Improving abundance estimates from

electrofishing removal sampling

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Abstract

Estimates of fish abundance from electrofishing surveys depend on accurate estimation

of capture probability. We examine in this paper how estimates of capture probability

and abundance of Atlantic salmon from multi-pass removal sampling can be improved

by comparing the results of an experimental program of closed electrofishing sites

within selected rivers in west-central Norway, and those obtained from open

22   electrofishing sites established for monitoring long-term juvenile Atlantic salmon

23   population abundance within the Burrishoole catchment, western Ireland. We first

24   establish that the Carle & Strub method provides a more robust estimate of population

25   abundance than the Zippin and Seber methods. We then show how prior information on

26   capture probability may be used to improve the accuracy of the abundance estimate in

27   open sites. We also show that the use of prior information with single-pass

28   electrofishing may improve the accuracy of the abundance estimate so that it is

29   comparable with that of multi-pass electrofishing in terms of stock prediction while

30   requiring less sampling effort.

31

32   *Keywords:* optimizing electrofishing; Zippin, Seber and Carle & Strub estimation

33   methods; calibrated single-pass, capture probability

34

35   **1   Introduction**

36

37   Effective management of salmon populations, especially those that are depleted,

38   requires information on the spatial and temporal distributions of juvenile abundance.

39   The principal method for obtaining this information is through the use of electrofishing

40   surveys (Nielsen, 1998) involving single or multiple fishing passes over the same stretch

41   of river. These surveys involve a trade-off between the information required (in terms of

42   river area coverage and accuracy of the estimate) and the expense involved in gaining

43   that information (inversely related to the number of samples and passes). When

44   estimating population characteristics such as population abundance from electrofishing

45   samples, it may be that a large number of relatively less accurate abundance estimates

46   are more useful than a small number of more accurate abundance estimates.

47   Two main types of statistical models are used to obtain estimates of fish abundance

48   using repeated sampling: (i) closed population models using mark-and-recapture (see

49   White, 2008) and (ii) multi-pass removal. Mark-and-recapture methods involve marking

50   a sample of fish, releasing them and resampling at a later date, from which the ratio of

51   unmarked to marked fish is used to estimate capture probability and abundance. Multi-

52   pass removal methods use repeated sampling over a short period of time, with samples

53   from each pass retained, and the decline in the number captured between successive

54   passes is used to estimate capture probability and abundance. Mark-and-recapture

55   methods are generally considered to have higher accuracy, but may be problematic

56   under certain circumstances. For example, marking may affect mortality rates and

57   recapture probability. In such circumstances, multi-pass removal methods may be

58   favoured. Additionally, an advantage of multi-pass removal is that it does not require

59   returning to the same site on separate dates, or marking, so the cost may be less. Given

60   this, multi-pass removal methods are commonly used in monitoring of population

61   abundance (Niemelä et al., 2000; LeBlanc and Chaput, 2003; Rivot et al., 2008).

62

63   The most prevalent methods for estimating population size using multi-pass removal

64   methods are those proposed by Zippin (Zippin, 1958), Seber (Seber and Le Cren, 1967),

65   and Carle & Strub (Carle and Strub, 1978) (Table 1). All methods estimate the

66   probability of capture, and use this to estimate abundance from the numbers captured.

67   The methods of Zippin and Seber are maximum-likelihood methods. That of Carle &

68   Strub is a weighted maximum likelihood method, which weights the likelihood function

69   by a prior beta distribution with parameters α and β (in the absence of prior

70   information, $\alpha = \beta = 1$), and uses an iterative method to derive the estimate. That is,

71   there may be some prior information on capture probability – for example from a

72 previously conducted electrofishing survey – that may be used to weight future

73 estimates. This background information may be particularly useful in informing the

74 estimate in sites where the data are not particularly appropriate for obtaining an

75 accurate estimate; for instance, sites where catch sequences suggest capture probability

76 varying according to pass.

77

78 Multi-pass removal methods rely on several assumptions: (i) that the population

79 remains closed during sampling; (ii) that capture probability (defined as the proportion

80 of the site abundance that is captured in the pass) does not vary in each pass

81 (Baumgartner, 2006); and (iii) that capture probability does not vary according to

82 individual. In reality, these assumptions are unlikely to be met. Migration into the site or

83 more likely out of the site can potentially occur between passes unless block nets are

84 used, possibly as a result of behavioural avoidance (Peterson et al., 2005). Capture

85 probability typically declines with each successive pass (Peterson et al., 2004). Capture

86 probability may vary according to individual; for example, the capture probability of

87 larger individuals is greater than that of small ones (Anderson, 1995; Dauwalter and

88 Fisher, 2007; Peterson et al., 2004). A decline in capture probability with successive

89 passes may occur if more catchable individuals are captured first (Seber, 1982). Multi-

90 pass removal methods assume an exponential decline in abundance with successive

91 passes: an accurate estimate of population size based on removal methods is not

92 possible if capture probability increases and/or there is immigration such that numbers

93 captured in the final pass are equal or greater than those in the first pass. Additionally,

94 multi-pass removal methods do not provide robust estimates of abundance when

95 numbers captured are low: Riley and Fausch (1992) set a threshold of there being at

96 least 30 individuals before estimating abundance using multi-pass removal. An

97   alternative to the multi-pass approach is the less resource intensive but arguably less

98   accurate method of single-pass.

99

100   There is a diversity of opinion on the relative merits of single-pass and multi-pass

101   methods. Single-pass has often been found acceptable for determining relative or

102   absolute abundance by some researchers (Bateman et al., 2005; Hedger et al., 2005;

103   Jones and Stockwell, 1995; Kruse et al., 1998) but other researchers have found less

104   consistent results (Odenkirk and Smith, 2005). To compensate for the fact that single-

105   pass may underestimate abundance, researchers have attempted to adjust single-pass

106   estimates by: (i) finding a relationship between single-pass and multi-pass estimates

107   (Lobon-Cervia and Utilla, 1993); or (ii) using a capture probability estimated from a

108   previous multi-pass estimate (Mitro et al., 2003).

109

110   Estimated capture probability in electrofishing removal sampling will often be very

111   uncertain and biased, especially when density is low (Korman et al., 2009). Errors in the

112   estimate of capture probability will cause errors in the estimate of population

113   abundance. Therefore, there may be much to gain in terms of the accuracy of the

114   abundance estimate by applying prior information on capture probability when this is

115   available. Priors may be specific to river, catchment, habitat type, age group, or species.

116

117   In this study we investigate how the use of prior information on capture probability

118   might be used to improve abundance estimates. Specifically, we investigate (i) which is

119   the best removal method (Zippin, Seber or Carle & Strub) in the absence of prior

120   information, (ii) how the use of a prior distribution will affect Carle & Strub estimates,

121   (iii) how the use of a prior distribution will affect single-pass estimates, and finally (iv)

122   how to establish prior information.

123

124   **2   Method**

125

126   *2.1   Field data*

127

128   Two electrofishing approaches were used: (i) closed-site electrofishing, conducted in

129   five rivers in west-central Norway in one year (Fig 1a), and (ii) open-site electrofishing,

130   conducted in 15 river tributaries of the Burrishoole catchment, western Ireland over a

131   period of 20 years (Fig. 1b). Closed sites allowed estimation of total site abundance in

132   which it was possible to be sure that the assumption of no migration was not violated,

133   enabling quantification of changes in capture probability according to electrofishing

134   pass. This allowed exploration of how the removal methods worked under near-optimal

135   conditions. Open sites were typical of those that are used in long-term monitoring

136   programs, enabling us to ascertain how suitable the methods would be under

137   circumstances when the assumption of no migration could potentially be violated.

138

139   **Closed sites.** Five rivers in west-central Norway (Ingdalselva, Vinddøla, Toåa, Homla,

140   Levangerelva) were chosen, and a site in each river was selected (two sites in Homla) so

141   that there would be minimal variation in habitat characteristics. All sites had

142   gravel/cobble substrates: the Ingdalselva site had a principal substrate class of coarse

143   gravel to small cobbles (20 – 100 mm), and the other four rivers had a principal

144   substrate class of large cobbles (100 – 250 mm). Mean width of the sites was 17 m (min.

145   = 10 m, max. = 22). Sites were electro-fished for Atlantic salmon (*Salmo salar* L.) over the

146   period from 2-13 September 2010 (Table 2) (see Sandlund et al., 2011). Additionally, the

147   Homla was again electro-fished on 4-5 November 2010. Sites were closed with block

148   nets, and passes were conducted until no more fish were captured (by 10-13 passes),

149   providing an estimate of fish abundance within each site. Captured individuals were

150   classified into 0+ and >0+ age groups according to length. Individuals classified as >0+

151   included all 1+, 2+ and 3+ individuals.

152

153   **Open sites.** Field data for an Atlantic salmon population were collected in the

154   Burrishoole system, W Ireland (53° 59′N, 09° 37′) (Table 3). The Burrishoole system

155   comprises multiple rivers (>15) which discharge into a freshwater lake (Lough Feeagh),

156   which in turn discharges into a brackish lake (Lough Furnace) through two small rivers,

157   and ultimately flows into Clew Bay on the Atlantic west coast of Ireland. Population

158   dynamics of Atlantic salmon within the system have been monitored since the 1970s as

159   fish traps between Loughs Feeagh and Furnace allow a total census of returning adults

160   and emigrating smolts from the catchment. In total, three-pass electrofishing was

161   conducted in 404 sites in 15 river tributaries of the Burrishoole catchment from 1991 to

162   2010. The number of sites sampled varied inter-annually (Table 3). Individuals were

163   classified into 0+ or 1+ age groups according to length frequencies (NB: the vast

164   majority (>95%) of salmon individuals smoltify before two years of age in this

165   catchment). Site width and site gradient were measured for establishing relationships

166   between capture probability and habitat. Mean site width was 3.41 m (min. = 0.8, max. =

167   8.0 m). Mean site gradient in terms of change in elevation over longitudinal distance was

168   0.03 (min. = 0.01, max. = 0.12).

169

170   *2.2   Determining the optimal estimation method using closed sites (Norwegian*

171   *study area)*

172

173   Firstly, the relative merits of the estimation methods in the absence of prior information

174   on capture probability were determined using the closed sites. The Zippin, Seber and

175   Carle & Strub (with a non-informative prior) methods were used to derive estimated

176   capture probability ($\hat{P}$) and estimated abundance ($\hat{N}$) in each site and for each age group

177   (0+ and >0+) from the captures in the first three passes. The *removal (FSA)* function

178   written by Derek H. Ogle (www.rforge.net/FSA/index.html) in R (R Development Core

179   Team, 2009) was used. Observed capture probability (P_i) was then calculated for each of

180   the first three passes for each age class to aid evaluation of estimated capture

181   probability (Table 1). Here, the total number of individuals capture in all 10-13 passes

182   for the age class in question was used as a conservative estimate of total abundance.

183   Secondly, the effect of using an informative prior on the error of abundance estimates

184   (i.e. the systematic difference between this estimate of abundance and observed

185   abundance) was determined for the Carle & Strub method. The informative prior was

186   drawn from a beta distribution, with parameters α and β parameterized using the

187   moments approximation method (Gelman et al., 2004, p.582). Two types of informative

188   priors were used. The first had both age classes pooled. The second was calculated

189   separately according to age class. The use of both types of priors allowed investigation

190   of whether priors should depend on age class.

191

192   The performance of each method was determined by (i) mean standard error of the

193   abundance estimate; (ii) the percentage of occasions when an abundance estimate was

194   not possible; and (iii) the Pearson correlation between estimated and observed

195 abundance (which provided an indication of the spread in the relationship between the

196 abundance estimate and total capture).

197

198 *2.3 Determination of the optimal estimation method for use in a field survey of*

199 *open sites (Burrishoole study area)*

200

201 **Estimation methods in the absence of prior information.** Capture probabilities and

202 abundances were estimated separately for ages 0+ and 1+ using the three removal

203 methods (Zippin, Seber and Carle & Strub with a non-informative prior). The

204 relationship between estimated capture probability and total capture was determined

205 using a power function.

206

207 **Establishing prior information.** The initial approach for establishing prior information

208 on capture probability was to examine the effect of habitat (site width, site gradient),

209 day of year of fishing and total capture on the estimated capture probability of fish of

210 ages 0+ and 1+ separately using generalized additive models (GAMs) (*gam(mcgv)*

211 function in R). GAMs were used because we had no *a priori* information on the functional

212 form of the relationship. Variables were correlated, but variance inflation factors

213 (*corvif(AED)* function in R)) were less than two, suggesting that they could all be used as

214 predictors in the same model (see Zuur et al., 2009). A model was fitted to all variables

215 together, and variables were removed in descending order of significance if their

216 removal caused a decrease in AIC. The only consistently significant variable that affected

217 capture probability, with the 95% confidence intervals of the smoothing curves mainly

218 not encompassing a zero effect on capture probability, was total capture. Therefore, it

219 was possible to use total captures from years 1991-2010 at one site alone as prior

220   information for applying the methods to the entire catchment (years 1991-2100, 404

221   sites in total). This single calibration site was chosen as that which had greatest

222   variation in first-pass captures from the rivers which had been sampled for the largest

223   number of years. For determining the informative prior for application to all sites within

224   the catchment, capture probabilities of ages 0+ and 1+ were first estimated in the

225   calibration site for each year using the Carle & Strub method with a non-informative

226   prior.

227

228   **Estimation methods using prior information.** Three methods for including prior

229   information were used to estimate abundances of ages 0+ and 1+ in all sites: (i) Carle &

230   Strub with an informative prior; (ii) calibrated single-pass with constant capture

231   probability; and (iii) calibrated single-pass with variable capture probability (depending

232   on total capture). Alpha and beta parameters for the Carle & Strub method with an

233   informative prior were determined from capture probabilities estimated in the

234   calibration site (Table 1). For the calibrated single-pass with constant capture

235   probability, the mean of the Carle & Strub estimated capture probabilities ($\hat{P}$) for all

236   years in the calibration site was used as the capture probability, and the numbers

237   captured on the first pass in all sites in the catchment were divided by this capture

238   probability (Table 1). For the calibrated-single pass with variable capture probability, a

239   power function relationship between the Carle & Strub estimated capture probability

240   ($\hat{P}$) and the numbers captured in the first pass in each year and in each year in the

241   calibration site was derived, and this relationship was used to predict capture

242   probability at all sites within the catchment (Table 1). If there is a zero capture in the

243   first pass, the calibrated single pass with constant capture probability will return an

244 abundance estimate of zero, whereas the calibrated single pass with variable capture

245 probability will not be able to return an abundance estimate (due to division by zero).

246

247 **Determining the relative merit of the estimation methods.** It was not possible to

248 calculate the error in the abundance estimate relative to the true abundance because we

249 had no information on the actual abundance within the sites. Therefore, the relative

250 merit of the estimation methods in the open sites was determined using the following

251 metrics: (i) mean standard error of the abundance estimate as calculated by the removal

252 method (see Table 1); (ii) the percentage of occasions when an abundance estimate was

253 not possible; (iii) the percentage of sites with outlying abundance estimates ($\widehat{N}$ > 1.5 ×

254 the abundance predicted by a power function model fitted to all the data); and (iv) the

255 Pearson correlation between the abundance estimate and the total capture.

256

257 **Use in stock prediction.** The relationship between mean estimated 0+ annual

258 abundance (the mean of all sites for each year) and egg deposition in the preceding year

259 was then analyzed using linear regression. The total number of eggs delivered into the

260 catchment (McGinnity et al., 2009) was used as a proxy for the annual 0+ population

261 abundance within the catchment. A strong relationship exists between spawner

262 abundance and smolt numbers within the Burrishoole catchment, so it is reasonable to

263 assume that total annual egg abundance is a satisfactory proxy for annual 0+ population

264 abundance (Baglinière et al., 2005; Crozier and Kennedy, 1995).

265

266 ## 3   Results

267

268   *3.1   Optimal estimation method using closed sites*

269

270   For the closed sites in Norway, 16.7% of cases (both for 0+) did not have a sequential

271   decline in numbers captured with successive pass for the first three passes. Observed

272   capture probability did not remain constant with successive passes (Fig. 2), and was

273   higher on the second pass than the first pass in 33.3% of cases. Thus the assumption of

274   capture probability remaining constant with successive passes inherent in the

275   estimation methods was not met. Observed capture probability often increased

276   subsequent to the third pass: 0+ age group $\bar{P}$ = 0.21 (passes 1 to 3), $\bar{P}$ = 0.28 (passes 4 to

277   9); >0+ age group $\bar{P}$ = 0.35 (passes 1 to 3), $\bar{P}$ = 0.39 (passes 4 to 9). Estimated capture

278   probabilities from all estimation methods for both size classes were generally greater

279   than observed capture probabilities. Mean observed capture probability of the age >0+

280   was greater than that for the age 0+ in all sites; this was true of estimated capture

281   probability in five of the six sites. Estimated mean capture probabilities were 0.35 (0+)

282   and 0.54 (>0+) for the Zippin method, 0.39 (0+) & 0.53 (>0+) for the Seber method, and

283   0.40 (0+) and 0.52 (>0+) for the Carle & Strub method. A slight trend of declining

284   capture probability with increasing abundance existed, but this trend was not significant

285   (Fig 3a).

286

287   Estimated abundance was almost always less than observed abundance (Fig. 3b), to such

288   an extent that the 95% confidence interval of the estimate only encompassed observed

289   abundance on 41.7%, 33.3% and 25% of occasions for the Zippin, Seber and Carle &

290   Strub (with non-informative prior) methods, respectively. The Carle and Strub method

291   with a non-informative prior had a smaller mean standard error of the abundance

292   estimate than the Zippin or Seber methods (Table 4). The Zippin method greatly

293   overestimated abundance in one occasion (in Vinddøla) when there were more fish

294   captured on the second pass than during the first or third pass, resulting in a high mean

295   error to the abundance estimate and a relatively low correlation between observed and

296   estimated abundance. The Seber method was not able to produce an estimate for age 0+

297   in this site. Therefore, it is concluded that, in the absence of prior information, the Carle

298   & Strub method is best. Use of an informative prior did not improve the estimate,

299   increasing the mean standard error and reducing correlation between estimated and

300   observed abundance. Additionally, using an informative prior with age groups separated

301   produced greater error than when age groups were pooled.

302

303   *3.2   Optimal estimation method for use in a field survey of open sites*

304

305   No capture occurred in approximately a fifth of the 404 open sites electrofished in the

306   Burrishoole catchment (0+, 20.0%; 1+, 22.8% of sites), A sequential decline in the

307   number of captures as a function of pass did not occur in 33.1% of the remaining sites

308   for fish of age 0+ and 37.2% of the remaining sites for fish of age 1+.

309

310   Estimated capture probability declined with increasing total capture for all estimation

311   methods with no prior information, and the estimated capture probability for age 1+

312   was greater than that of age 0+ for a given total capture (Fig 4a). Mean estimated

313   capture probabilities were 0.47 (0+) and 0.63 (1+) for the Zippin method, 0.45 (0+) and

314   0.59 (1+) for the Seber method, and 0.49 (0+) and 0.65 (1+) for the Carle & Strub

315   method. The Carle & Strub method was the optimal method in terms of having minimum

316   mean standard error of the abundance estimate, greatest percentage of sites where it

317   was possible to estimate abundance, smallest percentage of outliers, and greatest

318   correlation between abundance estimate and total capture (Table 5). Estimated

319   abundances for the Zipping and Seber methods were particularly high when there was a

320   small decline in numbers captured as a function of fish pass: for example, the site where

321   46, 44 and 42 age 0+ individuals were captured in the first, second and third pass

322   respectively resulted in an estimated abundance of greater than 700 using the Zippin

323   method and greater than 1000 for the Seber method, when less than 150 individuals

324   were captured (Fig. 4b). Overall, 95% confidence intervals of the estimate abundances

325   enclosed the total capture more often for the Carle & Strub method (84.8% of 0+

326   estimates and 93.3 % of 1+ estimates) and the for Zippin method (82.3% of 0+ estimates

327   and 92.3 % of 1+ estimates) than the Seber method (75.9% of 0+ estimates and 86.5% of

328   1+ estimates).

329

330   The strongest predictor of estimate capture probability for fish of both age 0+ and 1+

331   was total capture of the respective age class (Fig. 5). Significant relationships were also

332   found for site gradient and day of year for fish of age 0+, and site width for age 1+, but

333   relationships were weaker. Additionally, the standard error of the smoothing curves for

334   these variables suggested a poor fit, encompassing a zero effect on the capture

335   probability for a wide range of predictor values. Therefore, it was considered acceptable

336   to just use total capture alone for establishing prior information.

337

338   The relationship between estimated abundance and total catch was strongly dependent

339   on whether and how prior information was used (Fig. 6). Use of the Carle & Strub

340   method with an informative prior removed all outliers in the relationship. The

341   calibrated single-pass method with constant or variable capture probabilities produced

342   more outliers and less linear relationships than the Carle & Strub method with an

343   informative prior.

344

345   All methods using prior information produced stronger relationships between the

346   number of eggs deposited in the preceding year and mean annual estimated 0+

347   abundance than the Carle & Strub method with a non-informative prior (Fig. 7).

348

349   **4   Discussion**

350

351   *4.1   Observed capture probability and abundance in the closed parcels*

352

353   Observed capture probability varied among passes, and declined with successive pass

354   during the first three passes in only 66.7% of cases in the closed sites. This decline in

355   observed capture probability is consistent with capture probability varying according to

356   individual (the more catchable individuals being captured first) and/or a behavioural

357   response of the site population (individuals becoming more wary of capture in response

358   to capture attempts in previous passes). Thus, at least one of the key assumptions of the

359   estimation methods was violated, even under ideal circumstances of no migration.

360

361   It is possible that some individuals were not captured (even though 10 – 13 passes were

362   used), so observed abundance will have been an underestimate of true abundance.

363   However, observed capture probability often increased at passes subsequent to the

364   third pass, and it is inferred that the difference between true abundance and total

365   capture will have been small. For example, the mean probability of an individual

366   remaining uncaptured by the end of pass nine (across the sites) was 5.7% (0+) and 1.9%

367   (>0+).

368

369   *4.2   Estimated capture probability, site type and age class*

370

371   Estimated capture probabilities in the closed sites were less than those of the open sites.

372   In contrast, Niemelä et al. (2000) found significantly higher capture probabilities of

373   Atlantic salmon when using closed sites ($\hat{P}$ = 0.52 for 0+, $\hat{P}$ = 0.67 for >0+) than open

374   sites ($\hat{P}$ = 0.42 for 0+, $\hat{P}$ = 0.52 for 1+). The divergence between our results and those of

375   Niemelä et al. may be attributable to the fact that the closed sites were in a different

376   catchment to the open sites, and thus both population and habitat characteristics will

377   have differed between the study areas. The wide range in capture probabilities found

378   within this study was consistent with the wide ranges found by other authors for

379   salmonids. LeBlanc and Chaput (2003), for example, found mean capture probabilities of

380   Atlantic salmon ranging from 0.26 to 0.80 (0+) and 0.34 to 0.71 (1+). Kruse et al. (1998)

381   found capture probabilities of cutthroat trout (*Oncorhynchus clarki*), rainbow trout (*O.*

382   *mykiss*), brown trout (*Salmo trutta*), and brook trout (*Salvelinuus fontinalis*) ranging

383   from 0.35 to 0.99. Korman et al. 2009 reported a similar large range in capture

384   probability of rainbow trout with 80% of estimates lying between 0.27 and 0.75

385   (Korman et al. 2009). Differences in capture probability between these studies and ours

386   are probably related to differences in electrofishing method, habitat, species, body size,

387   age, and abundance.

388

389   Estimated capture probability was greater for age >0+ than age 0+ in the closed sites,

390   and did not significantly decline with increasing abundance. Estimated capture

391   probability was greater for age 1+ than age 0+ in the open sites, and declined with

392   increasing total capture for both age groups. The greater estimated capture probability

393   of the older (and larger) Atlantic salmon age groups is consistent with the literature,

394   which has shown a greater capture probability for larger individuals (Anderson, 1995;

395   Dauwalter and Fisher, 2007; Niemala et al. 2000; Peterson et al., 2004). Possible causes

396   of the higher capture probability for the older age groups are: (i) fewer available spaces

397   for the larger individuals to hide; and (ii) greater ease of the field workers at spotting

398   larger individuals. A decline in estimated capture probability with increasing total

399   capture has been less frequently reported in the literature, although this has been

400   observed for Atlantic salmon juveniles by Riley et al. (1993) and for age >0+ Atlantic

401   salmon parr but not for age 0+ fry by Niemelä et al. (2000). Behavioural avoidance may

402   be greater in sites with greater abundance because electrofishing may take longer in

403   these sites, with this increased disturbance elevating the amount of emigration; that is,

404   the estimate of capture probability is not solely dependent on depletion between passes

405   but also on behavioural avoidance. The fact that there was not a significant decline in

406   estimated capture probability with increasing abundance in the closed sites, where

407   emigration was not possible, would support this hypothesis.

408

409   *4.3   Choosing the optimal estimation method – Zippin, Seber and Carle & Strub*

410

411   There was relatively little difference between the relative merits of the estimation

412   methods for the closed sites in the absence of prior information on capture probability,

413   although the Carle & Strub method performed best. All estimation methods – Zippin,

414   Seber and Carle & Strub with a non-informative prior – generally overestimated capture

415   probability in the closed sites, and consequently underestimated abundance. In one case,

416   however, the Zippin method greatly overestimated abundance and the Seber method

417   was not able to provide an estimate. The Carle & Strub method was clearly superior in

418   the open sites in the absence of prior information. Differences between the closed and

419   open sites in terms of the relative merit of the Carle & Strub method suggest that the

420   Carle & Strub method was most effective when the assumption of non-emigration was

421   violated. This method has been noted for its robustness in comparison to the Zippin

422   method (Gerdeaux, 1987) and the findings of our study support this. The Carle & Strub

423   method should therefore be used in the absence of prior information on capture

424   probability. Use of prior information did not improve the estimates of the Carle & Strub

425   method in the closed sites, and in fact led to a small increase in error. The Carle & Strub

426   method with no prior information may have been achieving an optimal estimate of

427   capture probability in each site under ideal conditions of no migration, and influencing

428   this capture probability by the inclusion of prior information from other sites, may have

429   had a detrimental effect.

430

431   *4.4   Using prior information in a field survey of open sites*

432

433   Prior information on capture probability in this study was obtained using a single

434   calibration site, with this prior being established according to age class and total

435   capture. Only one species was used in this study, but if a multi-species study is in place,

436   priors should be specific to each species. It may be advisable to use multiple calibration

437   sites if there is strong evidence that capture probability varies according to habitat. No

438   relationship between capture probability and habitat was found in this study. It may be

439   that the habitat metrics we used did not have a large effect on capture probability – site

440   gradient and site width may be positively correlated with current speed which could

441   affect capture probability, but there was a large number of other habitat characteristics

442   (for example, substrate size and depth) which were not measured and which may have

443   obscured any relationship. The literature has presented a mixed picture. Some authors

444   have identified no relationship (e.g. Saunders et al., 2011), but habitat effects have been

445   found by other researchers (Dauwalter and Fisher, 2007; Hense et al., 2010; Peterson et

446   al., 2004). Differentiating between the effects of habitat and population abundance may

447   be difficult given that abundance varies according to habitat – if a strong relationship

448   with abundance can be found, it may not be necessary to survey habitat characteristics

449   to obtain information on how capture probability varies according to habitat.

450

451   Prior capture probability may be adjusted according to how efficiently the fishing is

452   conducted. It may be useful to identify the capture probabilities of the separate teams

453   doing the electrofishing so that they could be categorized as "inexperienced",

454   "experienced", or "very experienced" and the prior corrected accordingly. Alternatively,

455   the prior could be corrected according to the difficulty of fishing conditions. Outliers in

456   this study were often associated with difficult fishing conditions; for example, when

457   biting midges (Diptera: Ceratapogonidae) hampered efforts.

458

459   The estimation method to be used should depend on the type of information required.

460   The Carle & Strub method with an informative prior produced a strong relationship

461   between estimated abundance and total capture, and it is inferred that the individual

462   estimates would have been more reliable than those of the Carle & Strub with a non-

463   informative prior or calibrated single-pass method. The Carle & Strub method with an

464   informative prior might be recommended if sampling is conducted for the purpose of

465   showing habitat relationships, where accurate individual estimates are required. This

466   method might also be recommended if the intent is to obtain an accurate estimate of the

467   size distribution of the population: proportionally more of the larger fish may be

468   captured in the first pass if there are several size groups, so single-pass may lead to an

469   underestimation of the relative abundance of smaller individuals. Calibrated single-pass

470   may be a better option if sampling is being conducted to provide an overall view of

471   abundance within the system, which might be required in a long-term monitoring

472   program. The relationship between mean 0+ abundance estimated from calibrated

473   single-pass and the total number of eggs in this study was as strong as that estimated by

474   the Carle & Strub method with an informative prior, suggesting that single-pass

475   electrofishing may provide an acceptable estimate of population abundance for less

476   effort. Additionally, electrofishing has harmful effects on fish (Snyder, 2003) so another

477   advantage of single-pass is that it only applies this effect once, rather than multiple

478   times. Finally, multi-pass estimation methods using electrofishing data are less reliable

479   at low abundances. A large proportion of total site captures in the Burrishoole system

480   were less than 30 ($\sim$45 % for 0+ and $\sim$80% for 1+), so it is possible that a multi-pass

481   approach is not valid for a system with a depleted, or low, population, and that a

482   calibrated single-pass approach might be more useful.

483

484   **5   Conclusion**

485

486   The results from this study suggest that in the absence of prior information on capture

487   probability, the Carle & Strub method is the best of the removal methods. Use of prior

488   information on capture probability (preferably established separately according to age

489   class) improves abundance estimates in open sites when using the Carle & Strub

490   method, and this may be the optimal method if the objective is an accurate abundance

491 estimate within the site. The relationships between the calibrated single-pass estimates

492 (both that based on a constant capture probability and that based on a variable capture

493 probability) and annual total egg abundance had similar strengths to that between the

494 Carle & Strub method with an informative prior and annual total egg abundance, and

495 given that calibrated single-pass requires less sampling effort, this may be the optimal

496 method for a long-term monitoring program for juvenile Atlantic salmon.

497

498 **Acknowledgements**

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507

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631 **Tables**
632
633 Table 1. Methods for estimating abundance using removal methods (Zippin, Seber and Carle & Strub)
634 and calibrated single pass methods.

Variables

i = pass number

k = number of passes (3)

C_i = number captured in pass i

C_p = number captured in preceding pass to pass i

T = total number of individuals captures in all passes

P_i = observed capture probability in pass i:

$$P_i = \frac{C_i}{T - C_p}$$

$\widehat{N}$ = estimated abundance

$\widehat{P}$ = estimated capture probability

$SE_{\widehat{N}}$ = standard error of estimated abundance

$SE_{\widehat{P}}$ = standard error of estimated capture probability

X = an intermediate statistic:

$$X = \sum_{i}^{k} (k - i)C_i$$

Zippin method

The Zippin method, modified by Carle and Strub (1978), uses an iterative process for obtaining estimated abundance ($\widehat{N}$) by substituting values for N in the following equation, with the smallest $N \geq T$ that solves the equation being the estimate:

$$(N + 0.5)(kN - X - T)^k - (N - T + 0.5)(kN - X)^k \geq 0$$

Estimated capture probability is calculated as follows:

$$\widehat{P} = \frac{T}{kN - X}$$

The standard error of estimated abundance is calculated as follows:

$$SE_{\widehat{N}} = \sqrt{\frac{\widehat{N}(1 - q^k)q^k}{(1 - q^k)^2 - \left(\widehat{P}k\right)^2 q^{k-1}}}$$

where $q = 1 - \widehat{P}$

The standard error of estimated capture probability is calculated as follows:

$$SE_{\widehat{P}} = \frac{\left(q\widehat{P}\right)^2 \left(1 - q^k\right)}{\widehat{N}\left(q(1 - q^k)^2 - \left(\widehat{P}k\right)^2 q^k\right)}$$

Seber method

$$\widehat{N} = \frac{6X^2 - 3XT - T^2 + T(T^2 + 6XT - 3X^2)^{0.5}}{18(X - T)}$$

$$\widehat{P} = \frac{3X - T - (T^2 + 6XT - 3X^2)^{0.5}}{2X}$$

The standard errors of estimated abundance and capture probability are calculated in the same way as for the Zippin method.

Carle & Strub method

The Carle & Strub method uses an iterative process for obtaining estimated abundance ($\widehat{N}$) by substituting values of N in the following equation, with the smallest $N \geq T$ that solves the equation being the estimate:

$$\left(\frac{N+1}{N-T+1}\right)\prod_{i=1}^{k}\left(\frac{kN-X-T+\beta+k-i}{kN-X+\alpha+\beta+k-i}\right) \leq 1$$

where α and β are parameters of a beta distribution, based on observed capture probability (P_i) in each pass:

$$\alpha = P_1\left(\frac{P_1(1-P_1)}{var(\{P_1,P_2,P_3\})}-1\right); \quad \beta = (1-P_1)\left(\frac{P_1(1-P_1)}{var(\{P_1,P_2,P_3\})}-1\right)$$

where $var(\{P_1,P_2,P_3\})$ is the variance of the numbers captured in the three passes.

The standard error of estimated capture probability is calculated in the same way as for the Zippin method. The standard error of estimated abundance is calculated as follows:

$$SE_{\widehat{N}} = \sqrt{\frac{\widehat{N}(\widehat{N}-T)T}{T^2 - \widehat{N}(\widehat{N}-T)\left(\left(k\widehat{P}\right)^2/q\right)}}$$

The standard error of the estimated capture probability is obtained in the same way as for the Zippin method.

Calibrated single pass

$$\widehat{N} = C_1/\widehat{P}_{cal}$$

where $\widehat{P}_{cal}$ is the estimated capture probability in the calibration station.

For the calibrated single pass with constant capture probability, $\widehat{P}_{cal}$ is the mean capture probability across all years estimated using the Carle & Strub method in the calibration station.

For the calibrated single pass with variable capture probability:

$\widehat{P}_{cal} = aC_1{}^b$

where C_1 is the number of individuals captured in the first pass, and a and b are parameters determined by a power function fitted between capture probability estimated using the Carle & Strub method (response variable) and the number of individuals captured in the first pass (predictor variable) in the calibration station:

$\widehat{P}_{cal} = aC_{1,cal}{}^b$

635
636

637 Table 2. Closed sites electrofished in 2010 (Norwegian study area). One site was
638 electrofished per river, except in Homla where two sites were electrofished.

River	Month of fishing	Number of passes	Atlantic salmon abundance	
			0+	>0+
Homla	September	12	294	158
Homla	November	10	151	160
Ingdalselva	September	10	151	119
Levangerelva	September	13	154	210
Toåa	September	11	25	228
Vinddøla	September	10	35	248

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641   Table 3. Open sites electrofished from 1991-2010 (Burrishoole study area).

River	Total number of sites sampled	Number of sites in river	Number of years of sampling (initial year – final year)	Mean annual capture by 3-passes	
				0+	1+
Altahoney	17	2	12 (1995-2010)	5.5	3.7
Black	3	1	3 (2000-2007)	97.0	12.7
Cottage	7	1	7 (1997-2006)	43.9	14.3
Fiddaunahoilean	32	4	11 (1991-2010)	10.2	0.8
Fiddaunveela	54	3	18 (1991-2010)	32.3	6.1
Glenamong	27	4	11 (1997-2010)	15.7	25.1
Goulaun	87	6	16 (1991-2010)	78.7	22.1
Lena	2	1	2 (1992-2000)	13.5	0
Lodge	18	7	5 (1991-2003)	74.8	33.6
Main channel	10	1	10 (2001-2010)	76.2	43.9
Maumaratta	13	1	13 (1991-2010)	29.1	20.7
Srahrevagh	91	9	18 (1991-2010)	58.2	14.2
Stream A	17	1	(1991-2010)	5.9	0.9
Stream B	8	1	(1991-2010)	0.0	0.0
Stream C	18	1	(1991-2010)	0.3	0.1

642
643

644 Table 4. Performance of the estimation methods for estimating population abundance in the
645 closed sites (Norwegian study area). Metrics are (i) mean standard error in the estimate of
646 abundance; (ii) inability to provide an estimate of abundance; and (iii) correlation between
647 observed abundance and the estimate of the abundance. For each method, 12 estimates are
648 derived (six sites and two age classes).

Method	Mean ($SE_{\widehat{N}}$)	Inability to provide an estimate (%)	r ($N, \widehat{N}$)
Zippin	137.85	0	0.67
Seber	18.63	8.3	0.98
Carle & Strub (non-informative prior)	15.22	0	0.97
Carle & Strub (informative prior - age groups pooled)	16.38	0	0.96
Carle & Strub (informative prior - age group separated)	24.77	0	0.96

649
650

651 Table 5. Performance of the estimation methods for estimating population abundance in the
652 open sites (Burrishoole study area). Metrics are (i) mean standard error in the estimate of
653 abundance; (ii) inability to provide an estimate of abundance; (iii) percentage of outliers; and
654 (iv) correlation between observed abundance and the estimate of the abundance. Metrics
655 have been derived from sites where fish were captured – sites with zero abundance have
656 been excluded. Mean error in the estimate of abundance is calculated directly from the
657 removal equations, so no comparable error estimates are available for the calibrated single
658 pass methods.

| Stage	Method	Mean $(SE_{\widehat{N}})$	Inability to provide an estimate (%)	% of outliers	$r\,(C_{123}, \widehat{N})$
0+	Zippin	124.63	2.48	3.5	0.50
	Seber	44.42	9.29	3.4	0.75
	Carle & Strub (non-informative prior)	15.24	0	3.4	0.94
	Carle & Strub (informative prior)	12.92	0	0	1.00
	Calibrated single pass (constant capture probability)	NA	0	3.4	0.98
	Calibrated single pass (variable capture probability)	NA	0	6.5	0.98
1+	Zippin	3.46	0.96	3.2	0.96
	Seber	7.45	6.73	3.8	0.86
	Carle & Strub (non-informative prior)	2.43	0	1.3	0.98
	Carle & Strub (informative prior)	2.27	0	0	1.00
	Calibrated single pass (constant capture probability)	NA	0	7.1	0.97
	Calibrated single pass (variable capture probability)	NA	2.24	6.9	0.97

659
660

661 **Figures**

(a)
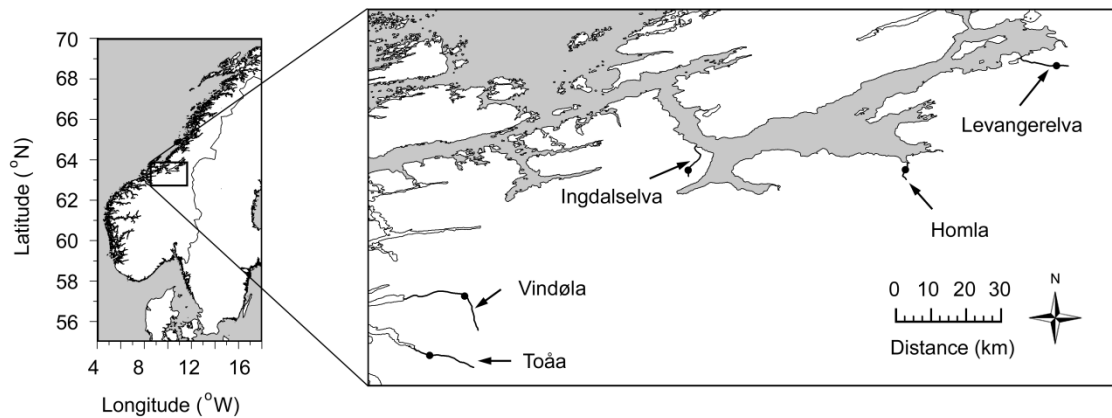
(b)
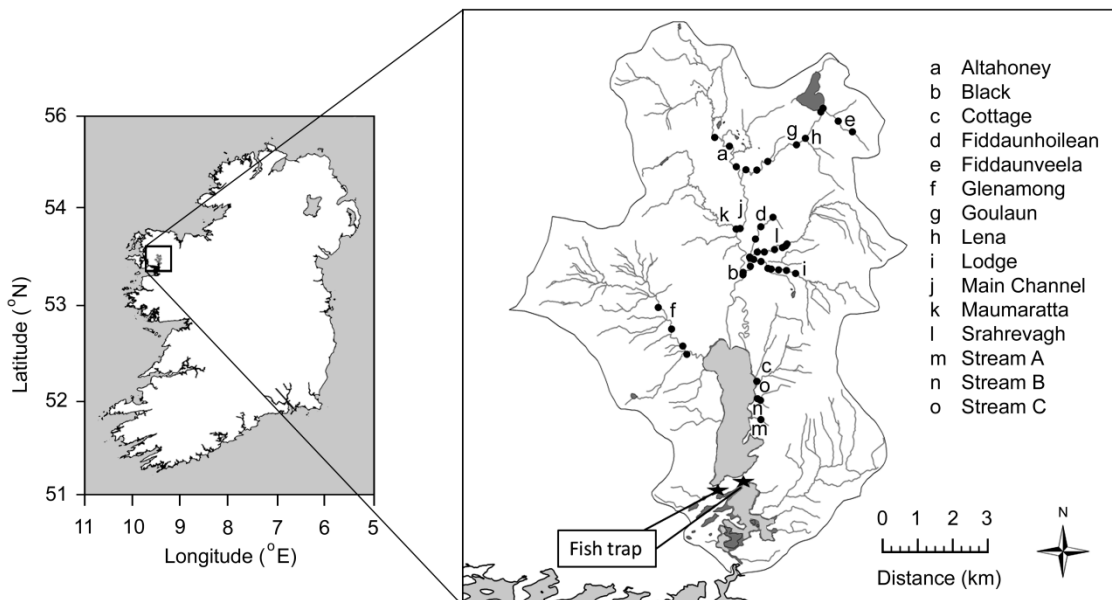
662
663 Fig. 1. Study areas: Norwegian rivers (a); and Burrishoole catchment, Ireland (b). Sample
664 sites within the rivers are shown by filled circles.
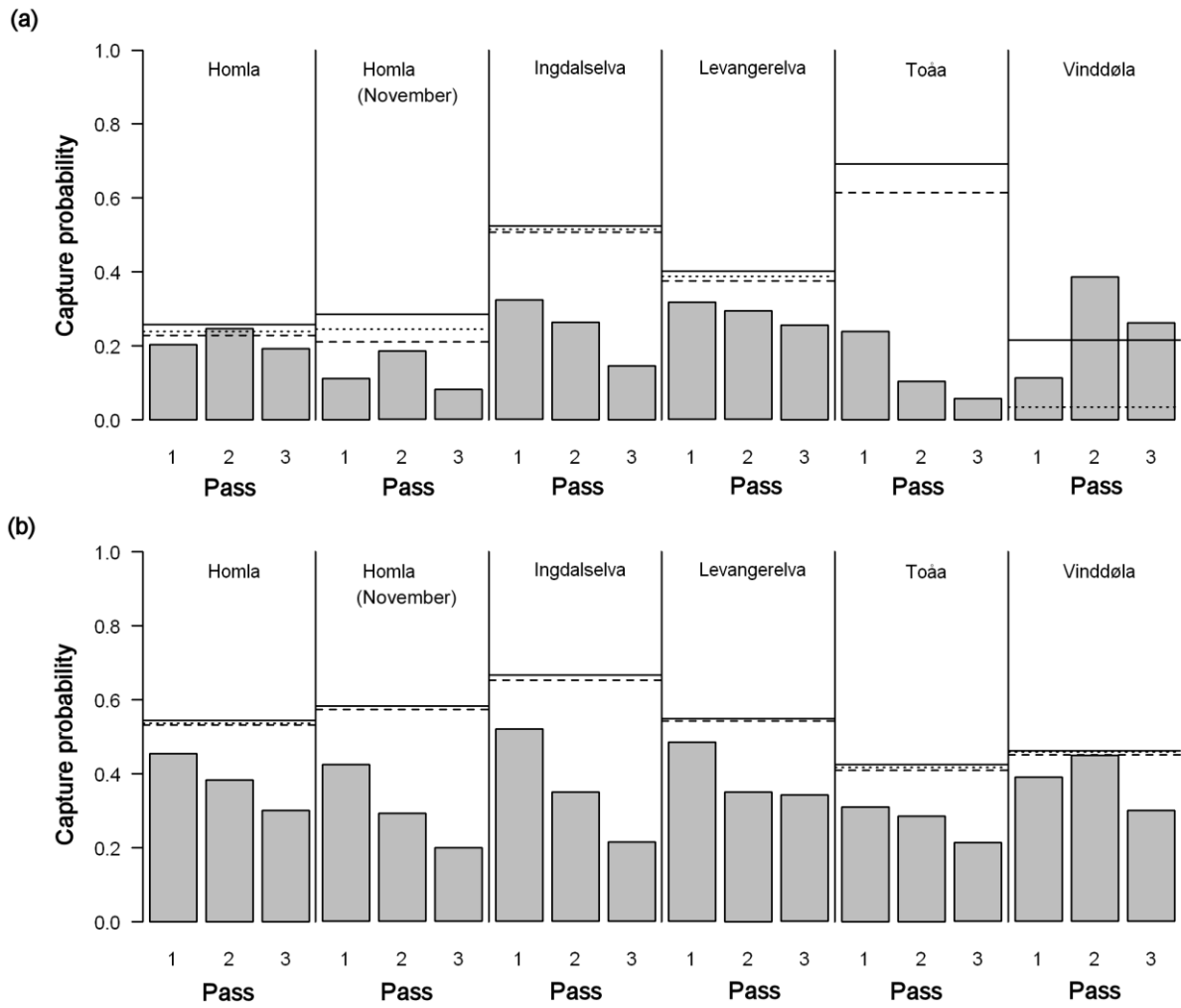
Fig. 2. Observed capture probability as a function of pass and estimated capture probability in the closed sites of five Norwegian rivers of age 0+ (a) and age >0+ (b). The River Homla was electrofished a second time in November. Bars show observed capture probabilities for passes 1 – 3. Horizontal lines show estimated capture probabilities for Zippin (dotted line), Seber (dashed line) and Carle & Strub (continuous line) methods.
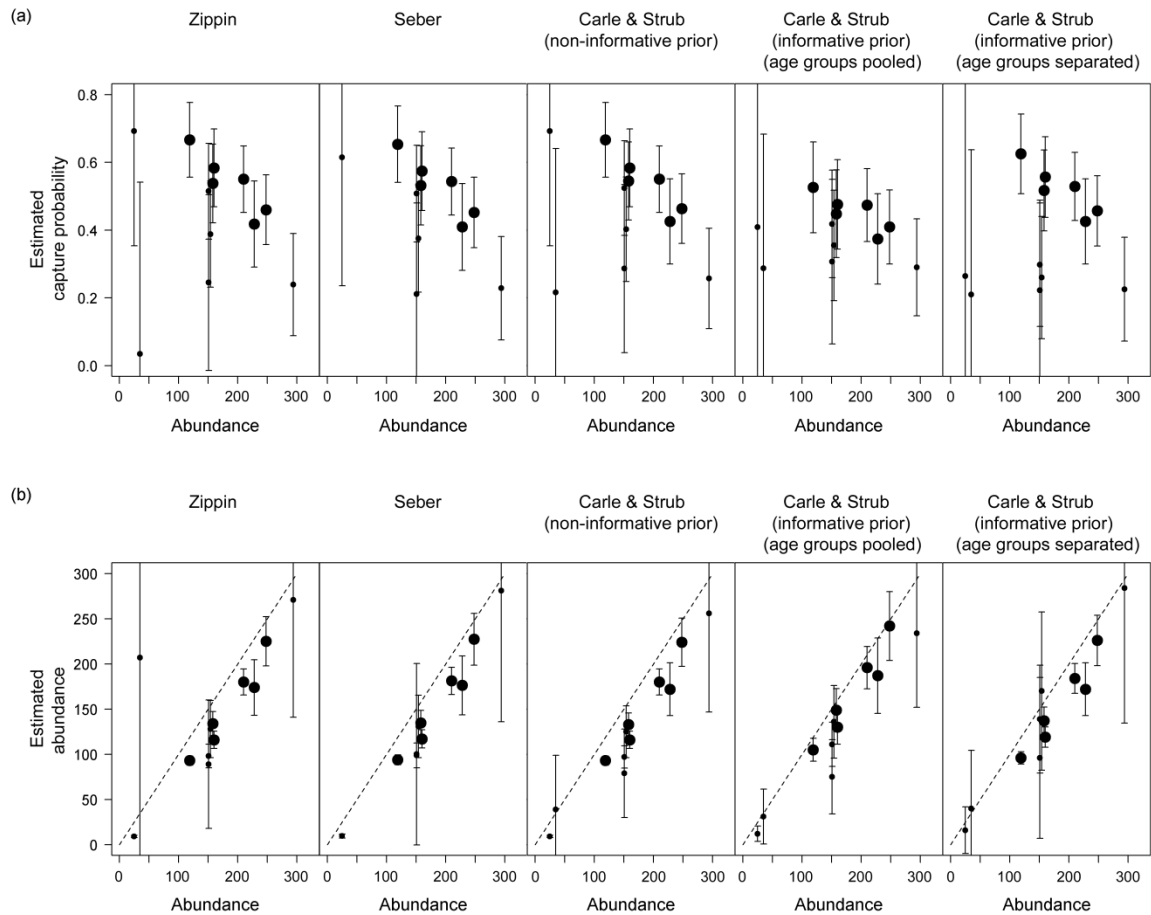
671
Fig. 3. Estimated capture probability (a) and estimated abundance (b) as a function of
observed abundance for closed sites. Age 0+ is shown by small filled circles and age >0+
is shown by large filled circles. Methods are Zippin, Seber, Carle & Strub with non-
informative prior, Carle & Strub method with informative prior (age-groups pooled),
Carle & Strub method with informative prior (age groups separated). Whiskers show
95% confidence intervals.

(a)

(b)
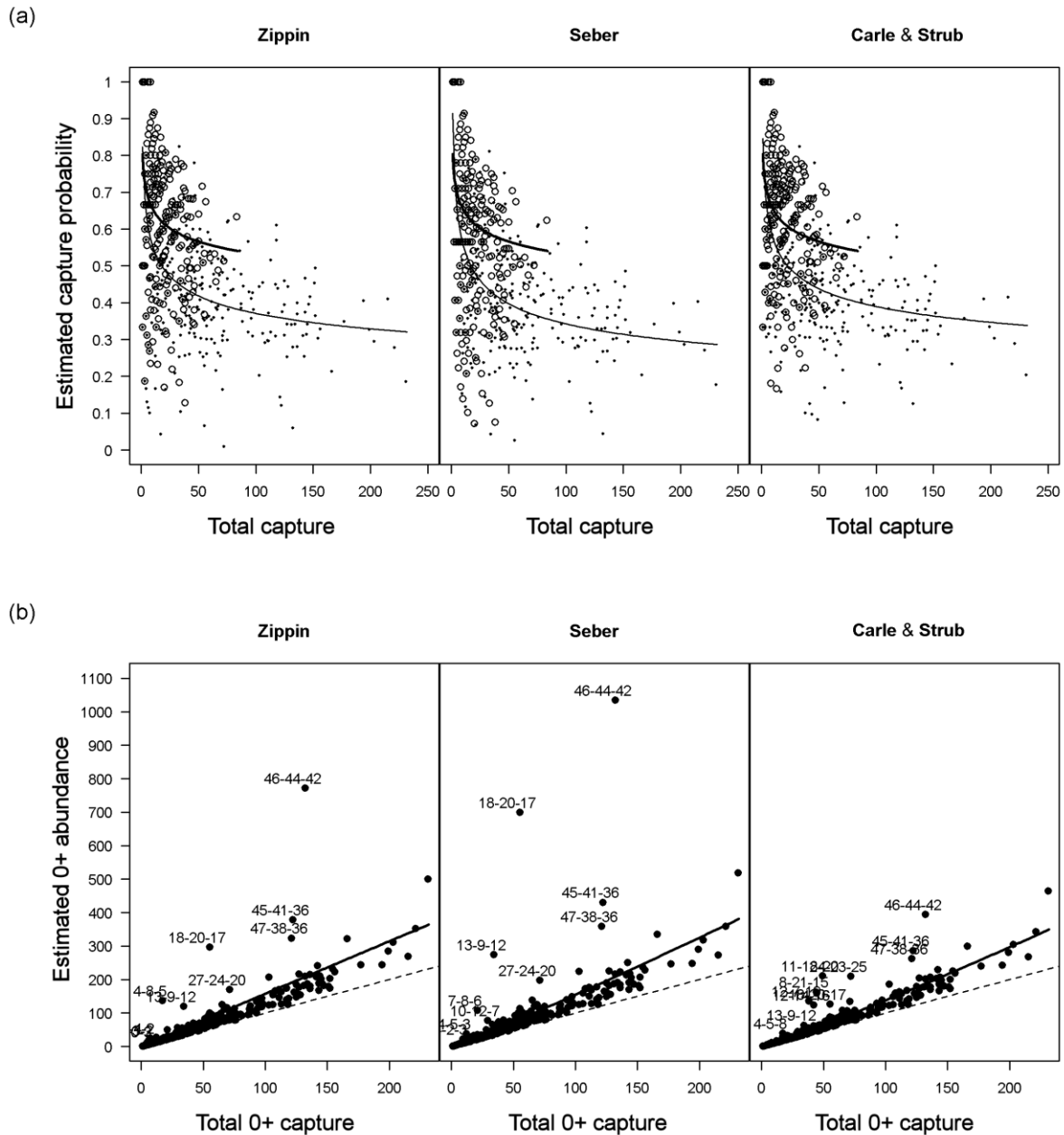
678
679 Fig. 4. Estimated capture probability (a) and estimated abundance (b) as a function of
680 total capture for Zippin, Seber and Carle & Strub methods. For estimated capture
681 probability, age 0+ is represented by dots and age 1+ is represented by empty circles.
682 Non-linear power functions ($y=ax^b$) have been fitted to the capture probabilities (thin
683 lines for 0+, thick lines for 1+). Only 0+ individuals are shown for estimated abundance.
684 The dashed line corresponds to the point where the estimated abundance is equal to the
685 total capture. The continuous line is a power function ($y=ax^b$) fitted to the data. Outliers
686 have the numbers captured in first, second and third passes attached.

(a)

(b)
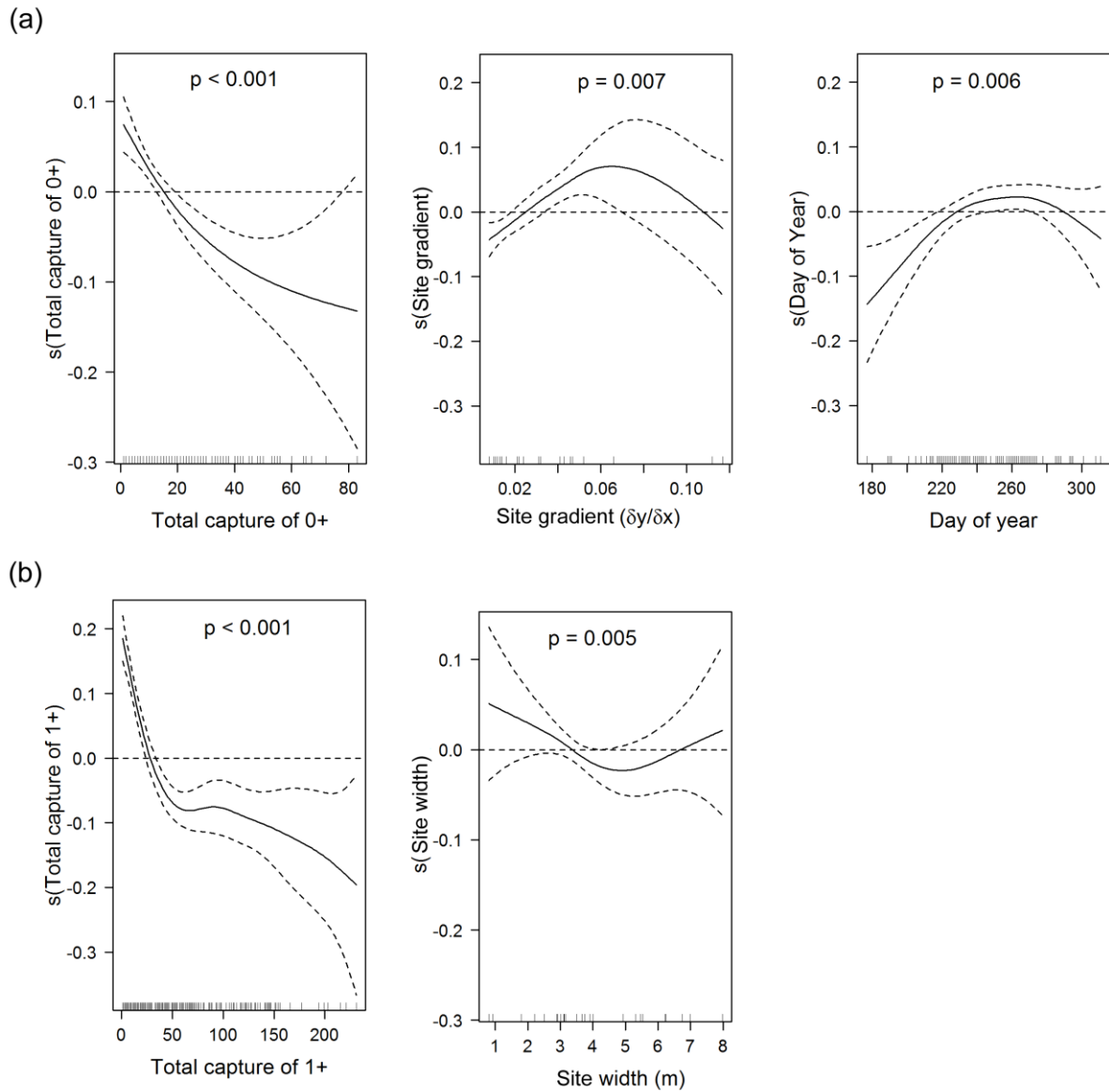
687
688 Fig. 5. Relationship between estimated capture probability of age 0+ (a) and age 1+ (b)
689 and predictors as identified by GAMs. The continuous line shows the smoothing curve,
690 the dashed lines show the 95% confidence intervals. Only significant relationships are
691 shown.
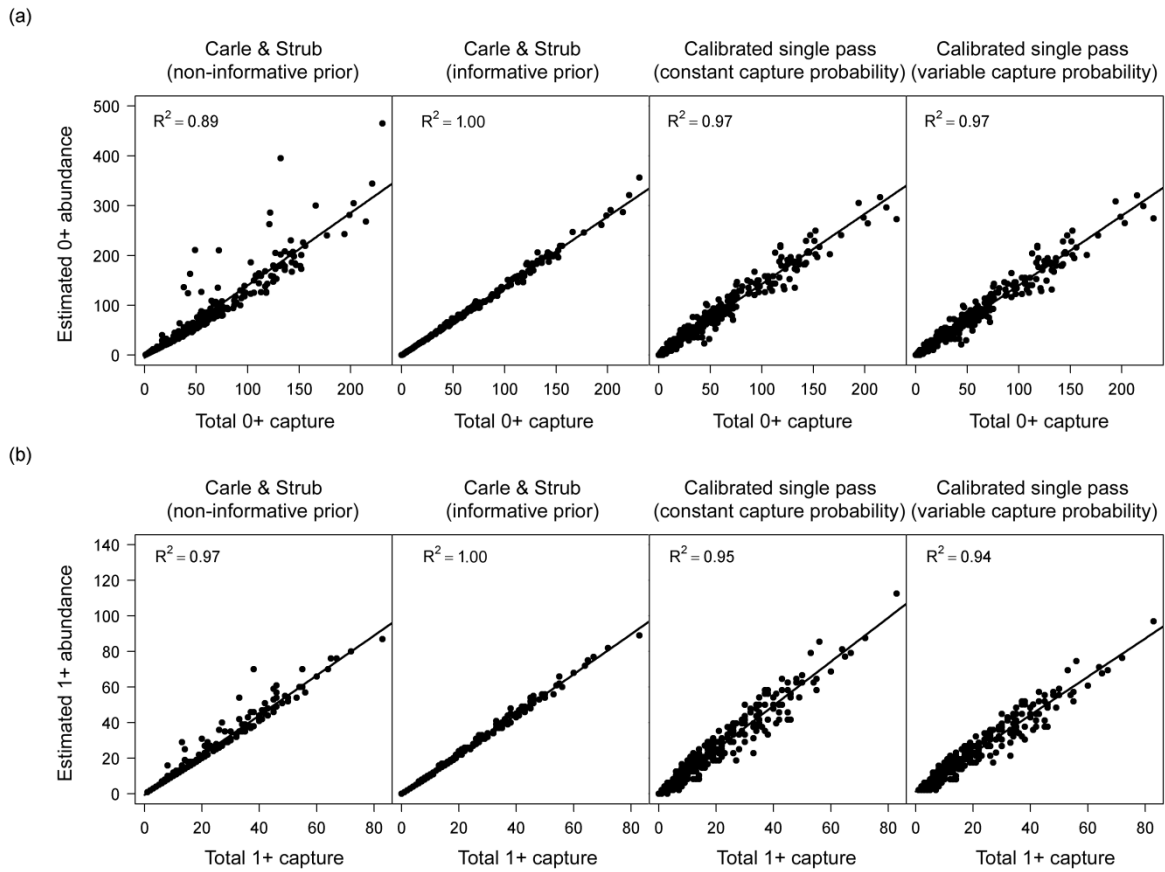
Fig. 6. Estimated abundance of age 0+ (a) and age 1+ (b) as a function of total capture for the Carle & Strub and calibrated single pass methods.
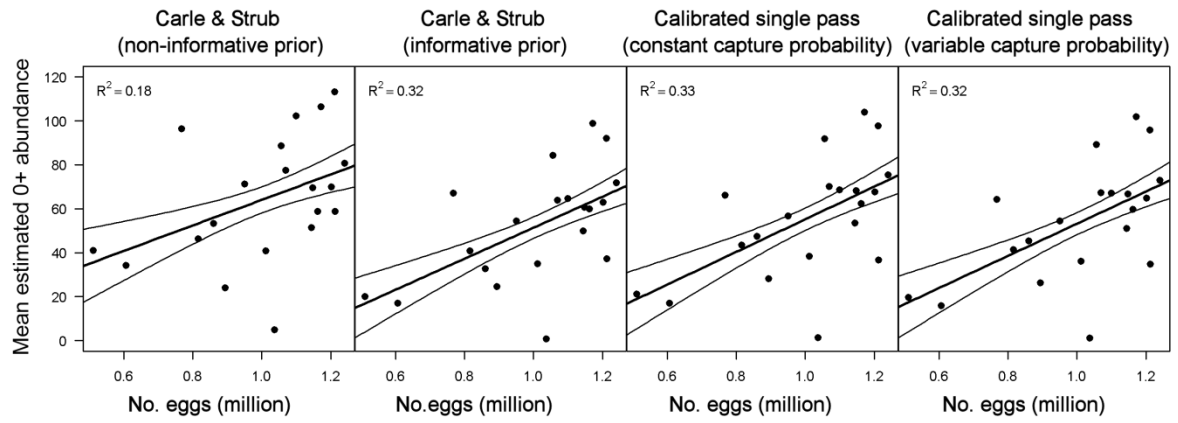
696
697 Fig. 7. Mean annual estimated abundance of age 0+ as a function of number of eggs
698 deposited in the catchment for Carle & Strub and calibrated single pass methods.
699