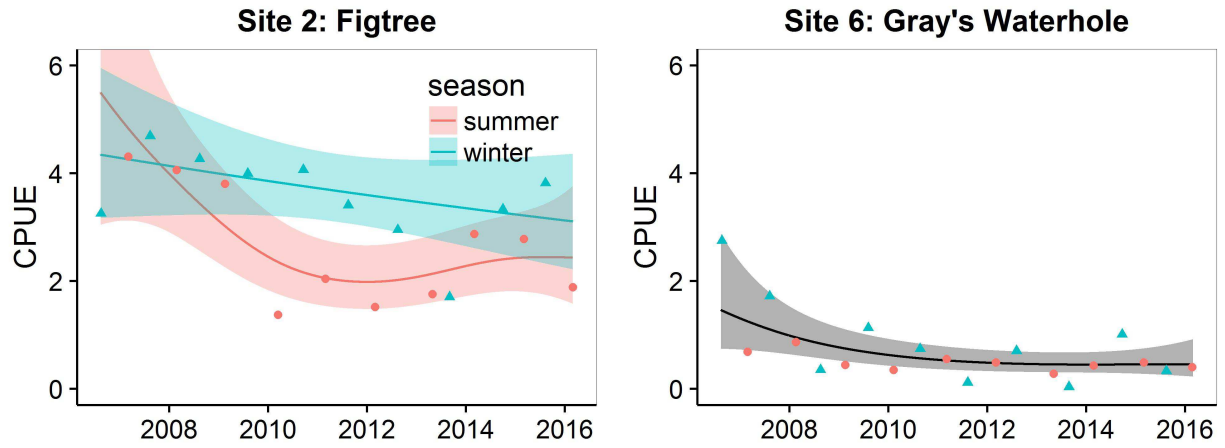
Figure 4. Temporal patterns in CPUE for Site 2 and 6 for models without environmental covariates.

Table 2: Summary of statistical results for all sites. Rows are grouped by predictor variable: time (date) or other covariate. For time, it could be linear (i.e. a slope), a spline for both seasons combined, or separate splines for summer and winter. If the best model was a linear slope, the slope estimate ($\pm$ SE) is listed, with the p-value in round brackets. For time splines, estimated EDF are listed with p-value in the round brackets (see Figures for shape of spline). For the other covariates, estimates are slope ($\pm$ SE), except for season which is the estimate of the change in CPUE from summer to winter. Again, p-values are in round brackets.

Type	Variable	Site 1	Site 2	Site 4	Site 5	Site 6	Site 7	Site 8
Time	Linear	-0.03 ± 0.040 (0.45)	-0.01 ± 0.027 (0.65)		**-0.33 ± 0.090 (<0.001)**	-0.08 ± 0.060 (0.18)	**-0.10 ± 0.048 (0.036)**	0.03 ± 0.041 (0.42)
	Summer			**3.0 (<0.001)**				
	Winter			1.0 (0.92)				
Other	Flow rate	-0.08 ± 0.061 (0.16)	**-0.10 ± 0.034 (0.005)**		-0.02 ± 0.082 (0.81)	-0.09 ± 0.065 (0.17)	0.02 ± 0.066 (0.73)	
	Conductivity	0.29 ± 0.194 (0.14)	-0.05 ± 0.159 (0.75)	-0.62 ± 0.529 (0.24)	0.35 ± 0.518 (0.50)	-0.32 ± 0.397 (0.42)		
	Temperature	-0.47 ± 0.459 (0.31)	-0.13 ± 0.361 (0.71)	**4.58 ± 1.692 (0.007)**	**-1.97 ± 0.950 (0.038)**	-0.11 ± 0.698 (0.87)		
	Season			**2.17 ± 0.675 (0.001)**				0.39 ± 0.240 (0.10)

5 Mark-recapture analysis

This section is divided into multiple subsections. First, an initial exploratory analysis was conducted to help determine the suitability of these data for a mark-recapture analysis, as well as possible processes (e.g. movement, length patterns) in the system. Then, several mark-recapture analyses were conducted.

5.1 Capture/recapture summary

The table below summarises the capture/recapture data for all sites. Site 2 (Figtree) had the highest recapture rates, with 22.4% of the fish being recaptured at least once. Site 1 (Isis) also had large numbers Site 6-8 have lower numbers but deemed large enough to attempt a mark-recapture analysis.

Table 3. Descriptive statistics for recaptures. Each column shows the number of captures for each site. For instance, column '1' indicates the number of fish that were captured just once. Note - fish that were measured but not tagged were dropped.

Site No.	Site Name	Total Fish	1	2	3	4	5	6
	Total	6352	5515 (86.8%)	699 (11%)	115 (1.8%)	17 (0.3%)	5 (0.1%)	1 (0%)
1	Isis	1703	1548 (90.9%)	142 (8.3%)	11 (0.6%)	1 (0.1%)	1 (0.1%)	0
2	Figtree	1962	1523 (77.6%)	343 (17.5%)	79 (4%)	12 (0.6%)	4 (0.2%)	1 (0.1%)
4	Kalliwa	94	93 (98.9%)	1 (1.1%)	0	0	0	0
5	Mingo	518	506 (97.7%)	12 (2.3%)	0	0	0	0
6	Gray's Waterhole	458	411 (89.7%)	38 (8.3%)	8 (1.7%)	1 (0.2%)	0	0
7	Claude Wharton	969	872 (90%)	87 (9%)	10 (1%)	0	0	0
8	Mundubbera	671	605 (90.2%)	57 (8.5%)	8 (1.2%)	1 (0.1%)	0	0

5.2 Movement patterns

Overall, 25 fish were recorded moving between sites, with one fish (ID# 33454342) moving from Site 2 (Figtree) to Site 5 (Mingo) and back again from Site 5 to Site 2. Therefore, there is evidence of migration between sites.
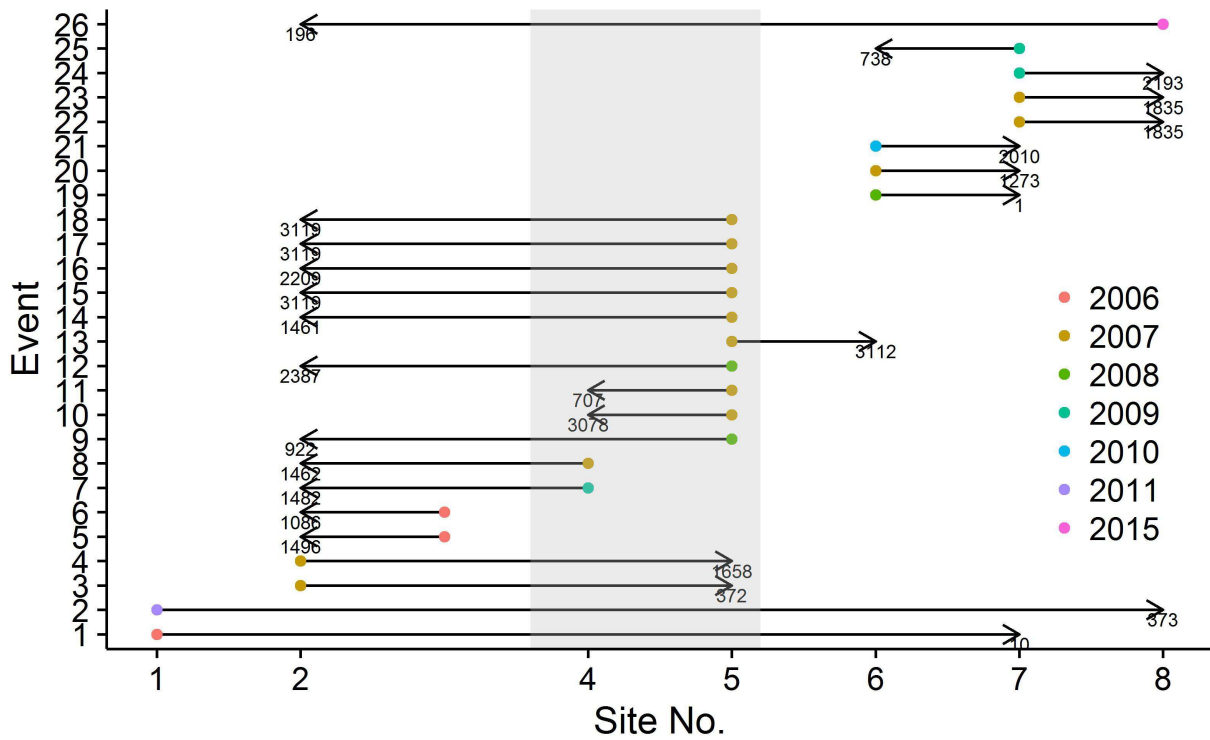
Figure 5. Summary of marked fish that moved between sites. Points show the original site of the fish (colour of the points indicate the year of the last sighting before movement) and the arrow indicates the end site. The numbers indicate the number of days between captures. Shaded grey region indicates roughly the Paradise impoundment area.

5.3 Recapture histories for fish with multiple recaptures

In Figure 6, capture histories for fish with >1 recapture were plotted. These results indicate high survival for lungfish and the low number of recaptures indicate low detection rates. The long spans between catches might indicate temporary migration in and out of sites and/or low catachability.
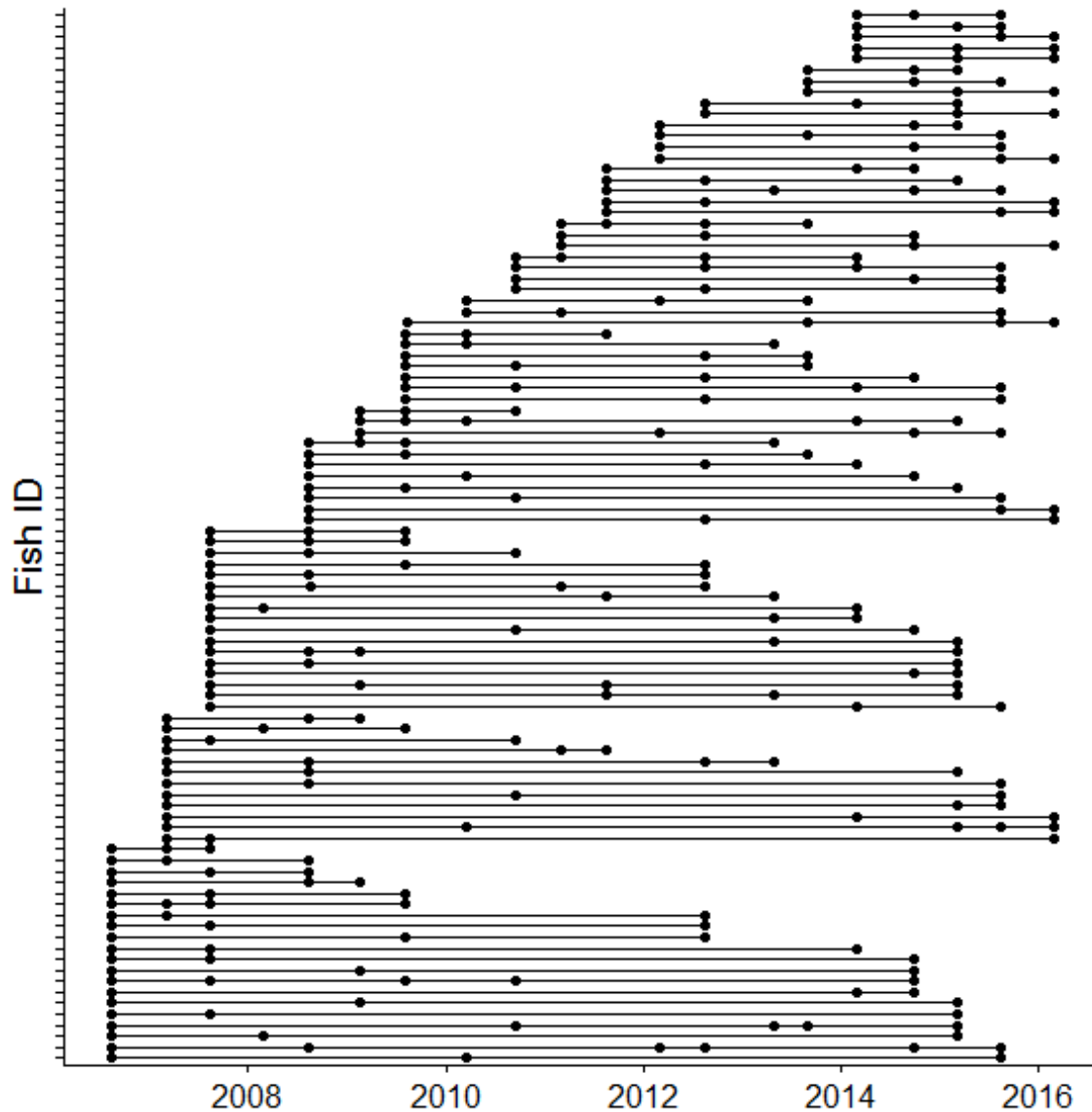
Figure 6. Capture histories for fish with multiple recaptures. Dots represent capture events and lines indicate time from first to last capture. Capture histories are ordered by date of first capture (and then by date of last capture).

5.4 Temporal patterns in distribution of fish lengths

Here, temporal patterns in fish lengths at each site are described. This analysis provides insights into possible recruitment events and changes in the age structure of the fish population over time. As with CPUE results, temporal patterns may reflect differential changes in catchability across different size classes.

5.4.1 Statistical methods

For fish length data, a quantile regression was performed to understand how distribution of lengths vary across site and across years. This analysis was used because quantile regression allowed the asking of specific questions about the distribution of lengths, instead of just questions about the mean length. Here, the following quantiles of the length distribution were modelled: 0.05, 0.5, 0.90. These quantiles were chosen in order to pick up changes in small (smallest 5% of the fish), medium, and large fish (largest 10%). For the models, date (linear slope) and site (categorical) were included as predictors, as well as the interaction between site and date. Thus, this model allows us to ask in the 0.05 quantile case if the size of the smallest fish caught was changing over time at a site, as well as if sites differ in this pattern. Similar interpretations were for the medium (0.5) and large (0.9) scenarios. The models were run using the *rq()* function in the *quantreg* (Koenker 2016) package in R. To determine if the interaction between date and site was improved the model, models were compared with and without the interaction using AIC. Finally, to determine if quantiles differed in slopes, joint tests for equality in slopes between quantiles were performed using the Wald's test. Note - time was adjusted so that time is in years and time=0 is the first sampling event.

5.4.2 Results

The best model (i.e. the most parsimonious model) included the interaction between site and date for each quantile level (>2 AIC units for each model). Additionally, the best model indicated that slopes for quantiles differed ($F_{1,26}$=15.047, p < 0.001). Results from this model can be seen in Figure 7.

Several key finding should be noted. For the smallest fish (quantile=0.05), sites 4 and 6 were significantly larger fish length (148-205 mm bigger) than sites 1 in 2006 (Figure 7;Table 4). However, sites 2, 5, 7, and 8 have increasing fish lengths for its smallest fish over time by ~ 32mm per year (Figure 7;Table 4). Therefore, by 2016, the fish in the smallest quantile increased by ~250mm at these sites.

The medium fish (quantile=0.50) were increasing in size at sites 2, 4, 5, 7, and 8 over time by 6 to 31mm per year, and the only changes in the largest fishes (0.95 quantile) were increases at sites 2 and 5.
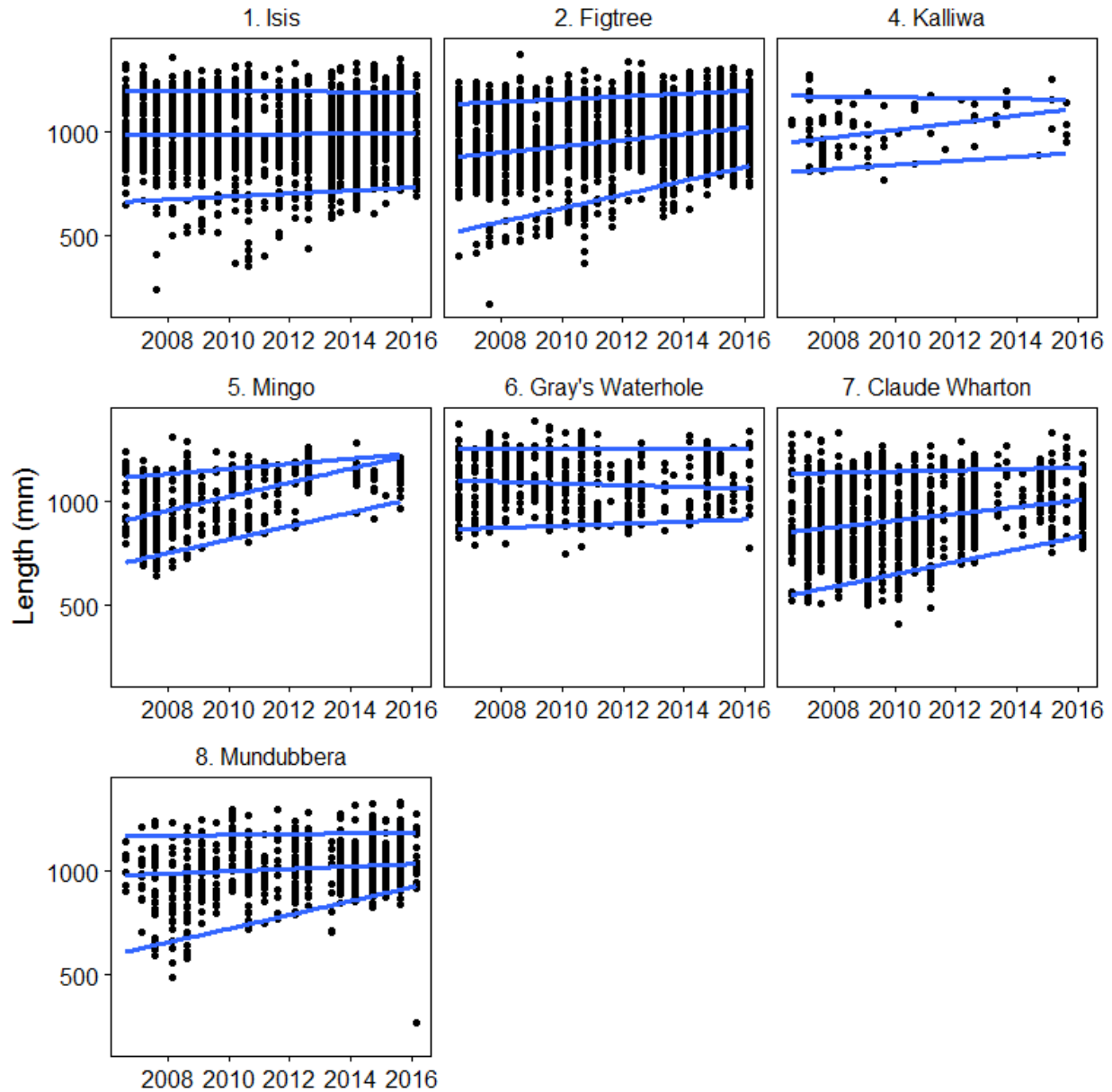
Figure 7. Distribution of fish lengths over time and sites. Each panel shows fish lengths from a site. Blue lines are fitted 0.05, 0.50, and 0.95 quantile regressions.

Table 4. Summary of quantile regression for fish length. Row indicate the predictor variable. The intercept row is fish length for Site 1 in 2006, broken up by quantile. Site 2-Site 8 indicate the change in fish length for that quantile for each site in 2006. For instance, Site 2 has significantly lower fish lengths for its medium fish by 105.94 mm. Similarly, the year row shows the effect of year on fish length for Site 1. 'Year for site X' shows the change in slope from Site 1. For instance, for Site 2, every year the smallest fish are getting bigger by 33.76 mm (= 7.63 + 26.13). Estimates are listed as quantile estimate $\pm$ one standard error with p-values in round brackets.

Variable	Small (0.05)	Medium (0.5)	Large (0.9)
Intercept	662.1 ± 33.0	988.5 ± 9.5	1202.7 ± 10.7
	(<0.001)	(<0.001)	(<0.001)
Site 2	-145.9 ± 67.4	-105.9 ± 11.3	-58.7 ± 15.1
	(0.031)	(<0.001)	(<0.001)
Site 4	148.0 ± 34.8	-36.0 ± 44.7	-26.6 ± 24.7
	(<0.001)	(0.42)	(0.28)
Site 5	39.0 ± 37.2	-70.1 ± 16.9	-85.0 ± 18.4
	(0.29)	(<0.001)	(<0.001)
Site 6	205.2 ± 37.8	108.7 ± 22.6	52.3 ± 13.7
	(<0.001)	(<0.001)	(<0.001)
Site 7	-124.4 ± 37.4	-133.1 ± 14.5	-64.5 ± 15.5
	(<0.001)	(<0.001)	(<0.001)
Site 8	-52.8 ± 42.3	-9.4 ± 18.4	-34.7 ± 22.0
	(0.21)	(0.61)	(0.12)
Year	7.6 ± 4.1	0.7 ± 1.6	-0.9 ± 2.2
	(0.06)	(0.65)	(0.68)
Year for site 2	26.1 ± 8.0	14.1 ± 1.9	6.9 ± 2.6
	(0.0011)	(<0.001)	(0.0084)
Year for site 4	2.2 ± 6.9	16.7 ± 8.5	-1.0 ± 6.3
	(0.75)	(0.05)	(0.88)
Year for site 5	26.1 ± 6.2	30.6 ± 3.7	13.1 ± 3.7
	(<0.001)	(<0.001)	(<0.001)
Year for site 6	-2.6 ± 5.2	-4.3 ± 4.0	0.9 ± 2.9
	(0.62)	(0.28)	(0.76)
Year for site 7	23.5 ± 4.7	15.5 ± 2.2	4.3 ± 3.6
	(<0.001)	(<0.001)	(0.24)
Year for site 8	25.7 ± 5.2	5.2 ± 2.7	2.9 ± 3.6
	(<0.001)	(0.05)	(0.43)

5.5 Mark-recapture models

5.5.1 Statistical methods

An open mark-recapture model was created for Figtree, Isis, Claude Wharton's, and Gray's waterhole. The Jolly-Seber model is an open-population model, which is appropriate for this study given the 10 year span. This model allowed for an estimation of recruitment (either immigration or fish reaching catchable size) and apparent survival [probability a fish remains in the population (i.e. does not emigrate or die)]. The model was run using the POPAN formulation implemented in RMARK (Laake 2013) and calculated in program MARK (v8.x) (Cooch and White 2001) and hence can be used to provide a population estimate.

The following are the main assumptions of the POPAN model:

1. Sampling is instantaneous.
2. Animals do not lose their tags and tags are read properly.
3. There is no temporary migration. Hence, any emigration is permanent
4. The study area remains constant (i.e. no expansion or shrinkage of area).
5. Survival probabilities are the same for both marked and unmarked.
6. Marked and unmarked animals have the same capture probability each sampling occasion.

The POPAN formulation has four main parameters: apparent survival (φ), detection/catchability (p), recruitment (b), and the superpopulation size (N). *A priori* it was expected that several covariates may affect these parameters. For catchability, river flow rate (*flow*), season, and fish lengths (*length*) were assumed to potentially affect catchability. For apparent survival, fish length was the only covariate expected to affect survival rates. For recruitment, no covariates were included. Since fish grow over time, fish length was defined as the mean length recorded for each fish. N was kept constant.

Though significant numbers of individual fish were caught at the sites, recapture rates were low (as shown above). Consequently, caution was exercised to prevent over-parameterization of the models. To this end, the following model selection was followed. First, a null model was created with no covariates or temporal periods [$\varphi(1)p(1)b(1)N(1)$]. Next, a covariate model was fitted in which the above covariates were added as described above [$\varphi(length)p(length + flow + season)b(1)N(1)$].

Then a series of models allowing the parameters to vary over time were created. These models allowed us to ask if survival varied over time. For these models, the 10 year study was divided into three periods: 2006 (Winter) to 2009 (winter), 2010 (Summer) to 2012 (Winter), and 2013 (Summer) to 2016 (Winter). These periods were chosen in relation to water flow. Prior to 2010, the dam was below capacity. Dam reached capacity in March 2010 and summer flooding was common from 2010 and onward. By reducing time to three periods, this helped prevent overparameterization of the model but still allowed us to ask if there were temporal changes in survival and/or recruitment. Three models were run: 1) allowed recruitment to vary over time periods [$\varphi(length)p(length + flow + season)b(period)N(1)$; 2) allow survival to vary over time periods [$\varphi(length + period)p(length + flow + season)b(1)N(1)$; and 3) allow both to vary [$\varphi(length + period)p(length + flow + season)b(period)N(1)$]. Finally, a reduced model was run in which nonsignificant covariates were removed and if the time period pattern had a linear pattern, a linear effect of time was substituted for the categorical effect of time. All models were compared using AICc and the best model was determined by selecting a model with the lowest AICc in which all parameters were estimable (Hurvich and Tsai 1989).

5.5.2 Mark-recapture results

Only the best model as defined in the methods is presented. Model AICcs and estimates from each fitted model can be found in Appendix 3.

Site 1 Isis results

The best simplified model $[\varphi(length + time)p(length + flow + season)b(period)n(1)]$ included an effect of fish length and a linear effect of time on survival, an effect of flow, fish length and season on catchability, and allowing recruitment to vary over time period. This model was substantially better than the null model ($\Delta AICc$=87) and the covariate model ($\Delta AICc$=8).

Using the best simplified model, it was found that population size increased. The apparent survival rate increased over time from upper 80% to near 99%, whether this is due to reduced migration or actually increased survival cannot be teased apart in this model. The model predicted significant recruitment events in time period 1 (2006-2009) and lower recruitment in time period 2 and 3, though there was large uncertainty around these estimates. Finally, larger flow events reduced catchability of fish and larger fish had decreased catchability. Even after controlling for flows, summer had reduced catchability.

Figure 8. Population estimates from the best model for Isis. Panels show population size, recruitment numbers, catchability, and survival. Error bars are 95%CI.

Site 2 Figtree results

The best simplified model [$\varphi(length)p(flow+season)b(period)n(1)$] included an effect of fish length on survival, an effect of flow and season on catchability, and allowing recruitment to vary over time. This model was substantially better than the null model ($\Delta AICc$=134) and the covariate model ($\Delta AICc$=25).

Using the best simplified model, it was found that population size at Figtree increased, especially after 2012 (Figure 9). The apparent survival rate was high and constant at 95.3% (95%CI: 93.3%, 96.8%) for an average sized fish. However, it should be noted that the best model was basically indistinguishable from the model that included an effect of time period on survival ($\Delta AICc$=0.2). In the time period model, survival dipped in the 2010-2012 time period to 91.3% from 98.3% in the 2006-2009 time period.

The model predicted significant recruitment events in time period 2 and 3. Finally, the model found a negative effect of flow rate on catchability and lower catchability in summer. Unlike Isis, fish length was not found to affect catchability.

Figure 9. Population estimates from the best model for Figtree. Panels show population size, recruitment numbers, catchability, and survival. Error bars are 95%CI.

Site 6 Gray's waterhole results

The best simplified model $[\varphi(length + period)p(season)b(1)n(1)]$ included an effect of fish length and time period on survival, an effect of flow fish length on catchability, and allowing recruitment to vary over time . This model was substantially better than the null model ($\Delta AICc$=11) and the covariate model ($\Delta AICc$=6).

Using the best simplified model, it was found that population size at Gray's waterhole decreased over time (Fig 10). The apparent survival rate varied over time starting at 85.6% before dropping to 74.8% during 2010-2012 and then rising again to 84.5%, which are much lower estimates than downstream sites. Recruitment was also estimated at a lower level (Fig 10). Finally, only season was found to affect catchability, with summer being lower.

Figure 10. Population estimates from the best model for Gray's waterhole. Panels show population size (N), recruitment numbers, catchability, and survival. Error bars are 95%CI.

Site 7 Claude Wharton results

The best simplified model $[\varphi(1)p(season)b(period)n(1)]$ included an effect of season on catchability and allowing recruitment to vary over time. This model was substantially better than the null model ($\Delta AICc$=75) and the covariate model ($\Delta AICc$=39).

Using the best simplified model, it was found that population size at Claude Wharton decreased over time (Fig 11). The apparent survival rate was lower than downstream sites, being at 83.1% (95%CI: 80.0, 85.8). Again, summer had lower catchability.

Figure 11. Population estimates from the best model for Claude Wharton. Panels show population size (N), recruitment numbers, catchability, and survival. Error bars are 95%CI.

Site 8 Mundubbera results

The best simplified model $[\varphi(1)p(length + season)b(period)n(1)]$ included an effect of fish length and season on catchability and allowing recruitment to vary over time. This model was substantially better than the null model ($\Delta AICc$=51) and the covariate model ($\Delta AICc$=13).

Using the best simplified model, it was found that population size at Mundubbera increased over time (Fig 12), mainly during the 2013-2016 time period. The apparent survival rate was similar to downstream sites at 96.5% (95%CI: 86.6, 99.1). As seen in other sites, catchability was lower during summer.
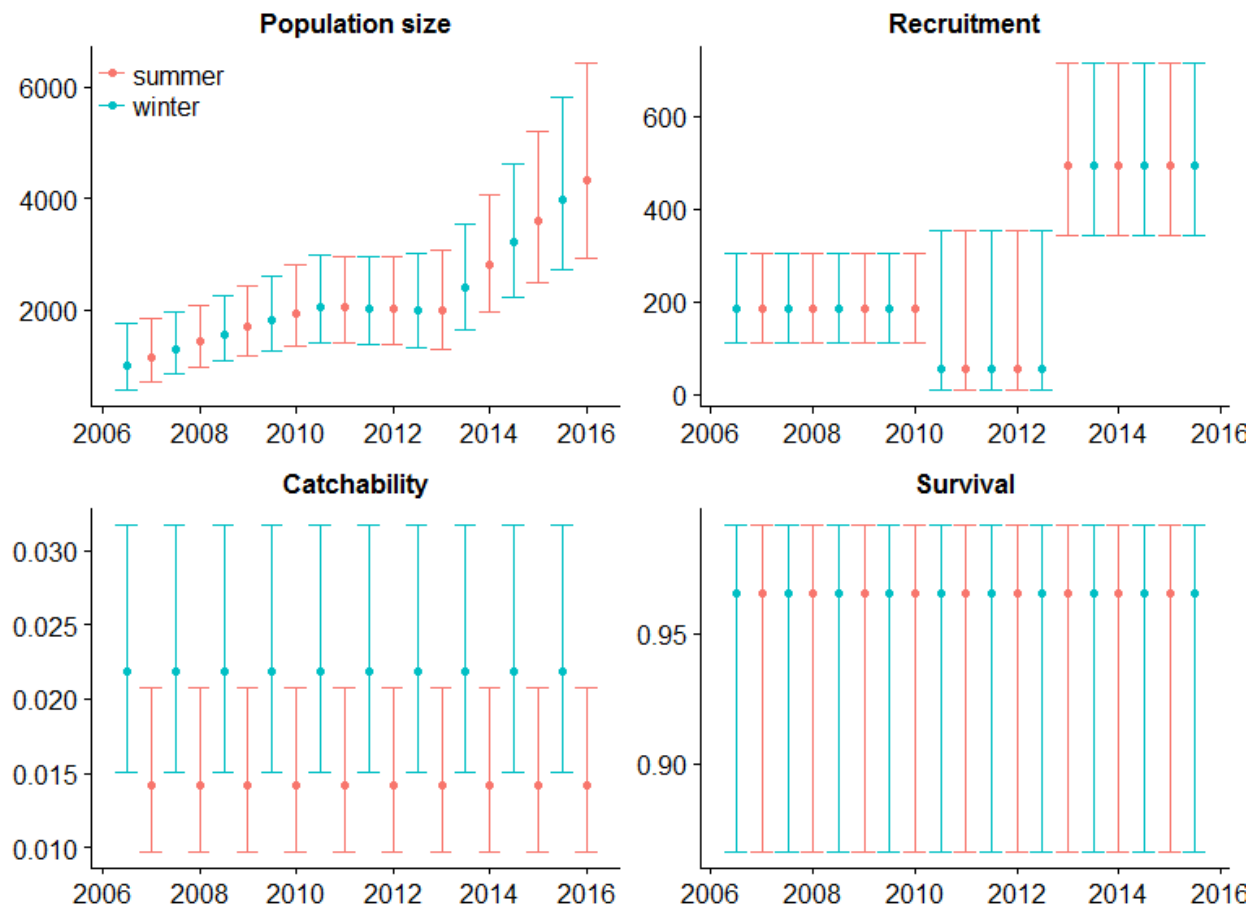

Figure 12. Population estimates from the best model for Mundubbera. Panels show population size (N), recruitment numbers, catchability, and survival. Error bars are 95%CI.

6 Discussion

6.1 CPUE findings

Using CPUE as a proxy for temporal changes in population size relies on the assumption that catchability of fish remain constant over time or can be statistically adjusted to correct for changing catchability. If time and factors affecting catchability did not correlate, then temporal patterns in CPUE should be unbiased, but the added noise of changing detectability could hide any temporal changes in CPUE. Thus, interpreting the CPUE patterns with lungfish in this study should be predicated on the available evidence showing how catchability may have changed over time.

In the regard to the covariates, water flow was only found to have a significant effect on CPUEs for Site 2 (Figtree). However, as noted above, running the model with only water flow for Site 1 resulted in a model explaining 21% of the variance, with the slope estimate for water flow being significant. The correlation between the predictors resulted in the final model explaining 32% of the variance, but no variable was significant, as the variables compete to explain the same variance. A similar pattern was found for Site 6, though water flow only explains 4.4% of variance and only marginally significant. Encouragingly, the slope estimates are very similar across the three sites when the only water flow is included in the models (-0.15 ± 0.04, -0.10 ± 0.02, and -0.12 ± 0.05 for sites 1, 2, and 6, respectively), suggesting that the water flow effect is consistent at the stream sites.

Water temperature was found to be significant for Site 4 and 5, which had no water flow estimates. Water temperature correlates with season (and with water flow) and it is not possible to separate seasonal effects and water temperature.

Conductivity was not a good predictor of CPUE, suggesting that it does not strongly affect catchability of lungfish, within the range observed.

After correcting for the above covariates, temporal declines in CPUE were found at sites 4, 5 and 7 (Kalliwa, Mingo, and Charles Wharton Weir, respectively). Site 4 and 5 were in the dam impoundment. Site 4 had the lowest overall CPUE of all sites and the decline in CPUE was only detected during the summer and leveled off after 2010. Site 5 showed a steady decline of ~28% per year, dropping to similar CPUE as Site 4. Whether this decline was due to decreases in lungfish densities and/or decreases in electrofishing effectiveness due to increased water depths cannot be disentangled.

Sites 7 differs in being upstream of the dam impoundment. The model estimated a ~10% decline per year at the site (roughly ~70% total decline over 10 years). Despite the decline, CPUE remain much higher than Site 4 and 5 in 2016.

Downstream sites (1 and 2) had the highest CPUE of all the sites. No significant temporal pattern in CPUE was found for Site 1, whether covariates were included or not. Site 2 did not have a significant decline when the covariates were included in the model, but without the covariates, Site 2 had a significant temporal decline, but only during summer. As water flow increased mainly during summer, this finding further supports the conclusion that water flow affected catchability of lungfish.

6.2 Temporal patterns in fish lengths

The distribution of fish lengths showed distinct patterns over years and sites. A consistent finding that most sites had reduced or reducing numbers of juvenile lungfish caught, except for Isis. Isis was fairly stable over the sampling periods, though it appears that the model did not detect a 2009-2012 dip in the smallest fish length. Figtree showed declining numbers of juvenile fish being caught. Whether the patterns in fish length reflect actual age-structure at each site depends, obviously, on the catchability of each size class of fish at the sites and how those catchabilities change over the years. Interestingly, winter and summer patterns in fish length were similar for sites 1, 2, and 7, suggesting that seasonal differences (like water flow, temperature) did not affect catchabilities between fish length classes.

6.3 Mark-recapture results

A POPAN model was applied to downstream and upstream sites. For the downstream sites, conclusions from these models were consistent across the two sites. Apparent survival was high at both sites, being on average around 95%, although not surprising for a long lived species such as lungfish. It should be re-emphasized that apparent survival is the probability of remaining at the site between sampling events. It is not possible to distinguish between permanent emigration and mortality in these models. Therefore, a fish that is not caught again may have died, permanently emigrated, or is still there but was just not caught (a distinct possibility given the low catchability). Thus, the high apparent survival indicates survival rates are high and permanent immigration is low at these sites.

At both sites, the models had lungfish populations increasing over time. Site 1 increased from ~5000 to ~7000 and Site 2 increased from ~2500 to ~4000. The higher estimate for Site 1 was due to the much lower catchabilities at Site 1. This explained why CPUE were higher for Site 2, but the population estimates were much lower. Understanding why the catchability is much lower at Site 1 is important in interpreting these results. For instance, if temporary migration is much higher at Site 1 , resulting in fish constantly moving in and out of the area, this could lead to the situation in which the density of fish is similar between Site 1 and 2, but the population estimates for Site 1 included a much larger area (i.e. more neighboring fishes).

Interestingly, the recruitment patterns predicted from the models differed between Site 1 and 2. Site 1 indicated more recruitment during the 2006-2009 time period, then dropping off for the 2010-2012 period, before increasing again during 2013-2016. In contrast, Site 2 recruitment was low pre-2010 but then increased afterwards. No change in the distribution fish lengths was found for Site 1, suggesting that the population structure remained fairly constant during the study period (i.e. no large influx of just juveniles or adults). The main recruitment appeared to occur during the drought period, which could reflect lungfish migrating downstream to Site 1 (Isis). This may explain why apparent survival was lower during this period if fish were migrating.

In contrast, for Site 2 the analysis indicated higher recruitment after 2010. The distribution of fish lengths indicated that there were decreasing levels of juveniles in the population over time, suggesting that juvenile recruitment does not seem to explain this pattern. Instead, a potential cause of this increase may be migration of adult fish from upstream. This hypothesis is supported by fact that of those marked fish found to move between sites, a large proportion moved from Site 4 and 5 to Site 2.

For upstream sites, the patterns were variable. The upstream site closest to the dam, Site 6, had a consistent decline due to lower apparent survival rates. Whether this was due to fish leaving the site or dying cannot be determined. The distribution of fish lengths suggesting little evidence of recruitment

from juveniles which was in agreement with the lower recruitment rate estimate. Site 7 also had a decreasing population trend, but this differed from Site 6 in that population size appeared to remain stable pre-2010 and then post-flood event. The distribution of fish lengths were suggestive of juvenile recruitment prior 2010 and then little recruitment post 2010. The lack of effect of time on apparent survival suggests that there was no large change in apparent survival over time.

Finally, Site 8 differed from the other sites by having an increasing population trend, mainly driven by larger recruitment post-2012. Apparent survival was similar to the downstream sites. Recruitment was mostly steady until the 2013-2016 time period in which the model predicted an increase. Given that the change in fish length distribution indicated that there were fewer small fish, it appears that the higher recruitment would be due to the immigration of adult fish.

As with most models, these estimates should be viewed with caution. First, it should be noted that time period was coarsely divided and smooth changes as seen here were unlikely in reality, so care should be exercised in interpreting temporal pattern. Also, catchability was low at all sites with Site 2 having around 5% and Site 1 having 2%, although these results are similar to the catchability of other freshwater species such as golden perch and Murray cod (Lyon et al., 2014). These low catchabilities precluded us from estimating parameters at each sampling event. These low catchabilities can be problematic as it is much harder to identity factors changing catchability (there is so much less recapture data to work with, despite the relatively large sample sizes). Furthermore, small changes in these catchabilities can lead to large changes in the population estimates. Therefore, there may be unmodelled temporal factors that have been changing catchabilities over time that could be driving the population patterns, leading to strong biases in the population estimates.

Besides caution about over catchability rates, differential catchability between marked and unmarked can lead to temporal patterns. A key assumption in the POPAN model is that capture probability and survival probabilities were the same between unmarked and marked lungfish over time. This assumption is key to the population estimates created in the POPAN model. Changes in the ratio of marked to unmarked are used as indications of changing population sizes in the model. Thus, if marked lungfish became harder to catch, unmarked to marked ratios increased, suggesting an increasing population size, as seen in the results here.

Another difficulty in interpreting the population estimates here is defining the actual area sampled. It was assumed the same area was sampled each year at each site. However, fish likely move in and out of the area, which may contribute to the low catchability. Assuming that this movement is random, this is not particularly problematic for the estimates, though defining the actual sampling area is difficult (since 'neighboring' fish were being sampled as well). As long as the rate of temporary, random migration is constant over time, then the estimates will be comparable.

6.4 Conclusions

This report had two main objectives: analyse temporal trends in standardised CPUE and develop mark-recapture models. These analyses where performed to provide insight into possible changes in lungfish populations along the Burnett river in relation to the Paradise Dam construction in 2006. Combining these analyses led to the following conclusions.

For the impounded sites (4 and 5), only CPUE results were obtained as there was insufficient data for more complex models. CPUE data suggested that theses sites had much lower CPUE than either upstream or downstream sites. Site 4 started at low CPUE whereas Site 5 decreased to low CPUE by 2009/2010. These results most likely reflect the increase in water depth at the sites, which occurred

later for Site 5. As water depth affects electrofishing effectiveness, the methodology used may be insufficient to assess temporal patterns in population densities. However, Site 5 had the largest percentage of fish that emigrated from the site, suggesting potentially large emigration.

For the upstream sites (6 to 8), CPUE and population estimates were obtained. CPUE decreased at Site 7, but the other sites had no significant change. Population sizes were estimated to have decreased at Site 6 and 7, but increased at Site 8. Site 6 and 7 had low apparent survival rates. CPUE and the POPAN results are both suggestive of a declining population at these sites. Site 8 had similar apparent survival rates as the downstream sites. This high apparent survival rate with an increasing population estimate and no changes in CPUE are suggestive of no change or an increasing population at Site 8.

For the downstream sites, temporal trends in CPUE were not significant, but the POPAN models predicted increasing population sizes. Together, these results suggest that lungfish population was not declining, and possibly increasing. Supportingly, apparent survival estimates were high for both of these sites. For Site 2, this increase in population size occurred after 2010 when the drought broke. Movement data suggested several fish from sites 4 and 5 were discovered at Site 2 (but not Site 1) after 2010, suggesting an increase in population size could be due to immigration from the dam impoundment site.

As with statistical models in general, the POPAN models rely on multiple assumptions about the dynamics of the system and the sampling process. Violating these assumptions can lead to biased results. For instance, differential catchability of marked to nonmarked fish, non-random temporary migration, and individual variation in catchability can bias population estimates. With the low catchability of fish, we suspect that these violations will be harder to detect and the model's results may be more sensitive to violations of these assumptions. Therefore, the POPAN model results should be viewed with healthy skepticism, but also as a starting point for interpretation of the data.

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Appendix

A.1 Overview of data and data cleaning performed

A.1.1 Data supplied for analysis

Data were supplied in two excel files (*'Data for Charles.xlsx'* and *'PRODUCTION2051009-v1-Burnett_River....xls'*; supplied 21DEC2016). The first excel file had two tabs, one containing lungfish capture history and the other sampling information.

The following modifications were made to the flow data provided in the *lungfish details* datasheet:

1. There were several duplicates in the datasheet. All records that had the same fish id, date, length, and weight were reduced to a single record.

2. For fish that were caught more than once during the same sampling event, the average length was calculated and the fish was then only counted once.

3. Fish with missing tag information were included in the CPUE and length analysis, but was dropped in the marked-recapture section.

4. Site 3 was incomplete and hence dropped from the analyses.

The following modifications were made to the flow data provided in the *CPUE & Recaps* datasheet:

1. No flow data was available for Site 5 prior to 2008. Water flow was assumed to be zero given the similar level of rainfall in 2006 and 2007 to 2008 and 2009.

2. When checking flow rates from the flow excel file to the *CPUE & Recaps* datasheet, several discrepancies were noted. For instance, Site 1 had several 24 ML/day but this 24 is most likely copied from the wrong column in the flow file. Therefore, I replaced all flow values by merging flow data from the file excel file.

3. For missing water temperature and conductivity data for Site 1, the average temperature and conductivity for that season was used across all years.

A.1.2 Estimating flow rates

Flow rates (if applicable) were estimated for each site from the *'PRODUCTION2051009-v1-Burnett_River....xls'* file. Below describes the how flow rates were obtained.

*   Site 1: flow rates were estimated from release data for Ned Churchward Weir.

*   Site 2: flow rate was estimate from a gauging station at Figtree.

*   Site 4: the site was in a ponded area and no flow data was available.

*   Site 5: the site was located at the upper extent of the impoundment of Paradise dam and flow data from SunWater's headwater data (2172) was used.

- Site 6: streamflow data was obtained from gauging stations near the sites. Note - a missing flow rate was estimated from surrounding days.

- Site 7: flow rates were estimated from release data for Claude Wharton Weir.

- Site 8: the site was in a ponded area and no flow data was available. Flow rate was zero.

A.2 Descriptive statistics on sampling events

This section just the actual number of fish caught per sampling period for each site.

Table A.1. Descriptive statistics for each sampling event. The total number of fish caught at each sampling event for each site.

Year	Season	1) Isis	2) Figtree	4) Kalliwa	5) Mingo	6) Gray's Waterhole	7) Claude Wharton	8) Mundubbera
2006	winter	92	119	3	18	49	39	9
2007	summer	84	132	16	104	31	93	13
2007	winter	82	153	21	92	59	82	33
2008	summer	89	100	8	29	42	109	29
2008	winter	115	143	5	74	18	68	35
2009	summer	93	95	8	18	20	75	45
2009	winter	108	117	5	15	46	62	22
2010	summer	68	79	1	30	19	71	30
2010	winter	163	121	4	20	36	80	35
2011	summer	24	72	2	12	22	53	17
2011	winter	61	114	1	13	5	14	14
2012	summer	70	60	1	11	31	90	49
2012	winter	93	139	6	57	24	71	44
2013	summer	87	113	3	1	8	11	10
2013	winter	100	106	3	1	1	6	39
2014	summer	112	171	1	9	17	13	50
2014	winter	114	154	1	8	37	25	105
2015	summer	82	166	3	1	22	41	48
2015	winter	177	234	4	19	13	16	104
2016	summer	61	133	1	1	15	57	17

A.3 Tables for mark-recapture analysis

Table A.2. Model selection for POPAN models. Only the best two models and the null model are shown for each site.

Site	Model	Npar	AICc	DeltaAICc	Weight
Site 1 Isis	φ(length + time)p(flow + season + length)b(period)n(1)	11	2147	0.00	0.70
	φ(length + period)p(flow + length + season)b(period)n(1)	12	2148	1.92	0.27
	φ(1)p(1)b(1)n(1)	4	2233	86.65	0.00
Site 2 Figtree	φ(length)p(flow + season)b(period)n(1)	9	5071	0.00	0.40
	φ(length + period)p(flow + length + season)b(period)n(1)	12	5071	0.20	0.36
	φ(1)p(1)b(1)n(1)	4	5205	134.44	0.00
Site 6 Gray's waterhole	φ(length + period)p(season)b(1)n(1)	8	800	0.00	0.75
	φ(length + period)p(flow + length + season)b(1)n(1)	10	804	3.45	0.13
	φ(1)p(1)b(1)n(1)	4	812	11.33	0.00
Site 7 Claude Wharton	φ(1)p(season)b(period)n(1)	7	1466	0.00	0.43
	φ(length)p(flow + length + season)b(period)n(1)	10	1467	0.93	0.27
	φ(1)p(1)b(1)n(1)	4	1540	74.53	0.00
Site 8 Mundubbera	φ(length)p(length + season)b(period)n(1)	9	1054	0.00	0.73
	φ(length + period)p(length + season)b(period)n(1)	11	1057	2.89	0.17
	φ(1)p(1)b(1)n(1)	4	1103	48.34	0.00

Table A.3. Parameter estimates for the best POPAN model for each site.

Site	Parameter	Estimate	SE	95% lower	95% upper
Site 1 Isis	φ:(intercept)	1.81	0.43	0.97	2.65
	φ:length	29.57	9.75	10.45	48.68
	φ:time	0.19	0.06	0.07	0.30
	p:(intercept)	-4.31	0.13	-4.56	-4.06
	p:flow	-0.08	0.03	-0.14	-0.03
	p:seasonwinter	0.18	0.08	0.03	0.34
	p:length	-16.57	4.03	-24.47	-8.68
	b:(intercept)	-1.69	0.29	-2.25	-1.13
	b:period2	-2.60	2.13	-6.78	1.57
	b:period3	-0.69	0.37	-1.42	0.03
	n:(intercept)	9.28	0.11	9.07	9.49
Site 2 Figtree	φ:(intercept)	3.02	0.20	2.63	3.40
	φ:length	31.93	6.04	20.09	43.78
	p:(intercept)	-3.11	0.07	-3.25	-2.97
	p:flow	-0.04	0.01	-0.07	-0.02
	p:seasonwinter	0.12	0.06	0.01	0.24
	b:(intercept)	-2.97	0.32	-3.60	-2.35
	b:period2	0.82	0.30	0.22	1.42
	b:period3	0.98	0.26	0.47	1.49
	n:(intercept)	8.52	0.06	8.39	8.64
Site 6 Gray's waterhole	φ:(intercept)	1.78	0.23	1.33	2.24
	φ:length	10.84	3.61	3.77	17.91
	φ:period2	-0.69	0.28	-1.23	-0.15
	φ:period3	-0.09	0.37	-0.81	0.64
	p:(intercept)	-3.46	0.20	-3.85	-3.06
	p:seasonwinter	0.20	0.09	0.02	0.38
	b:(intercept)	-2.52	0.24	-3.00	-2.04
	n:(intercept)	7.94	0.16	7.63	8.25
Site 7 Claude Wharton	φ:(intercept)	1.60	0.10	1.39	1.80
	p:(intercept)	-3.39	0.13	-3.64	-3.15
	p:seasonwinter	-0.34	0.06	-0.46	-0.21
	b:(intercept)	-1.70	0.21	-2.10	-1.30
	b:period2	-12.77	211.35	-427.02	401.48
	b:period3	-0.89	0.16	-1.22	-0.57

Site 8 Mundubbera	n:(intercept)	8.77	0.11	8.56	8.99
	φ:(intercept)	3.32	0.74	1.87	4.78
	p:(intercept)	-4.24	0.20	-4.62	-3.86
	p:length	9.77	3.05	3.79	15.74
	p:seasonwinter	0.44	0.08	0.29	0.59
	b:(intercept)	-1.67	0.49	-2.62	-0.72
	b:period2	-1.17	1.26	-3.64	1.29
	b:period3	0.99	0.26	0.48	1.49
	n:(intercept)	8.53	0.15	8.24	8.81