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ARTICLE

Efficiency of electrofishing in turbid lowland rivers: implications for measuring temporal change in fish populations

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Abstract: To quantify how electrofishing capture probability varies over time and across physiochemical and disturbance gradients in a turbid lowland river, we tagged between 68 and 95 fish·year^{-1} with radio transmitters and up to 424 fish·year^{-1} with external and passive integrated transponder (PIT) tags. We surveyed the site noninvasively using radiotelemetry to determine which of the radio-tagged fish were present (effectively closing the radio-tagged population to emigration) and then electrofished to estimate the proportion of available fish that were captured based on both this and standard mark–recapture methods. We replicated the electrofishing surveys three times over a minimum of 12 days each year, for 7 years. Electrofishing capture probability varied between 0.020 and 0.310 over the 7 years and between four different large-bodied species (Murray cod (*Maccullochella peelii*), trout cod (*Maccullochella macquariensis*), golden perch (*Macquaria ambigua ambigua*), and silver perch (*Bidyanus bidyanus*)). River turbidity associated with increased river discharge negatively influenced capture probability. Increasing fish length increased detection of fish up to 500 mm for Murray cod, after which capture probability decreased. Variation in capture probability in large lowland rivers results in additional uncertainty when estimating population size or relative abundance. Research and monitoring programs using fish as an indicator should incorporate strategies to lessen potential error that might result from changes in capture probabilities.

Résumé : Afin de quantifier les variations de la probabilité de prise à la pêche électrique dans le temps et le long de gradients physicochimiques et de perturbation dans une rivière turbide de basse terre, nous avons doté de 68 à 95 poissons·année^{-1} de radioémetteurs et jusqu'à 424 poissons·année^{-1} d'étiquettes externes et de transpondeurs passifs intégrés (PIT). Nous avons sondé le site de manière non intrusive par radiotélémétrie afin de déterminer lesquels des poissons radioétiquetés étaient présents (excluant du fait l'émigration pour la population radioétiquetée), puis effectué une pêche électrique pour estimer la proportion de poissons disponibles capturés selon cette méthode et des méthodes de marquage–recapture normales. Nous avons répété les levés par pêche électrique trois fois sur au moins 12 jours chaque année, pendant sept ans. La probabilité de capture par pêche électrique variait dans une fourchette de 0,020 à 0,310 sur les sept ans et pour quatre espèces de gros poissons (la morue de Murray (*Maccullochella peelii*), la perche Macquarie (*Maccullochella macquariensis*), la perche dorée (*Macquaria ambigua ambigua*) et la perche argentée (*Bidyanus bidyanus*)). La turbidité de la rivière associée à un débit accru avait une incidence négative sur la probabilité de capture. Plus la longueur des poissons était grande, plus la détection était élevée pour les poissons allant jusqu'à 500 mm en ce qui concerne la morue de Murray; au-delà de cette longueur, la probabilité diminuait. Les variations de la probabilité de capture dans les grandes rivières de basse terre introduisent une incertitude supplémentaire dans l'estimation de la taille ou de l'abondance relative des populations. Les programmes de recherche et de surveillance qui se servent des poissons comme indicateurs devraient comprendre des stratégies visant à limiter l'erreur qui pourrait résulter des variations de la probabilité de capture. [Traduit par la Rédaction]

Introduction

A cornerstone of biological sampling methods is the estimation of the presence or abundance of target organisms (Phillips et al. 2009; Magurran et al. 2010; Kepner et al. 2000). Most often, direct observation or capture of the entire population is not plausible, so a census method needs to include a design that permits estimation of the number of unobserved animals (Seber 1973). Capture probability is often used as a coefficient that scales the relationship between the catch and true population size. It can be influenced by environmental (e.g., season, temperature), biological

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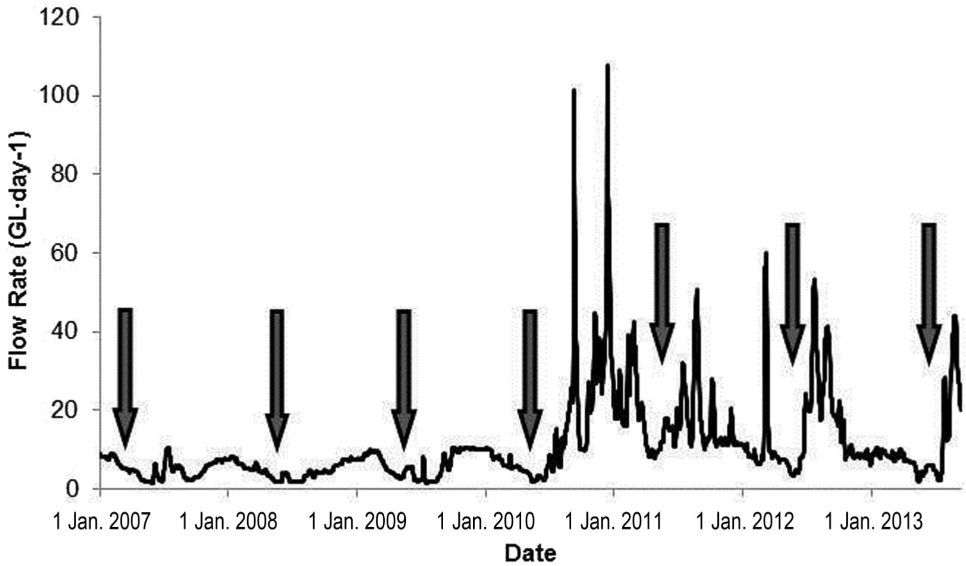
Fig. 1. Murray River flows (10^6 L·day^{-1}) downstream of Yarrawonga from 2007 to 2013. Arrows indicate sampling occasions.



(species and size), and sampling equipment (selectivity) variability, so robust census methods should ideally include ways to estimate its associated variance. Capture probability can also vary temporally and spatially, so valid inferences about changes in population size need to take these into account.

In riverine ecosystems, monitoring fish populations is widely used to track river health, as fish are often viewed as a tangible "end product" of environmental improvement or fisheries management (Cowx and Gerdeaux 2004; Woolsey et al. 2007) and are increasingly used to assess the actual and potential impacts of climate change (Bond et al. 2011; Parra et al. 2012). Such monitoring data are regularly used to measure how management interventions such as stock enhancement, the provision of environmental flows, or habitat improvement influence waterways. River restoration programs around the world, including the assessment of the ecological status of European Union surface waters (Schmutz et al. 2007), the AU$500 million Living Murray program in Australia (http://www.mdba.gov.au/what-we-do/managing-rivers/TLM-environmental-works-and-measures), or the US$7.8 billion Kissimmee River Restoration Project in the USA (Koebel 1995), use fish monitoring data to assess ecological health. The increased emphasis on improving river catchments and fish populations over the past two decades has been immense (Lake et al. 2007; Whiteway et al. 2010). With such a large investment comes the requirement for extensive monitoring; however, given the scale of the investment in environmental improvement, there is surprisingly little effort made to test the reliability and accuracy of fishery assessment methods or indeed the outcomes of fishery improvement measures.

Electrofishing is a widely adopted tool for assessing fish populations in rivers and small water bodies (Cowx 1995; Rosenberger and Dunham 2005; Schmutz et al. 2007); it is relatively safe for fish (compared with other capture methods) and easily applicable to a wide range of waterways and habitats. However, electrofishing has limitations (Zalewski and Cowx 1990), and given the weight of the management decisions increasingly justified based on data collected via electrofishing, accurate data interpretation is essential.

Considerable literature exists describing the conditions that can affect capture probability using electrofishing (Zalewski and Cowx 1990; Pygott et al. 1990; Bayley and Austen 2002). These can include water depth, turbidity, conductivity, habitat structure, and operator experience. However, this literature typically describes patterns of capture probability in smaller streams with high water clarity, and little is known about larger lowland streams with deep, turbid waters, where estimation is difficult (but see Harvey and Cowx 1996). Here we present the results of a 7-year electrofishing efficiency trial in a large, fifth-order stream in southeastern Australia. We investigated whether different species, fish size, and environmental variables influenced fish capture probability.

Materials and methods

Estimating absolute abundance for electrofishing in rivers is challenging because the true number of fishes available for sampling is usually unknown. Mark–recapture methods are commonly used to estimate population parameters in such a scenario, but are complicated in our case (and in many others) by the migration of fish out of the sampling area between sampling occasions. Previous attempts at fully accounting for the population (via poisoning or blocking the stream) have proven successful in some scenarios (Price and Peterson 2010), but are unlikely to be effective in a large river setting. Instead, we used a combination of radio transmitters and standard mark–recapture methods to estimate capture rates while accounting for temporary migration in and out of the study area.

Electrofishing capture probability trials were conducted during May and June (to coincide with low flow conditions) between 2007 and 2013 (i.e., 7 consecutive years; Fig. 1; Table 1). We chose a 2 km stretch (the maximum distance we could efficiently electrofish with two boats in 1 day) of the Murray River (a large lowland river in southeastern Australia) as the study site. This river length was further divided into 16 subunits (approximately 250 m long and 50 m wide), which equated to approximately the length of river the electrofishing boats could fish before the holding wells on the boat were full of collected fish. Within this 2 km reach, we radio-tagged between 68 and 95 fish, and PIT-tagged (passive integrated transponder) or externally tagged up to 424 fish, annually (see Table 2). We sampled the same site yearly to take advantage of radio transmitters that were still active from previous years, thus reducing costs and increasing our sample size.

At the start of the annual trials, we used two electrofishing boats (Smith Root Inc., Portland, Washington, USA — a commonly used gear type) to sample the 16 subunits. Each boat was randomly allocated eight subunits (i.e., boats did not operate together in any subunits). Both boats were fitted with Smith Root 7.5 GPP boat-mounted electrofishing units. Drivers and netters on both boats were highly competent, with a minimum 5 years of electrofishing

Table 1. Mean and standard deviation for discharge, turbidity, conductivity and stream gauge height (i.e., water level) during electrofishing capture efficiency investigations in the Murray River.

Year	Mean discharge (GL·day^{-1})	Mean turbidity (Secchi) (m)	Mean conductivity (S·m^{-1})	Mean gauge height (m)	Change in depth from 2007 (m)
2007	1.75±0.08	1.35±0.05	0.0028±0.00008	0.29±0.02	0
2008	2.36±1.14	1.30±0.01	0.0034±0.000113	0.43±0.26	+0.11
2009	3.19±0.27	1.44±0.09	0.0047±0.000112	0.65±0.05	+0.36
2010	2.34±0.54	0.97±0.07	0.0034±0.000458	0.45±0.13	+0.15
2011	15.59±2.46	0.63±0.03	0.0045±0.000295	2.35±0.29	+2.06
2012	3.92±0.41	0.85±0.10	0.0072±0.000147	0.79±0.07	+0.49
2013	4.28±0.55	0.87±0.13	0.0061±0.000134	0.85±0.09	+0.55

experience each. We operated the electrofishing gear with 1000 V, 60 Hz, a duty cycle of 40%, and between 5.5 and 7.5 amps (mean = 6 amps).

The fishing procedure involved one boat driver and one dip-net operator and ensured that, as far as practically possible, each subunit was sampled in its entirety (i.e., the whole 250 m × 50 m area was sampled). In some years when resources allowed, a chase boat (Daugherty and Sutton 2005) followed the electrofishing boat at a safe distance to collect any additional stunned fish that had not been collected by the dip-net operator. We placed all fish collected in an aerated live well on board the boat. At the completion of an electrofishing subunit, we identified collected fish to species, measured total length (nearest mm), and weighed (nearest g) and tagged each with both a uniquely coded subdermal PIT tag and an external floy tag, before fully resuscitating them. We retained up to 100 in total of the following species — Murray cod (*Maccullochella peelii*), trout cod (*Maccullochella macquariensis*), golden perch (*Macquaria ambigua ambigua*), and silver perch (*Bidyanus bidyanus*) — weighing ≥200 g for surgical implantation of a radio transmitter in any one year. In addition, we tagged previously unmarked fish with external or PIT tags and recorded the species, mass, total length, subunit of capture, and tag number if already tagged. All captured fish were then returned to the water unharmed. We radio-tagged a wide range of size classes of the target species to test the effect of fish size on electrofishing capture probability (Table 2).

The tags used were two-stage, 35 pulses per minute, 150 MHz radio transmitters with 300 mm antennae (model F1835, F1850, and F1815/F1505 Advanced Telemetry Systems, Isanti, Minnesota, USA) that weighed between 7 and 55 g in air and had a guaranteed life span of between 160 and 1200 days. We selected the tag model for each fish to ensure that the transmitter mass never exceeded 1.5% of body mass, thus minimizing disproportionate effects of tag size on behaviour. All tags had a "mortality switch" (a mercury motion sensor), which indicated when the animal had either died or shed its tag. Tags on all captured fish were checked to ensure that they were still transmitting (to ensure that nontransmitting fish were not recorded as telemetry recaptures). Tags were implanted following standard surgical procedures (O'Connor et al. 2009).

After a minimum of 3 days following their release, we tracked all fish with radio transmitters from a boat using a receiver and antenna (Koehn 2006). We began tracking before 0800, and then after 0900, two independent electrofishing teams separately fished eight subunits using the same procedures used to capture fish for radio transmitter insertions. The dominant behaviour for Murray cod, trout cod, and golden perch during daylight hours is sedentary (Koehn 2009; Crook 2004; Thiem et al. 2008), and we expected little movement of individuals away from the study reach during the day of electrofishing. However we expected some movement of fish at night between sampling occasions and possibly in response to the capture and tagging process. To account for such movement, the tracking team remained on site during electrofishing to confirm whether radio-tagged fish had moved away from the 2 km reach between the morning recording and the time of sampling by the electrofishing boat. The tracking team applied discreet procedures to ensure that the electrofishing team did not know whether radio-tagged fish were present during electrofishing. The tracking of approximately 100 tagged fish to their exact location was not possible within the constraint of needing to have completed most tracking before electrofishing began. However, we were able to narrow the position of radio-tagged fish to within two subunit lengths (500 m). We were thus able to estimate the likelihood of fish emigrating from the sampling area, thereby removing this potential source of bias from estimates of capture probability (analysis described below).

We repeated tracking and electrofishing a total of three times annually, with a minimum 3-day interval between each occasion (i.e., over a minimum of 12 and maximum of 45 consecutive days annually). Stress-related hormones have been observed in fish for up to 24 h after electrofishing (Mesa and Schreck 1989), so we assumed that the interval between electrofishing sampling occasions was sufficient for the fish to recover from any residual effect from the previous electrofishing experience.

We collected environmental descriptors for each of the 16 subunits to estimate their influence on capture probabilities. The mean depth of each subunit using visual observation of the vessel's depth sounder while fishing was done in each year of sampling. The volume of structural woody habitat in each subunit was estimated using the methods outlined in Kitchingman et al. (2013). Depth and volume of structural habitat were correlated (Pearson's R = 0.85), and we only included structural woody habitat to minimize collinearity. The primary environmental variables hypothesized to affect sampling conditions between years were river discharge (for which we obtained values from the Murray Darling Basin Authority), mean river depth (m), turbidity (Secchi depth, m), and conductivity (S·m^{-1}). We used Secchi depth as a descriptor of flow-related sampling conditions given it was highly correlated with discharge (which in turn was correlated with annual mean river depth; R = 0.88) and less correlated with depth (R = 0.65). Secchi depth varied yearly (along with discharge that varied yearly during sampling between 1.64 and 19.97 GL·day^{-1} in 2007 and 2011, respectively), but was stable within years (Fig. 1; Table 1). We assumed that turbidity conditions were consistent between subunits. Water conductivity also influences electrofishing success, and we also obtained daily values of this from the Murray Darling Basin Authority. We centred all continuous variables on the mean across all years and for fish length. We also centred lengths on each species' mean lengths. Where squared values were used in modelling, we squared the centred values.

Analysis

Movement of fish within and between sampling subunits was a potential source of bias, both in terms of estimating overall capture probabilities due to emigration of tagged fish and to spatial and temporal variability in the influence of predictor variables. We therefore used the combination of telemetry and capture–recapture data in a state-space model (King 2012) to infer the likely locations and capture probabilities of fish given their location. We assumed that (*i*) fish could move freely within and out of the

Table 2. Species data and mean (range in parentheses) total length (TL) used during electrofishing capture efficiency investigations in the Murray River.

	2007	2008	2009	2010	2011	2012	2013	Total
Murray cod (*Maccullochella peelii*)								
Mean no. of radio-tagged fish	51 (47–54)	46 (41–49)	39 (37–42)	35 (32–37)	24 (19–29)	22 (18–26)	20 (19–23)	237
% Recaptures radio-tagged fish	19 (15–23)	13 (4–21)	25 (24–26)	23 (22–24)	7 (4–10)	16 (5–33)	13 (11–17)	
No. of transmitter mortalities	2	1	0	0	0	0	0	3
Total no. of conventionally tagged fish	127	81	66	45	22	30	58	429
Total no. of recaptured conventionally tagged fish	32	30	23	14	7	8	15	129
TL mean (mm)	368 (213–1260)	395 (221–1320)	386 (160–1150)	414 (228–1180)	493 (238–1280)	545 (288–1150)	433 (215–1340)	
Trout cod (*Maccullochella macquariensis*)								
Mean no. of radio-tagged fish	12 (11–12)	14 (11–17)	17 (16–17)	15 (13–17)	29 (26–32)	39 (38–39)	24 (23–25)	150
% Recaptures radio-tagged fish	0	7 (6–9)	10 (6–13)	18 (12–23)	6 (0–12)	4 (3–5)	5 (0–12)	
No. of transmitter mortalities	0	1	0	0	0	0	0	1
Total no. of conventionally tagged fish	122	148	191	148	71	180	64	924
Total no. of recaptured conventionally tagged fish	17	23	21	17	9	31	7	125
TL mean (mm)	301 (201–556)	286 (182–530)	285 (154–538)	297 (178–538)	354 (165–536)	361 (154–498)	367 (223–500)	
Golden perch (*Macquaria ambigua*)								
Mean no. of radio-tagged fish	26 (23–28)	28 (20–36)	14 (11–18)	16 (13–18)	14 (12–18)	30 (28–32)	38 (26–54)	166
% Recaptures radio-tagged fish	10 (9–11)	6 (0–14)	14 (9–17)	4 (0–6)	7 (0–22)	5 (3–7)	7 (4–9)	
No. of transmitter mortalities	0	0	1	0	0	0	1	2
Total no. of conventionally tagged fish	54	62	36	42	51	119	109	473
Total no. of recaptured conventionally tagged fish	9	6	3	2	6	10	12	48
TL mean (mm)	432 (308–535)	420 (265–581)	422 (260–526)	426 (295–532)	429 (226–542)	420 (249–553)	414 (230–547)	
Silver perch (*Bidyanus bidyanus*)								
Mean no. of radio-tagged fish	0	0	1	2 (1–3)	2 (1–2)	0	0	5
% Recaptures radio-tagged fish	0	0	0	0	0	0	0	
No. of transmitter mortalities	0	0	0	0	0	0	0	0
Total no. of conventionally tagged fish	31	51	42	135	37	95	24	415
Total no. of recaptured conventionally tagged fish	1	3	1	1	1	2	0	9
TL mean (mm)	367 (282–445)	368 (260–438)	371 (237–474)	281 (152–423)	331 (240–417)	305 (200–394)	356 (283–442)	

Note: Mean number of radio-tagged fish denotes only those that are available for capture (i.e., tracked within the study reach and averaged over sampling events).

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sampling area, (*ii*) fish could not be caught if they left the sampling reach, and (*iii*) capture probabilities and movement patterns varied with environmental and individual covariates. In the subsequent sections, we describe the movement and capture components of the model.

Movement model

We used a Gaussian random-walk model to estimate the locations of unobserved fish based on their last-known locations (distance in 250 m segments and side of the river). We assumed that the location (in metres along the river) of a fish at time t would be shifted from its location at time $t - 1$ by a normally distributed distance $D_{i,t}$. Thus, the model for location $L_{i,t}$ in metres was

$$L_{i,t} \sim \text{Normal}(L_{i,t-1} + D_{i,t}, \sigma_{\text{species}})$$

where the full model for $D_{i,t}$ was a linear combination of parameters including fish species, fish length, site-level structural woody habitat volume (m^3), Secchi disk depth (m), and whether or not the fish was captured in the previous occasion (0 or 1):

$$D_{i,t} = \beta 0_{\text{species}} + \beta 1\text{length}_i + \beta 2\text{wood}_{\text{site}} + \beta 3\text{Secchi}_y + \beta 4\text{capture}_{i,t-1}$$

where $\beta 0_{\text{species}}$ is a normally distributed random intercept for each species, and each β indicates a normally distributed parameter. We estimated the coefficients for factors relating to fish characteristics (length and previous capture) as normally distributed, taxon-specific random coefficients, whereas parameters that related to sampling conditions (wood, conductivity, and turbidity) were treated as fixed effects common across species. We recorded the capture location for each fish as the centroid of the 250 m subunit where it was first captured and tagged, along with the side of the river. Because sampling only occurred within the 2 km study reach, our data for estimating $D_{i,t}$ were restricted to observations within the 2 km study reach, which could potentially bias our estimates of $L_{i,t}$. We therefore additionally specified in the model that the $L_{i,t}$ were censored at 0 and 2 km.

We were also able to use the telemetry data to put finer bounds on the locations of radio-tagged fish. First, we were able to discern whether each radio-tagged fish was in the 2 km reach. If it was absent, we were able to assign its location as either in the upstream or downstream segments beyond the 2 km reach and therefore not catchable. For individuals within the sampling area, we were able to truncate the distribution for $L_{i,t}$ to a 500 m section, allowing for greater precision in the estimation of D.

To determine in which bank of the river a fish was given its last location, we assumed that whether or not the fish switched sides at time t was the outcome of an exchangeable random Bernoulli trial:

$$B_{i,t} \sim \text{Bernoulli}(\varphi_i)$$

where the parameter φ_i is the probability of switching for individual i. We tested logistic regression models for φ_i that included species, river discharge, site, and the logit of φ_i. Based on $L_{i,t}$ and $B_{i,t}$ we assigned the site ($S_{i,t}$) of each unobserved fish as being in one of the 16 subunits or outside of the sampling reach. We then used $S_{i,t}$ to determine the conditional capture probability for each fish.

Electrofishing observation model

We modelled the observed captures $Y_{i,t}$ of each fish as exchangeable Bernoulli trials:

$$Y_{i,t} | S_{i,t} \sim \text{Bernoulli}(\theta_{i,t,S_{i,t}})$$

where $Y_{i,j} = 1$ if a fish is captured at time j and 0 if it is not, and $\theta_{i,t,L_{i,t}}$ is the probability of capture conditional on individual, time-, and site-dependent factors. For fish that remained within the sampled reach, we modelled $\theta_{i,t,L_{i,t}}$ using a logistic regression:

$$\begin{aligned}\text{logit}(\theta_{i,t,S_{i,t}}) = {} & \alpha 0_{\text{species}} + \alpha 1_{\text{species}}\text{length} + \alpha 2_{\text{species}}\text{length}^2 \\ & + \alpha 3_{\text{species}}\text{radio} + \alpha 4\text{wood} + \alpha 5_{\text{species}}\text{capture}_{t-1} \\ & + \alpha 6\text{Secchi} + \alpha 7\text{conductivity} + \alpha 8\text{wood}_{\text{site}} \\ & \times \text{length}_i + \alpha 9\text{conductivity} \times \text{length}_i\end{aligned}$$

where each α is a normally distributed parameter specific to each predictor, and $\alpha 0_{\text{species}}$ is a normally distributed random intercept for each species. Because of the differences in size, behaviour, and habitat choice in the four species used in this study, we included species-specific random coefficients for all fish characteristics (individual length, whether they had a radio tag implanted, whether they were captured in the previous occasion). For sampling-related parameters (for each subunit, structural woody habitat volume, water turbidity – Secchi disk depth for each day of sampling, and water conductivity), we tested models both with species-specific random effects and with effects assumed to be the same across species.

Model ranking

We took a multistepped approach to model ranking. We first ran all possible combinations of models in which the movement parameters varied and capture probabilities were assumed to be equal across all individuals. We recorded the deviance information criterion (DIC; Spiegelhalter et al. 2002) scores. We then built a set of 180 candidate models that included different combinations of random and fixed parameters in the conditional capture model. Where variables were potentially correlated (such as habitat complexity and site depth), we excluded combinations of strongly correlated variables. We compiled all models for the JAGS programming language (Plummer 2003) and ran them using the R2jags package (Su and Yajima 2012) in R (R Development Core Team 2013). Using a 24-core desktop computer, we ran each model with three chains in parallel for 200 000 iterations, with a burn-in period of 50 000 iterations and keeping every 150th sample using the GIBBSIT (Raftery and Lewis 1996) procedure in R (library = mcgibbsit) (Warnes 2011) to confirm that chains were sufficiently long. We also calculated Bayesian p for each model to provide an indication of goodness of fit. For the top-ranked model, we reported the mean value of the posterior distribution of Markov chain Monte Carlo (MCMC samples) for each parameter, as well as 95% Bayesian credible intervals.

Results

River discharge, water height, turbidity, and conductivity were relatively stable within years but varied between sampling years (Table 1; Fig. 1). In particular, during the first 4 years of the study, water levels were low and had comparatively low turbidity (i.e., high Secchi depth readings). In contrast, year five of the study was dominated by higher discharge and turbid sampling conditions. Years six and seven had moderate discharge and turbidity readings (Table 1). Within each 250 m subunit, structural woody habitat loadings were measured once during 2013 (Table 3), varied between 0 and 188 m^3, and were assumed to have been stable over time. During the 7-year electrofishing study, we captured and tagged 2241 fish and implanted 558 radio transmitters across all species (Table 2). Species-specific values are reported in Table 2.

The first step of model ranking revealed that a model including factors for taxon and a taxon-specific coefficient for fish length was the top-ranked by over 10 DIC points (DIC = 6630 versus 6640 for the next-highest ranked model). We therefore proceeded with model selection using these two factors in all subsequent models.

Table 3. Mean depth and structural woody habitat loadings within the 16 subunit sites.

Subunit	Mean depth 2007 (m)	Habitat loading (m^3)
1	1.1	46.2
2	1.2	117.5
3	1.1	74.03
4	1.1	14.62
5	0.6	14.62
6	0.5	119.34
7	1.5	102.34
8	1.5	99.58
9	1.7	58.48
10	0.9	99.58
11	0.7	102.34
12	2.1	188.16
13	2.2	16.48
14	1.8	14.62
15	1	0
16	0.9	74.03

The next step of model ranking revealed that the top-ranked model for conditional capture probability included a random intercept for taxon, a species-specific quadratic relationship with individual fish length, turbidity, conductivity, structural woody habitat loadings, presence of a radio tag and a species-specific interaction between conductivity and fish length. This model was also related to a similar model in which the conductivity × length interaction was exchanged for a species-specific interaction between structural woody habitat loading and fish length (Table 4). Both of these top-ranked models had high Bayesian p (0.46, Table 4), indicating good model fit.

We estimated the species-specific probability of being captured during any single survey in each year using the length, turbidity, conductivity, and taxon parameter estimates (Table 5), along with the mean lengths of species within each year and annual turbidity and conductivity. In general, Murray cod had the highest annual capture probabilities (mean = 0.24, range: 0.16 to 0.31), followed by trout cod (mean = 0.083, range: 0.05 to 0.11), golden perch (mean = 0.08, range: 0.03 to 0.08), and silver perch (mean = 0.005, range: 0.001 to 0.01) (Fig. 2). For all species, capture probabilities were lowest in 2010–2011 and highest in 2009. On average, capture probabilities increased when Secchi disk readings were higher.

For all species, fish length was related to capture probabilities, with some species (Murray cod, trout cod, golden perch) having a quadratic relationship with fish length (Table 5), although the linear parameter for length in all species was imprecise, with 50% credible intervals that overlapped 0. We therefore included only the quadratic term when describing the relationship between length and capture probability, resulting in a peaked relationship for most species. For Murray cod and golden perch, fish ~400 mm had the highest capture probabilities, whereas the maximum was ~350 mm for trout cod (Fig. 3). There was a weak negative relationship between conductivity and capture probabilities, with the difference in conductivity encountered (0.0028 $S \cdot m^{-1}$ in 2007 versus 0.0072 $S \cdot m^{-1}$ in 2012) resulting in a 20% increase in relative capture probabilities, although the 95% credible intervals for the conductivity parameter overlapped 0 (Table 5). In addition, the model showed a positive length × conductivity interaction for golden perch and a weakly supported interaction for trout cod and silver perch, indicating that larger fish were relatively more likely to be captured as conductivity increased. (We note here that the conductivity range tested during our experiment is small.) The amount of structural woody habitat at a subunit level influenced capture probability, with fish being almost twice as likely to be captured in sites with high structural woody habitat loads than in sites with low structural woody habitat loads. There was also a positive relationship between capture probability and wood volume × fish length, indicating that larger fish were more likely to be captured as wood volume increased (Table 5). The top-ranked models did not include a term for whether or not a fish had been captured on a previous occasion (Table 4).

Table 4. Model descriptions top-ranked models for capture probability according to the deviance information criterion (DIC).

Capture Model	pD	p	DIC	ΔDIC
Telemetry tag, Secchi, wood volume, length, length, conductivity, (wood volume × length)	320	0.460	6491	0
Telemetry tag, Secchi, wood volume, length, length, conductivity, (conductivity × length)	320	0.460	6491	0
Telemetry tag, Secchi, (wood volume + length)	321	0.425	6496	5
Telemetry tag, wood volume, length	314	0.427	6496	5
Telemetry tag, Secchi, wood volume, length, conductivity, (wood volume × length), (conductivity × length)	329	0.467	6498	7
Telemetry tag, wood volume, length, (wood volume × length)	322	0.443	6499	8
Telemetry tag, wood volume, length, conductivity, (conductivity × length)	322	0.443	6499	8
Telemetry tag, wood volume, length, conductivity, (wood volume × length), (conductivity × length)	327	0.444	6500	9

Note: All models included a random intercept for taxon and shared same movement model (taxon + length). Table headings: pD is a measure of the number of parameters used; p indicates Bayesian p and ΔDIC is the relative difference between each model and the top-ranked model. Where terms are subscripted by "species" in the text, the term is species-specific.

The movement model demonstrated that on average, fish did not move from their site, but that movements of up to two sites away in either direction (upstream or downstream) were possible. The mean distance moved was close to zero sites, with standard deviations of around one site for all species, and larger fish moved farther downstream between sampling occasions than did smaller fish (Table 5). Site and turbidity were not included in the top-ranked models; however, the top-ranked model did include a random effect for site in the probability of switching banks. On average, site-specific bank-switching probabilities ranged from 0.05 to 0.35 (mean = 0.15).

We did not find evidence for spatial autocorrelation between catch rate in adjacent subunits (Mantel's I; $p > 0.08$ for all species and years). In the movement model, fish mostly stayed within the subunit in which they were captured, and if they did move, it was most likely to an adjacent subunit. As a consequence, fish that were tagged in subunits closer to the margins of the 2 km reach were more likely to migrate out between sampling events, although some did return.

Discussion

Our experiment represents a method for estimating the capture probability of fish (electrofishing efficiency) — information necessary to construct protocols for the credible estimation of fish population parameters and trends. Without estimates of capture probability, the ability to track changes in fish population size as a function of environmental variation or in response to a particular condition is potentially compromised. Others have used alternative methods coupled with electrofishing, such as netting, trawling, piscicides, explosives, or draining of the water body, to estimate capture probability (e.g., Bayley and Austen 2002;

Table 5. Model-averaged parameter estimates for the two top-ranked models based on the deviance information criterion (DIC).

Parameters	Value
Intercept(mc)	–1.174 (–1.771, –0.479)
Intercept(sp)	–5.235 (–6.444, –4.273)
Intercept(tc)	–2.416 (–2.879, –1.938)
Intercept(gp)	–3.049 (–3.816, –2.351)
Conductivity	–0.008 (–0.021, 0.004)
Conductivity × length(mc)	0 (–0.003, 0.004)
Conductivity × length(sp)	0.012 (–0.004, 0.03)
Conductivity × length(tc)	0.004 (0, 0.008)
Conductivity × length(gp)	–0.008 (–0.021, 0.004)
Length^2(mc)	–0.027 (–0.08, 0.022)
Length^2(sp)	–0.085 (–1.072, 0.973)
Length^2(tc)	–0.194 (–0.526, 0.057)
Length^2(gp)	–0.314 (–1.199, 0.189)
Secchi	0.864 (–0.043, 1.687)
Telemetry(mc)	0.498 (–0.103, 1.146)
Telemetry(sp)	0.424 (–1.454, 2.148)
Telemetry(tc)	–0.044 (–0.702, 0.52)
Telemetry(gp)	0.744 (0, 1.551)
Wood volume	0.01 (0.008, 0.014)
Wood volume × length(mc)	0 (–0.003, 0.004)
Wood volume × length(sp)	0.012 (–0.004, 0.03)
Wood volume × length(tc)	0.004 (0, 0.008)
Wood volume × length(gp)	0.007 (–0.001, 0.017)
Movement parameters	
Length(mc)	–0.11 (–0.2, –0.01)
Length(sp)	–0.26 (–1.01, 0.29)
Length(tc)	–0.09 (–0.26, 0.11)
Length(gp)	–0.32 (–0.85, 0.03)
Intercept(mc)	–0.18 (–0.33, –0.06)
Intercept(sp)	–0.16 (–0.66, 0.24)
Intercept(tc)	–0.07 (–0.24, 0.12)
Intercept(gp)	–0.13 (–0.34, 0.1)
Standard deviation(mc)	1.08 (0.998, 1.098)
Standard deviation(sp)	1.09 (1.07, 1.12)
Standard deviation(tc)	1.09 (1.08, 1.11)
Standard deviation(gp)	1.11 (1.10, 1.12)

Note: All fish-specific parameters have taxon-specific estimates (mc, Murray cod; sp, silver perch; tc, trout cod; gp, golden perch). Data in parentheses indicate 95% Bayesian credible intervals around parameter estimates. Interaction terms are denoted with "×". Length parameters are based on length measured in millimetres.

Achleitner et al. 2012; Hedger et al. 2013), but our nonlethal approach is a more acceptable method, especially for native and threatened species.

Capture probability varies across several important environmental, biological, and methodological gradients in large lowland river systems (Bayley and Austen 2002; Speas et al. 2004) and is specifically related to habitat use by the target species (Mouton et al. 2012). It is therefore important to estimate the degree to which capture probability varies under specific sampling and environmental conditions so that the statistical robustness of population estimates can be assessed and, where possible, corrected accordingly as a function of the calibrated gear methodology (Bayley and Austen 2002). Specifically, we determined that peak electrofishing detection in this system varied according to species, but was generally at its maximum for all species in the range of 300–450 mm total length (Fig. 3). Larger fish are generally the most susceptible to electrofishing because of their greater electric potential differences (Zalewski and Cowx 1990) and nerve dimensions stimulated by the electrical field (Lamarque 1990; Reynolds 1996). However, in larger lowland rivers (>50 m wide), this trend could be counteracted by the tendency for larger fish to occupy deeper habitats that are more impacted by turbidity and where capture probability is generally lower (e.g., Bayley and Austen 2002; Mouton et al. 2012). Our results support this hypothesis, and

Fig. 2. Mean probability that a tagged fish of average size will be captured by an electrofishing survey given that it is present in a sampling site and given the mean sampling conditions (across all days of sampling and all sites sampled) in each year. Data for each year are calculated based on the model-averaged parameters in the top two capture models. 95% credible intervals are also indicated.

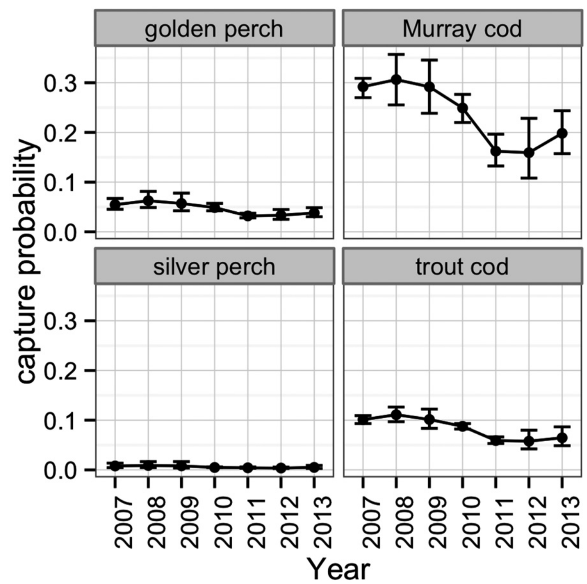
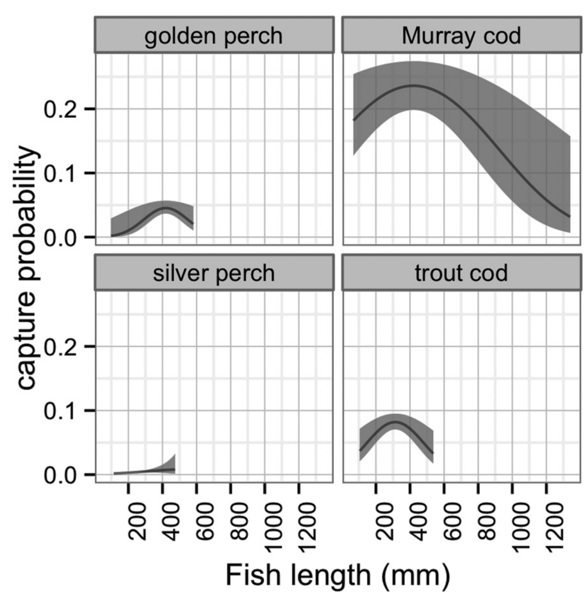


Fig. 3. The relationship between mean probability of being captured in a single survey and mean length for each of the four species studied: Murray cod, trout cod, silver perch, and golden perch. Grey areas indicate 90% credible intervals. Each curve is based on the model-averaged taxon-specific intercept and length squared parameters estimated in the two top capture probability models.



electrofishing might result in an under-representation of large adult fish in samples taken from lowland rivers.

We demonstrate that in the same site, using the same gear and settings, and with experienced electrofishing crews, capture probability can vary markedly both within and among years (Fig. 2). Our estimates of capture probability are consistent with other estimates for single- and multipass electrofishing in large rivers

(Bayley and Austen 2002), indicating that this capture method detects fish with a probability typically <0.5 (and in our case, well below that). Species-specific detection varied considerably over time; for example, Murray cod detection varied from 0.16 to 0.310 over the 7-year trial. By contrast, trout cod capture probabilities were relatively stable (0.07 to 0.12). Although morphologically similar (apart from differences in adult size), these two species occupy different habitats in riverine systems (Koehn 2009); therefore, differential habitat use is more likely to be the principal determinant of capture probability rather than differences in species morphology (see Mouton et al. 2012).

Mesa and Schreck (1989) found that cutthroat trout (*Onchorhynchus clarkii*) hid in more complex habitats after electrofishing. Lowland, warm-water species are often more cryptic than salmonids, and Australian freshwater cods and perches are strongly associated with complex habitats (Koehn 2006). Electrofishing teams can exploit this during sampling, and the increases in capture probabilities associated with wood volume likely reflects an increase in the efficiency of the electrofisher operators (who know where to "look" for fish when habitat is present). As such, we suggest that accounting for habitat volume and other interactions between the behaviour of fish and fishers in detection models will be important for estimates of population size.

Had our marked fish avoided the electrofishing teams, we would have expected a reduction in capture probability over time. Instead, we found no evidence that a fish captured in the previous sampling period was more or less likely to be captured again in the following period. As such, the high variance we observed likely represents random variation associated with this monitoring method and probably reflects normal fluctuation in fish behaviour. Indeed, Bohlin and Cowx (1990) found that a small proportion of any population appears to be invulnerable to capture by electrofishing and that this proportion varies between species and habitat complexity. Mesa and Schreck (1989) suggested that wild cutthroat trout require at least 24 h to recover from electrofishing, tentatively indicating this should be the minimum time elapsed between passes. Our minimum recovery time of 3 days between sampling events (noting that this was not a depletion trial — we returned all captured fish for potential resampling) was thus sufficient to avoid capture probability biases.

Sampling conditions also played an important role in determining capture probabilities. In deep and turbid waters, electrofishing capture efficiency is typically low (Bayley and Austen 2002), although in some shallower and moderately turbid waters, capture efficiency can be higher (e.g., for salmonids; Speas et al. 2004). Deep, turbid waters are characteristic of most lowland rivers, but we still observed a decreasing capture efficiency as turbidity and daily river discharge increased. In particular, our ability to detect Murray cod in 2011, where sampling was done during river discharge of around 15 GL·day^{-1}, was approximately half of when sampling was done at flows of 1.8–2.5 GL·day^{-1}. One explanation is that increased turbidity and river discharge hamper electrofishing crews from seeing stunned fish in the water (Pygott et al. 1990; Flotemersch et al. 2011). Further research is required to obtain an understanding of the individual effects of both depth and turbidity, and by recording maximum depth at the site of capture for each fish, a "proportion of the water visible" estimate can be calculated and included in models. Variation in water conductivity can also affect capture probability. In our case, water conductivity fluctuated little across time (between 0.0028 and 0.0072 S·m^{-1} over all sampling events). Even so, conductivity appeared consistently in our top-ranked models; and while this was true across all size classes, larger fish were more likely to be captured as conductivity increased. Because of the link between conductivity and turbidity, this interaction suggests that the relationship between conductivity and capture probability is driven more by electrochemical phenomena for larger fish, whereas for smaller fish, the relationship is mainly driven by water turbidity.

In summary, our results show that the effectiveness of electrofishing can vary considerably in large lowland systems. Unless the data can be corrected for such variation in capture probability, any population estimates arising should be viewed with caution (Cowx 1995; Flotemersch et al. 2011). We have shown how a model that can correct for variation in sampling conditions can account for some of this variation in capture probabilities. Unfortunately, estimating stream-specific capture probability is both difficult and expensive. To that end, Bayley and Austen (2002) recommended that "calibration" projects be implemented to estimate capture probability across a range of environmental conditions, fish species, and fish sizes. A benefit of such an approach is that it requires only a single investment, rather than trying to gather detection data for every project where electrofishing is used. In this case, care must be taken to account for variability between survey teams and other external conditions.

As such, we recommend that calibration should be a regular part of any sampling design where funding permits. As a general recommendation, sampling should include some level of replication to allow for assessment of the variation in capture that is due to sampling alone. Where possible, analysis of sampling efficiency can be augmented when sampling known populations, as we demonstrate here. We note that for many studies, this might be infeasible because of logistic constraints (Flotemersch et al. 2011). In some cases, it might be suitable to analyse relative change in fish population structure, or fish body condition, rather than total population size or comparisons of catch per unit effort. However, this approach should be used with caution, given that prevailing environmental conditions as well as the characteristics of individual fish can influence capture probabilities; thus, certain cohorts might go undetected in some conditions unless sufficient replication is applied. Furthermore, any calibration made on groups of fish that have different likelihood of detection — such as those that can emigrate undetected from the study area — should take into consideration the confounding effect of permanent or temporary migration. Failing to do so could introduce substantial bias into estimated parameters.

Sampling for cryptic taxa within inherently variable systems will always introduce some uncertainty. Given this, electrofishing is and will continue to be one of the safest, most cost-effective, and most easily replicated methods with which to survey large-bodied fish in freshwater environments. However, we promote active and ongoing research to increase our understanding of its limitations, which in turn will improve study design and increase the confidence of population parameter estimates.

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