Original Articles

Take the long way home: Minimal recovery in a K-selected freshwater crayfish impacted by significant population loss

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ABSTRACT

Extreme disturbance can cause catastrophic mortality, population collapse and localised extinction in animal species. The ability of species to resist and recover from such disturbance is paramount to the persistent of populations thus regulating species distribution and diversity. The present study assessed the status of a slow-growing, long-lived and recreationally harvested freshwater crayfish, the Murray crayfish *Euastacus armatus*, which experienced significant population loss imposed by an extreme hypoxic blackwater disturbance in the Murray River in the southern Murray-Darling Basin, Australia. Specifically, before-after-control-impact monitoring, which accounted for imperfect and variable detection, was employed to assess indicators of recovery (occupancy, abundance, sex ratio and length structure) at affected and non-affected sites over 3–5 years following the hypoxic blackwater. A stochastic population model was further utilised as an indicator of longer term trajectories of recovery under a range of management scenarios. The indicators employed in the study suggested minimal recovery as there was no significant improvement in occupancy or abundance and length structures emphasising the continued underrepresentation of juveniles across the affected populations. Modelling simulations reinforce these findings with lengthy recovery trajectories (e.g. 50 years to reach pre-disturbance population sizes) forecast under natural recovery scenarios and any scenario involving harvest pressure predicted to delay this recovery timeframe. The findings emphasise the need to acknowledge realistic recovery timeframes for K-selected species impacted by extreme disturbance. It is now a critical time for concerted conservation and fisheries management to facilitate the recovery of the species across its range.

1. Introduction

Extreme disturbance events – natural or human-induced – can cause catastrophic mortality, population collapse and localised extinction of animal species (see Fey et al., 2015; Pickett and White, 2013). These extreme disturbances can be abrupt or gradual in nature, and have local and global implications, with the impacts often at disparity with the duration of the event (Smith, 2011). Prominent examples include the mortality of 250,000 seabirds following the *Exxon Valdez* oil spill in Prince William Sound (Piatt and Ford, 1996), widespread deaths of common seals *Phoca vitulina* around the coast of Europe in 1989 (Harwood and Hall, 1990), and even human populations (Kelly, 2005; Morgan et al., 2006). The ability of animal species to resist and recover from extreme disturbances is paramount to the persistence of populations thus regulating species distribution and diversity (Pickett and White, 2013; Reice et al., 1990). Understanding the impact of, and

recovery from, disturbance is necessary as extreme climatic events and anthropogenic impacts are predicted to increase in the future (Bailey and Pol, 2016; Smith, 2011).

Animal populations naturally recover following extreme disturbance through reproduction of surviving individuals and/or re-colonisation (Hughes, 2007; Parkyn and Smith, 2011). These recovery mechanisms are governed by the: (1) pre-disturbance population size and connectivity; (2) extent and severity of the disturbance; (3) return of suitable habitat and resources; and (4) life-history traits, phenotypic plasticity, genetic diversity and dispersal ability of the species (Beever et al., 2016; Parkyn and Smith, 2011). Species with short generation times, high fecundity and rapid growth (i.e. r-selected) are considered to have high recovery potential, whereas gradual recovery is anticipated for large, long-lived, late maturing and dispersal limited species (K-selected: Hutchings et al., 2012). Impaired recovery is likely if population declines are rapid and large (e.g. in excess of 50%) to the

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extent that Allee effects are expressed, or if threats are not abated and effective conservation is lacking (Hutchings, 2015; Hutchings et al., 2012). For fisheries species, the release from harvest pressure is considered a major driver of recovery (Hilborn et al., 2014; Lotze et al., 2011).

Whilst the study of recovery has a long history (see Duarte et al., 2015; Niemi et al., 1990), universal definition and assessment indicators remain elusive, and often vary amongst fisheries and conservation settings (Lotze et al., 2011; Westwood et al., 2014). Typically, recovery is defined as the temporal process in which populations return to pre-impact levels and the disturbance is no longer posing a threat (Parker and Wiens, 2005). Presently, Before-After-Control-Impact (BACI) designs are considered the most robust to assess environmental disturbance (Underwood, 1994; Verdonschot et al., 2013). It is important for these designs to account for the spatial extent of the disturbance and be of sufficient temporal scale to adequately reflect prevailing dynamics (i.e. acknowledge shifting baselines) and track indicators over time (i.e. full recovery: Verdonschot et al., 2013). It is also acknowledged that predetermined endpoints are necessary as are multiple indicators to robustly assess recovery (Keeley et al., 2014; Verdonschot et al., 2013). As abundance is most commonly used as the indicator of recovery (Lotze et al., 2011), it is imperative to account for imperfect detection as not to make incorrect conclusions (cf. Gwinn et al., 2016; Kellner and Swihart, 2014).

Approximately one-third of freshwater crayfish across the world are at risk of extinction (Richman et al., 2015); with members of the Australian *Euastacus* genus considered among the most threatened (Furse and Coughran, 2011b; Furse et al., 2013). *Euastacus* species appear particularly vulnerable to environmental disturbance and anthropogenic change (Furse and Coughran, 2011c), with flash flooding (Furse et al., 2012), severe blackwater (McCarthy et al., 2014), wildfire (Johnston et al., 2014) and habitat degradation (Noble and Fulton, 2017) shown to contribute to population declines. The capacity of *Euastacus* species to recover through population growth or recolonisation is expected to be constrained (Furse and Coughran, 2011a) by life history traits (i.e. slow-growth, late maturity and low fecundity); restricted movement and dispersal ability; and limited gene flow and low levels of genetic diversity (Honan and Mitchell, 1995; Miller et al., 2014; Ryan et al., 2008). Additionally, many *Euastacus* species have already experienced declines in distribution and abundance (Furse and Coughran, 2011a), increasing the likelihood of smaller population sizes and population fragmentation, which will further act to limit capacity to resist and recover from disturbance (Allendorf et al., 2013; Frankham et al., 2010).

The Murray crayfish *Euastacus armatus* (von Martens, 1866) is a recreationally harvested freshwater crayfish occurring across the southern Murray-Darling Basin (MDB), Australia (Morgan, 1997). This long-lived (~28 years), slow-growing (K = 0.0933), late-maturing (~8–9 years) and low fecundity (up to 2000 eggs per mature female) has experienced substantial decline in distribution and abundance over the past 50 years attributed to river regulation, pesticides and pollutants, habitat degradation and harvest pressure and blackwater events (Furse and Coughran, 2011a,b; Horwitz, 1995; Walker and Thoms, 1993). Most recently over 2010–11, *E. armatus* populations, along with other freshwater crayfish (common yabby *Cherax* spp., freshwater shrimp *Paratya* spp. and freshwater prawns *Macrobrachium* spp) and freshwater fish, were impacted by an extreme hypoxic blackwater disturbance (King et al., 2012; Leigh and Zampatti, 2013; McCarthy et al., 2014); antecedent drought conditions and unseasonal inundation led to the accumulation and breakdown of large quantities of organic matter, which resulted in hypoxia, persisting for nearly six months, across much of the present range of the species (Whitworth et al., 2012).

During this extreme disturbance, *E. armatus* were observed emerging from the water in the affected areas, a behavioural adaptation to resist short-term periods of adverse water quality (King et al., 2012), but indicators (at the scale of 1–2 years) revealed a significant (81%)

population loss across affected areas, with all size classes and both sexes equally impacted (McCarthy et al., 2014). The impacts of the 2010–11 blackwater disturbance, and other recent research (Zukowski et al., 2011, 2012), led to amendments of the recreational fishery regulations, including closure of affected areas; shift from a minimum length limit (MLL = 90-mm) to a harvestable slot length limit (HSLL = 100–120-mm); the reduction of bag (five to two crayfish) and possession (10 to four crayfish) limits; and the contraction of the open fishing season (four to three months: NSW DPI, 2014). The legacy of this extreme disturbance could to be profound, with restricted movement (Ryan, 2005) and gene flow suggesting natural recovery of affected populations could occur across a decadal timescale (Whiterod et al., 2017).

This study aimed to assess the present status of *E. armatus* populations affected by the 2010–11 blackwater event as well as forecasting long-term indicators of recovery. Specifically, using a BACI design we assess key indicators, including abundance (adjusted for detection probability: Gwinn et al., 2016), sex ratio and length structure at hypoxic blackwater affected sites and non-affected sites before (2010: Zukowski, 2012) and shortly after (2012: McCarthy et al., 2014) with now three to five years (2014, 2015 and 2016). To achieve broader insight, we forecast long-term recovery indicators under potential management scenarios using a recently developed population model (Todd et al., in press). It was hypothesised that the abundance of the species will have increased little and affected populations will remain patchy and modelled simulations will reveal slow population growth trajectories indicating that recovery will be a gradual process.

2. Methods

2.1. Sampling region and protocol

The Murray River flows 2530-km from the south-eastern highlands of Australia, through the southern MDB, to the sea at Goolwa (Eastburn, 1990). The Murray River is highly-regulated by upland impoundments, low-level weirs and irrigation diversions along much of its length (Walker, 2006). The present study focused on a 1100-km section (i.e. 1094–2194 river-km upstream of the Murray mouth) of the Murray River previously sampled in 2010 (Zukowski, 2012) and 2012 (McCarthy et al., 2014) (Fig. 1). This section encompassed the lower sections of the headwater tract of the river along with the low-gradient and meandering river channel of the gently undulating riverine plains and Mallee trench tracts (Eastburn, 1990). Consistent with 2010 and 2012, a total of 16 sites were sampled across this section, which conformed to the Before-After-Control-Impact (BACI) design: six control sites upstream of the large and significant river red gum floodplain wetland system, Barmah-Millewa Forest that were "non-affected" by hypoxic blackwater in 2010–11 whereas 10 treatments sites within and downstream of Barmah-Millewa Forest were affected.

At all sites, twenty standard hoop nets (single 800-mm steel hoop diameter, 13-mm stretch mesh size, 0.3-m drop baited with ox liver) were first deployed by boat during daylight hours (0800–1700) and retrieved hourly over two deployments (maximum of 40 net lifts). Nets were typically set 3–10-m from the river bank at least 40-m apart over a 2-km reach and re-deployed approximately 10-m from its initial set position after the first lift. Nets where bait had been lost or were snagged upon lifting were excluded from the abundance analysis. As with 2010 and 2012, the 16 sites were sampled in random order during the austral winter (1–11 July 2014; 15–26 June 2015; 18–28 July 2016) when *E. armatus* catches are highest (Zukowski et al., 2012).

Sampled *E. armatus* were sexed and occipital carapace length (OCL, in mm: from eye-socket to rear of carapace) measured with vernier calipers (Kinchrome). Additionally, sampled individuals were marked (see Ramalho et al., 2010) to identify potential recaptures (none were obtained: *unpublished data*) before being returned to the water. Water temperature (°C) was measured during sampling at each site using a multiprobe system (556 MPS, Yellow Springs Institute, YSI) and mean
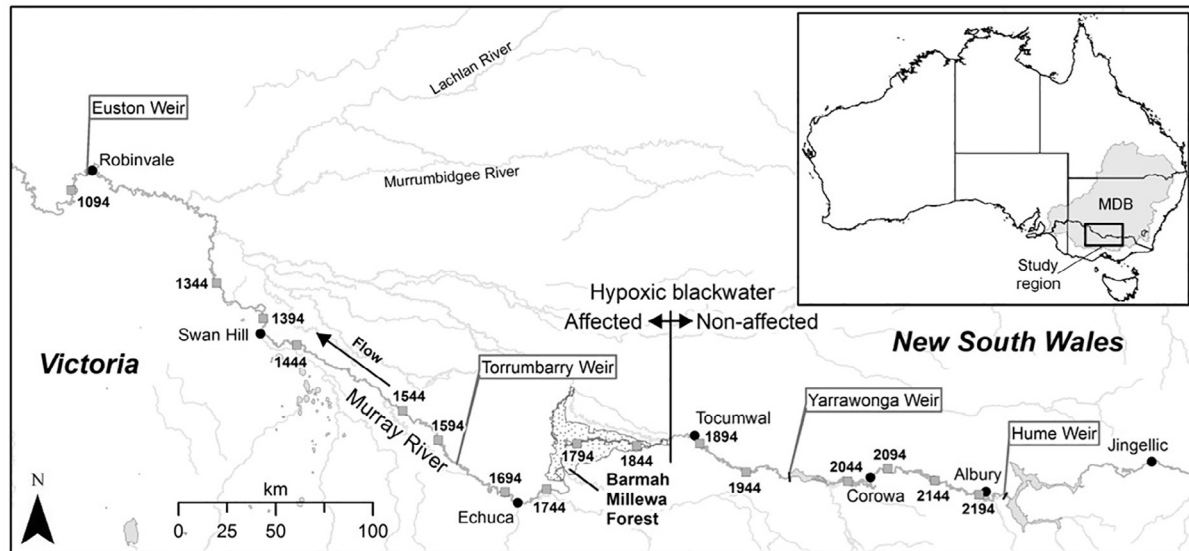
Fig. 1. Location of the 16 study sites along the Murray River in the Murray-Darling Basin (grey shade), Australia, that were sampled for *Euastacus armatus* before (2010) and after (2012; 2014, 2015 and 2016) the 2010–11 extreme blackwater disturbance generated by the flooding of Barmah-Millewa. Sites upstream and downstream of Barmah-Millewa Forest were "non-affected" and "affected" by the hypoxic blackwater, respectively (river-km represents the distance upstream of the mouth of the Murray River).

daily flow data (ML d^{-1}) on the day of sampling was obtained for the nearest gauging station to each site (data obtained from Murray-Darling Basin Authority).

2.2. Abundance and detection probability analysis

To provide an indication of patterns in abundance relative to the blackwater event, we developed a Bayesian hierarchical model that uses replicate samples at multiple sites to estimate abundance while accounting for incomplete and variable sampling efficiency (i.e. detection probability). The model was based on methods first proposed by Royle and Nichols (2003) and then extended into a hierarchical framework by Royle and Dorazio (2008) and Coggins et al. (2014) and contains a sub-model that describes patterns in abundances and a sub-model that describes patterns in detection probability. Because abundance cannot be observed directly, specified site abundance N_i as defined as a latent random effect with variation explained by a Poisson distribution as, $N_i \sim$ Poisson (λ_i), where λ_i represents the expected abundance at site i. Our data y_{ij} were the frequencies of *E. armatus* detections at site i with net j. We assume that y_{ij} was the result of binomial outcomes as $y_{ij} \sim$ Binomial(k_{ij}, p_{ij}), where p_{ij} is the probability of detecting at least one individual at site i with net j and k_{ij} is the number of replicate samples collected with net j at site i. The abundance sub-model was linked to the detection sub-model by specifying the relationship between p_{ij} and N_i, per Royle and Nichols (2003), as $p_{ij} = 1 - (1 - r_{ij})^{N_i}$, where r_{ij} is individual-based detection probability, as opposed to p_{ij}, which is the probability of detecting at least one individual at site i with net j. This formulation essentially models the detection probability p_{ij} as a random effect with a Poisson mixing distribution.

The study employed a BACI design that included control sites, treatment sites (i.e. *treat*), one time period before the blackwater event (i.e. 2010), and four time periods after the blackwater event (i.e. 2012, 2014, 2015, and 2016). Thus, we incorporated covariates into our model that describe potential temporal variation in abundance in the control sites and treatment sites to isolate and draw inference on the influences of the blackwater event. Potential covariates were incorporated into the abundance sub-model with a log link as:

$$\log(\lambda_i) = \beta_0 + \beta_1 2012_i + \beta_2 2014_i + \beta_3 2015_i + \beta_4 2016_i + \beta_5 treat_i$$
$$+ \beta_6 treat_i 2012_i + \beta_7 treat_i 2014_i + \beta_8 treat_i 2015_i + \beta_9 treat_i 2016_i$$
(1)

where β_0 is the intercept of the abundance model, which represents the mean abundance at the control sites in 2010. The parameters β_1-β_4 model potential variation in abundance through time in the treatment sites. The parameter β_5 models potential inherent differences between treatment and control sites in 2010 prior to the blackwater event. The parameters β_6-β_9 model the interaction between the treatment and the time variables. These parameters describe the potential effects of the blackwater event in the treatment sites through time. One of the main assumptions of our experimental design is that data collected in the control sites represents abundance patterns in absence of blackwater in the treatment sites. This assumption can be violated when sampling efficiency varies through time differently between the control and treatment sites. To account for this possibility, we incorporated covariates in the detection sub-model that were synonymous to those included in the abundance sub-model to account for potential variation in detection probability among the temporal and spatial experimental units of the study. Additionally, we included covariates to describe potential variation in detection probability of *E. armatus* with river discharge (*dis*) and water temperature (*temp*) as these variables commonly effect sampling efficiency of aquatic animals (Gwinn et al., 2016). Potential covariates were incorporated into the detection sub-model with a logit link as:

$$\text{logit}(r_{i,j}) = \eta_0 + \eta_1 2012_i + \eta_2 2014_i + \eta_3 2015_i + \eta_4 2016_i + \eta_5 treat_i$$
$$+ \eta_6 treat_i 2012_i + \eta_7 treat_i 2014_i + \eta_8 treat_i 2015_i + \eta_9 treat_i 2016_i$$
$$+ \eta_{10} dis_i + \eta_{11} temp_i$$
(2)

where η_0 is the intercept of the detection sub-model and parameters η_1-η_9 represent the BACI design parameters analogous to β_1-β_9 in the abundance sub-model. The parameters η_{10} and η_{11} model the potential effects of river discharge and temperature on net sampling efficiency. All continuous variables were centred on zero and scaled by one standard deviation to help with fitting and allow for unambiguous comparison of parameter estimates.

2.2.1. Model fit and variable selection

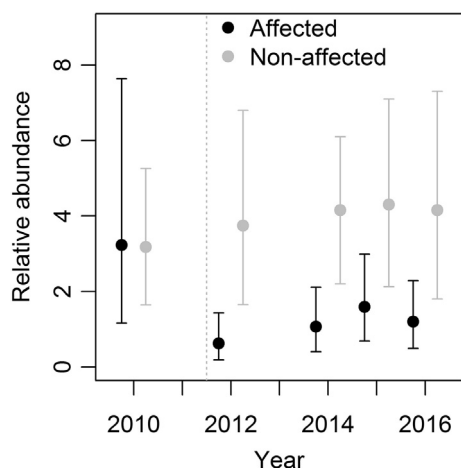Evaluation of the fit of our model was achieved with a posterior

Fig. 2. Predicted relative abundance and detection probability of *Euastacus armatus* in the control and treatment sites. The vertical dotted line represents the time of the blackwater event. Error bars represent the 95% Bayesian credible intervals.

predictive check (Broms et al., 2016; Hooten and Hobbs, 2015). For each net set at each site during each year, simulated (expected) number of detections (e), obtained from the posterior distributions of the model parameters, was compared with the observed number of detections (o) using a Chi-squared test statistic calculated as $X^2 = [(o-e)^2/e]$. In turn, the X^2 statistics was summed across all nets, sites, and years to provide a measure of overall model fit. To assess whether the observed value of the summed X^2 statistic was likely given the assumptions of the model, the posterior samples of the simulated data were used to approximate the sampling distribution of the fit statistic. The percentile of the fit statistic was reported as a measure of model fit with percentile values < 0.95 indicating adequate fit. The importance of covariates was evaluated using the Bayesian credible interval, where covariate effects were considered statistically significant when the 95% credible intervals did not include zero. The model was fitted in a Bayesian context using a Gibbs sampler implemented in JAGS (Plummer, 2003). Description of model fitting methods and code is in Appendix S1 of the online supplemental information.

2.3. Length and sex-ratio analysis

We assessed the potential impact of the blackwater event on the length composition and sex ratio of the population with logistic regression using an information theoretic approach (Burnham and Anderson, 2002). Each sampled crayfish was assigned into either 'small' (< 90-mm) or 'large' (≥90-mm) categories based on the size of onset of sexual maturity in 50% of females (SOM$_{50}$: Zukowski et al., 2012). The probability of crayfish being either male or female and small or large as a function of blackwater was assessed using a repeated measures logistic regression with both year and treatment as independent variables and site as a random effect. We considered all models that either included or excluded year or treatment variables in full factorial design (Table 2) and evaluated their relative support with using Akaike Information Criterion (AIC: see Burnham and Anderson, 2002).

2.4. Population modelling

We utilised the stochastic length-based age structure population model developed by Todd et al. (in press) to investigate long-term recovery indicators following significant population loss under a range of management scenarios. Briefly, the model summarises the life history of *E. armatus* by explicitly representing both male and female population size across age classes based on estimates of survival (across life stages) and fecundity as well as density dependence (i.e. top down: Todd et al., 2004) across the species' lifespan (i.e. 25 years: for details see Todd

et al., in press). The model was simulated to assess population trajectories under (1) natural (no harvest) and (2) previous regulation (90-mm MLL) scenarios along with a range of fishery scenarios that could be enacted following the observed population loss (i.e. 81%). These scenarios were: (3) continuation of the 90-mm MLL regulation; amending to the (4) present 100–120-mm HSLL without closure as well as with (5) 20-year closure or (6) permanent closure of the recreational fishery.

All simulations utilised the Murray River sub-model and started with an average adult population size of 50,000 individuals and were executed for 100 time-steps (i.e. 100 years) using 1000 model iterations with the disturbance event occurring after 10 time-steps and fishing harvest (take rate) set at 30% for relevant scenarios. For simplicity, immigration and emigration were not included in the model. The scenarios were compared by assessing the time to recovery (years) of the mean adult population size – deemed as when the mean trajectory of the scenario reached that of the mean harvest trajectory (defined as the 90-mm MLL scenario). The population model was developed and implemented in the simulation software package Essential, v2.20 (Todd and Lovelace, 2017).

3. Results

A total of 1573 *E. armatus*, ranging between 37 and 140-mm OCL, were sampled over the study, with catches varying across years from 182 to 324 individuals in the non-affected sites and 18 to 72 individuals in the affected sites.

Markov chain Monte Carlo (MCMC) chains for all models demonstrated adequate mixing and converged on the posterior distributions as indicated by all Gelman-Rubin statistics ≤ 1.1. Our model adequately fit the data with an X^2 statistic within the 95 percentiles of the predicted distribution ($X^2 = 827.17$, Percentile of expected distribution = 0.12). This value of the fit statistic suggests that abundance and detection did not vary substantially among sites beyond the variation described by the experimental design and environmental covariates and that our model was a useful approximation of the data-generating process.

3.1. Response to blackwater

3.1.1. Relative abundance

Our results showed clearly the impact of the blackwater event on the relative abundance and occurrence of *E. armatus* (Fig. 2). Between 2010 and 2012 there was an ~80% decrease in the estimated relative abundance and a ~52% decrease in the predicted occurrence at the blackwater affected sites which was statistically significant ($\beta_6 < 0$, Table 1). Concurrent to this change, relative abundance and occurrence remained constant at the non-affected sites ($\beta_2 \approx 0$, Table 1). Between the years of 2012 and 2016, we observed little evidence of recovery toward the pre-blackwater state at affected sites. Although the 2015 estimate of relative abundance in the affected sites was not statistically different from the pre-blackwater estimate in 2010 ($\beta_8 \approx 0$, Table 1), the 2014 and 2016 abundance estimates were statistically lower than 2010 (β_7 & $\beta_9 < 0$, Table 1) and all point estimate of relative abundance were > 50% lower than the 2010 estimate (Fig. 2). Additionally, the relative abundance in the non-affected sites demonstrated no statistical change from 2012 to 2016 (β_2, β_3, β_4, $\beta_5 \approx 0$, Table 1, Fig. 2), confirming that the observed changes at the affected sites were due to the blackwater event.

3.1.2. Length and sex-ratio

The proportion of small (< 90-mm) to large (≥90-mm) length categories was best explained (i.e. lowest AIC) by the interaction between year and treatment indicating differential change between affected and non-affected sites over time (Fig. 3a and Table 2). Prior to the blackwater disturbance, the proportion of small individuals at both affected and non-affected sites was greater than 0.8. In 2012, the proportion of

Table 1

Posterior probability summaries of parameters for covariate effects on relative density and detection probability of *Euastacus armatus*. Parameter mean, SD and 95% Bayesian credible intervals are based on model averaged posterior samples.

Parameter	Mean	SD	95% CI
Abundance model			
β_0 (intercept)	1.09	0.36	0.50, 1.66
β_1 (treatment)	−0.04	0.53	−0.90, 0.85
β_2 (2012)	0.10	0.57	−0.82, 1.05
β_3 (2014)	0.25	0.51	−0.58, 1.11
β_4 (2015)	0.24	0.48	−0.55, 1.01
β_5 (2016)	0.45	0.53	−0.41, 1.33
β_6 (treatment:2012)	−1.77[*]	0.82	−3.12, −0.43
β_7 (treatment:2014)	−1.32[*]	0.73	−2.53, −0.14
β_8 (treatment:2015)	−0.90	0.71	−2.08, 0.26
β_9 (treatment:2016)	−1.40[*]	0.73	−2.65, −0.22
Detection model			
η_0 (intercept)	−2.15	0.34	−2.73, −1.61
η_1 (treatment)	−0.66	0.49	−1.48, 0.11
η_2 (2012)	0.80	0.56	−0.15, 1.70
η_3 (2014)	0.78[*]	0.46	0.00, 1.51
η_4 (2015)	0.40	0.42	−0.28, 1.10
η_5 (2016)	0.70	0.50	−0.14, 1.49
η_6 (treatment:2012)	−0.05	0.71	−1.21, 1.11
η_7 (treatment:2014)	0.07	0.63	−0.94, 1.12
η_8 (treatment:2015)	0.01	0.63	−1.02, 1.04
η_9 (treatment:2016)	0.03	0.63	−1.01, 1.09
η_{10} (discharge)	−0.37[*]	0.12	−0.57, −0.17
η_{11} (temperature)	0.01	0.11	−0.18, 0.20

[*] Indicates statistical significance of parameter at α = 0.05.
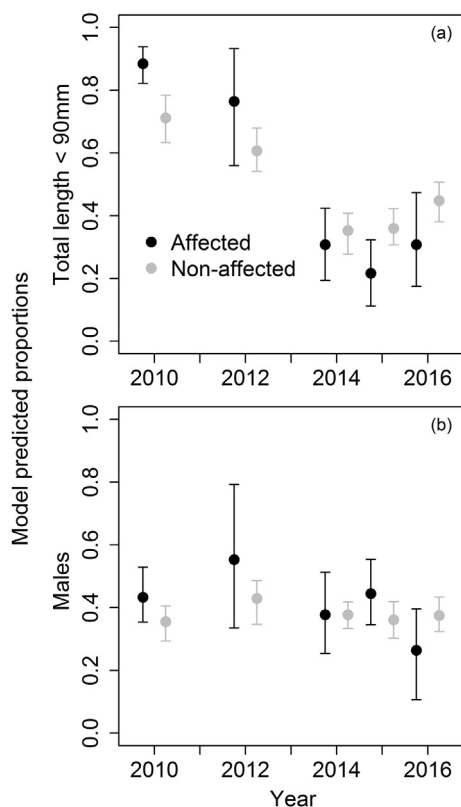
Fig. 3. Changes in (a) proportion of small (< 90-mm) individuals and (b) proportion of males for *Euastacus armatus* at 2010–11 hypoxic blackwater "affected" and "non-affected" sites over time. Grey = non-affected sites; black = affected sites.

small individuals declined only slightly at affected sites (although the estimate was more variable reflecting the low numbers sampled), but after 2014 a considerably lower proportion of small individuals (< 0.4) and no obvious pattern of increase was observed. A similar shift toward

Table 2

Logistic regression models of length category and sex ratio for *Euastacus armatus* with AIC and AIC weights. The dependent variables y_{size} and y_{sex} are binary indicators of crayfish < 90-mm and male, respectively. The independent variables *year* and *treat* are dummy variables indicated the year (i.e. 2012, 2014, 2015, or 2016; 2010 is default) and the treatment (i.e. blackwater affected; non-affected as the control), respectively.

Model	AIC	Δ AIC	AIC weight
Length category analysis			
y_{size} = NULL	1983.2	187.4	0.00
y_{size} = year	1807.7	11.9	0.00
y_{size} = treat	1982.1	186.4	0.00
y_{size} = year + treat	1809.6	13.9	0.00
y_{size} = year∗treat	1795.8	0.0	1.00
Sex ratio analysis			
y_{sex} = NULL	2110.7	0.0	0.58
y_{sex} = year	2115.0	4.1	0.07
y_{sex} = treat	2112.1	1.3	0.29
y_{sex} = year + treat	2115.9	5.2	0.04
y_{sex} = year∗treat	2118.3	7.6	0.01

a greater the proportion of large individuals was observed at non-affected sites after 2014, this is accounted for by changes in the fishing regulations (e.g. 90-mm MLL to 100–120-mm HSLL) that afford greater protection to larger individuals. The proportion of males in the sampled population ranged from 0.34 (affected sites in 2016) to 0.55 (affected sites in 2012), but the best model (i.e. lowest AIC) showed that variation was not explained by either year or treatment, indicating no statistical effect of the blackwater on sex ratio (Fig. 3b).

3.2. Detection probability

Mean detection probabilities ranged between 0.05 (affected sites in 2010) to 0.26 (non-affected sites in 2015); varying significantly with mean daily discharge ($\eta_{10} \neq 0$, Table 1) and among years due to unknown factors ($\eta_3 \neq 0$, Table 1). Detection probability declined from ~0.15 at the minimum mean daily discharge during the study (i.e. 1619 ML d^{-1}) to ~0.05 at the maximum mean daily discharge (i.e. 26,791 ML d^{-1}, Fig. 4a). There was no clear pattern of mean detection probability among years, although detection probability was statistically greater in 2014 compared to 2010 for all sites (Table 1, Fig. 4b). Furthermore, we observed a tendency for the detection probability to be greater in the non-affected sites than the affected sites (Fig. 4b), although this pattern was not statistically significant (Table 1). Despite these observed patterns, detection probability in the affected and non-effected sites demonstrated consistent patterns through time (η6, η7, η8, η9 ≈ 0, Table 1, Fig. 4b), suggesting that the non-affected sites served as operative controls in the BACI experimental design.

3.3. Population model simulations

Modelling simulations forecast lengthy recovery trajectories of affected populations under all post-disturbance scenarios when compared to the 90-mm MLL scenario (i.e. the harvest trajectory) (Fig. 5). For instance, if the 90-mm MLL regulation remained in place following the blackwater disturbance, it was anticipated that the mean population size would only converge with the mean harvest trajectory after almost 100 years. Implementing the 100–120-mm HSLL improved the mean recovery trajectory (to 60 years) and this timeframe was not improved greatly if an initial 20-year closure was also enacted (as trajectories merged once harvest pressure was again introduced). The shortest time (just under 50 years) to reach the mean harvest trajectory was realised under the permanent closure scenario, and the mean trajectory of this scenario approaching that of the natural population scenario after 80 years. Under all post-disturbance scenarios there was an initial lag period (~5 years) before populations began to increase in a meaningful
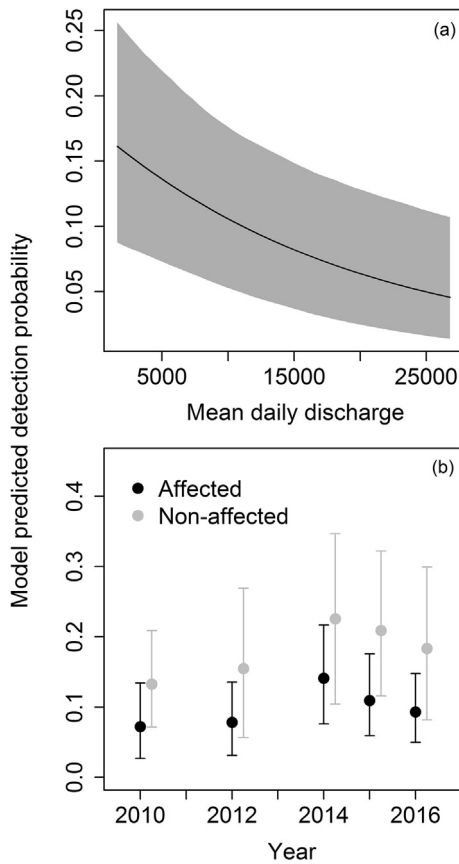
Fig. 4. Changes in the detection probability of *Euastacus armatus* with (a) discharge (ML.d^{-1}) and (b) year.

manner.

4. Discussion

This study revealed minimal recovery of *E. armatus*, a K-selected freshwater crayfish, in the five years following significant population decline. Specifically, the affected population did not display a significant improvement in occupancy or abundance. The affected population also continued to exhibit a truncated length structure compared to the unaffected population, i.e. dominated by adults with limited

juvenile representation, indicating little evidence of localised recruitment. Population simulations forecast a decadal timeframe will be required for the recovery of this species (cf. Lotze et al., 2011). These findings emphasise the critical need for concerted conservation and fisheries management to facilitate the recovery of the species across its range.

Modelling simulations under a natural recovery (i.e. no harvest pressure) scenario suggest that, on average, pre-disturbance population sizes of the species would not be reached for some 50 years. Imposing any level of harvest pressure, even with initial periods of closure, was predicted to delay this recovery timeframe for decades. The reality of these predictions must be acknowledged in the management of affected populations of the species (i.e. permanent closures may be necessary). Whilst these predictions are illustrative of likely recovery timeframes, some variation is conceivable for several reasons. Firstly, the simulations considered the mean population loss (i.e. 81%) with shorter timeframes forecast at sites where the blackwater impact was less pronounced (i.e. lower population loss or only adults impacted). Likewise, the recovery trajectories represent mean estimates (of 1000 model iterations), ensuring that both faster (and slower) timeframes were predicted under each scenario. Secondly, immigration was not considered in the model (Todd et al., 2017; Todd et al., in press), but recolonisation may promote more rapid increases in the size of affected populations. Similarly outside of the model framework was the fact that in small, recovering populations, which are released from density dependence and not expressing Allee effects, individuals may display faster growth rates leading to enhanced overall population growth (Frankham et al., 2010; Kuparinen et al., 2014). Finally, recovery timeframes may be accelerated through targeted reintroductions (Weeks et al., 2011), which are already underway in some blackwater affected areas where there has been no sign of recovery. Refining the model to allow spatially-explicit predictions, which account for differential levels of population loss as well as immigration and population growth, would enhance understanding of the impact of, and recovery from, disturbance events.

The findings of the present study provide some insight into the mechanisms that will drive the recovery of affected *E. armatus* populations. With the proportionally lower numbers of individuals below 90-mm, it is evident that localised recruitment is yet to contribute meaningfully to population recovery. It is conceivable, however, that greater numbers of small juveniles (< 40-mm), spawned in recent years, are yet to be reflected in the sampled population given their problematic detection (Alves et al., 2010). The greater proportion of larger individuals (> 90-mm) observed over 2014 to 2016 (cf. McCarthy et al.,
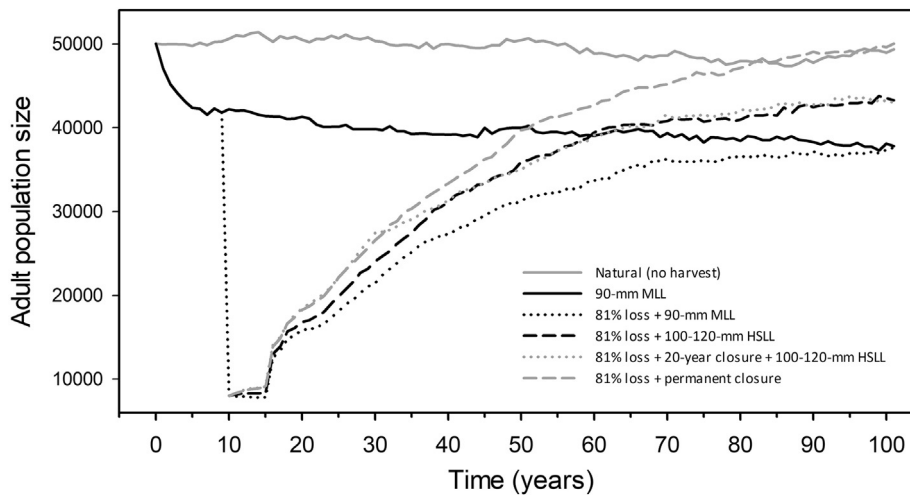

Fig. 5. Mean adult *Euastacus armatus* population size based on modelling simulations (using 1000 iterations) under a range of scenarios relating to natural populations, harvest pressure (relating to length regulations of minimum length limit, MLL; and harvestable slot length limit, HSLL) and hypoxic blackwater disturbance.

2014), suggests that large-scale dispersal, facilitated by active movement or entrainment during high flows, and subsequent recolonisation could be aiding the recovery of affected populations. Freshwater crayfish with r-selected life histories can disperse large distances (between 18 and 24.4 km year^{-1}: Hudina et al., 2009) and it has been predicted that adults of K-selected species, such as the giant Tasmanian freshwater crayfish *Astacopsis gouldi*, intersperse infrequent larger-scale movements (e.g. > 2-km) with long periods of inactivity or limited movement (Webb and Richardson, 2004). Whilst these larger-scale movements are incongruent with those observed in *E. armatus* in upland areas (Ryan et al., 2008), populations across lowland areas may possess greater capacity for such movements as inferred by genetic analyses (Whiterod et al., 2017). Finally, the downstream drift of small juveniles (Robinson et al., 2000) represents an additional recolonisation pathway but is largely unexplored in the species. There is an opportunity to better understand the recovery potential of K-selected species such as *E. armatus* through the concurrent determination of age and growth rates (Leland et al., 2015) and movement patterns of different life stages (Cooke et al., 2013; Hussey et al., 2015).

The present study employed a BACI design, which accounted for imperfect and variable detection, to best isolate the impacts of the blackwater event. These indicators demonstrated that detection probability varied consistently through time for the non-affected and affected sites so, it could be argued that, in our case, it is unnecessary to account for detection probability to achieve accurate inference on changes in *E. armatus* abundance relative to blackwater disturbance. However, when imperfect and variable detection is ignored, the robustness of the BACI design is questionable as the assumption of constant detection, among years and treatments, cannot be assessed (Popescu et al., 2012). Relevantly, we did observe some variation in the detection of *E. armatus* with river discharge (three-fold change) and among years (two-fold change) and detection probability is also known to be influenced by local (i.e. temperature, habitat, water clarity) and landscape variables (i.e. stream order, topography, landuse) as well as sampling methods (Gwinn et al., 2016; Magoulick et al., 2017). Finally, low detection probabilities were observed (i.e. 0.05–0.26), compared to other studies focusing on freshwater crayfish (Magoulick et al., 2017; Pearl et al., 2013). Thus, it is recommended that detection probability continued to be accounted during future assessments of recovery to lessen the possibility of spurious conclusions that hamper conservation of the species (Gwinn et al., 2016; Kellner and Swihart, 2014).

The findings of the present study emphasise an increasingly realised dilemma – an important and valued recreationally harvested species that is now threatened across much of its range. The noted historical declines experienced as a result of both ceased (i.e. commercial harvest) and enduring, but largely unknown, impacts (Furse and Coughran, 2011a) are anticipated to result in smaller, fragmented populations less resilient to abrupt disturbances. The 2010–11 blackwater event posed concomitant impacts across other lowland populations and other disturbances have impacted upland populations over recent times (Noble and Fulton, 2017). The findings of the present study ensure that greater emphasis must now be placed on the conservation of the species. In this context, the management of the recreational fishery must adopt a precautionary approach, with regulations (such as area closures and length limits) promoting the sustainability of the species (Gwinn et al., 2015; Todd et al., in press). The present 100–120-mm HSLL regulation appears most appropriate as evidenced by the shift toward a greater proportion of larger individuals observed at non-affected sites in the present study, and reinforced by complimentary population modelling (cf. Todd et al., in press).

Further, it is recommended that the combination of indicators assessed in the present study form the basis of a long-term monitoring strategy to allow evaluation of (1) areas that remain open to recreational fishing, (2) the legacy of the 2010–11 disturbance event and also (3) more recent and future (and most likely unforeseen) disturbances (Lindenmayer et al., 2012; Verdonschot et al., 2013). This is

particularly pertinent as another blackwater disturbance has influenced areas of the present range of the species over 2016–17 (MDBA, 2016). Targeted research is needed to explore recovery mechanisms and re-introductions on a scale larger than have already been instigated should be explored to promote recovery. Opportunities exist for more meaningful engagement of recreational fishers in monitoring and research to achieve more effective management (Aceves-Bueno et al., 2015; Cooke et al., 2016). The role that flow and habitat have played in the decline of the species and, more importantly, how it can aide recovery must also be considered.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2018.02.042.

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