1 **The generalization of Gulland's method: how to estimate maturity ogives**

2 **when juvenile data are missing while spawner demography is known**

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13

14 **Abstract**

15 The proportions of mature individuals at age or length, collectively known as the maturity ogive,

16 are a key population characteristic and serve as critical input to age-disaggregated stock assess-

17 ments. John Gulland showed in 1964 that it is possible to estimate maturity ogives even when

18 representative data on immature individuals are not available, provided that one can distinguish

19 newly mature individuals (first-time spawners) from those that had matured earlier (repeat

20 spawners). Gulland's method offers a valuable tool for obtaining information on an unobserved

21 part of a population and is also applicable to other ontogenetic transitions, such as metamor-

22 phosis, smolting, ontogenetic niche shifts, and sex change. Here we present a full derivation of

23 Gulland's method from first principles, applicable to the general case in which the survival of

24 immature, first-spawning, and repeat-spawning individuals may differ. Better observation

25 methods, in particular in sclerochronology and histology, are expected to make meeting this

26 method's data requirements—i.e., the separation of first-time and repeat spawners—more often

27 achievable, and estimating maturity ogives could serve as an additional incentive for allocating

28 resources to enhanced data collection. With the generalization presented here, we hope to make

29 Gulland's method better known and more widely accessible.

30

31 Keywords: maturity ogives, life-history transitions, reproductive potential, stock dynamics

32 **1. Introduction**

33 Maturity ogives measure the proportions of mature individuals at age or length and serve as a

34 key characteristic of populations, directly impacting their reproductive potential (Murua and

35 Saborido-Rey, 2003; ICES, 2008; Flores et al., 2015). The demographic structure of the mature

36 part of a population has profound consequences for recruitment and population dynamics

37 (Trippel et al., 1997; Ottersen et al., 2006; Köster et al., 2013; Hixon et al., 2014). At the same

time, fish maturation is a highly plastic process that is influenced by an array of environmental factors such as food availability and temperature (Stearns and Crandall, 1984; Trippel, 1995). This implies that it is important to see maturity ogives as dynamic, rather than static, population characteristics and that an accurate understanding of stock dynamics necessitates the regular updating of a stock's maturity ogive.

When representative measurements of both immature and mature individuals are available, it is straightforward to estimate a population's maturity ogive as the proportions of mature individuals among all individuals, mature and immature, across all age or length classes. Indeed, it would seem obvious that data on both immature and mature individuals were always needed for estimating maturity ogives. However, John Gulland has shown, already more than 50 years ago, that this is not necessary: age-dependent maturity ogives can be calculated based on age-specific proportions of first-time spawning individuals among all spawning individuals (Gulland, 1964). This is potentially a very important methodological discovery, because obtaining representative samples of both immature and mature individuals can be difficult. A number of challenges are evident: immature and mature fish may be spatially segregated, sampling gear may have reduced catchability for smaller sizes, and—when obtaining data from commercial fisheries—fishermen often face regulations specifically designed to reduce catching juvenile fish that may end up being discarded. Gulland's method therefore offers considerable promise in the many situations in which only the mature part of a population is amenable to quantitative sampling.

In reality, Gulland's method has seen only sporadic use, probably because it is rare that first-time and repeat spawners are separated as part of routine stock monitoring. However, in some fish populations, the age at first spawning can be estimated from scales or otoliths based on so-called spawning checks. This is the case for Northeast Arctic cod (*Gadus morhua*), for which spawning checks can be identified in otoliths (Rollefsen, 1933; Zuykova et al., 2009).

63 Indeed, Northeast Arctic cod is the stock for which Gulland first devised his method. Since then,

64 the method has recurrently been applied to this commercially and economically important stock

65 (Jørgensen, 1990; Heino et al., 2002; Svåsand et al., 2003; Zuykova et al., 2009; Yaragina, 2010)

66 and contributes to the maturity ogives used in the official stock assessment (Zuykova et al.,

67 2009; ICES, 2017). Another important example of such applications is Norwegian spring-

68 spawning herring (*Clupea harengus*), for which scales can be used to identify first-time spawn-

69 ers (Lea, 1928; Runnström, 1936; Engelhard et al., 2003). Gulland's method has been applied

70 to this stock in a few publications (Engelhard and Heino, 2004a, 2004b) and, since 2010, in the

71 official stock assessment (ICES, 2016). Species for which Gulland's method has not yet been

72 used, even though first spawning can be identified from otoliths or scales, are as diverse as

73 shortnose sturgeon (*Acipenser brevirostrum*; Taubert, 1980), steelhead trout (*Oncorhynchus*

74 *mykiss*; Narver, 1969), Atlantic halibut (*Hippoglossus hippoglossus*; Devold, 1938), and orange

75 roughy (*Hoplostethus atlanticus*; Francis and Horn, 1997). Future developments in sclerochro-

76 nology could make this list much longer.

77   Gulland (1964) presented his method through a worked example rather than in terms of

78 general equation(s). He also noted that differential survival between immature and mature fish

79 will bias the results, but considered this bias unimportant and did not present a correction. Terje

80 Jørgensen (1990) was the first to express Gulland's method as a general equation. He also pre-

81 sented a way to account for the difference in survival between mature and immature fish, albeit

82 indirectly, by adjusting the counts of repeat spawners. However, he did not present the deriva-

83 tion of the equations, nor did he allow for the survival of first-time spawners to differ from the

84 survival of repeat spawners. Here we present a full derivation of Gulland's method from first

85 principles, applicable to the general case in which the survival of immature, first-spawning, and

86 repeat-spawning individuals may differ. With this generalization, we hope to make Gulland's

87 method better known and more widely accessible.

2. Logic of Gulland's method

88

89 We first describe the general idea underlying Gulland's method. When survival of all types of

90 individuals of the same age is equal, the method is straightforward and can easily be illustrated

91 graphically (Fig. 1). This simplifying assumption is then relaxed in the next section.

92   The goal of Gulland's method is to estimate the age-specific proportions o_t of mature

93 individuals for the population's cohorts at each age t from the observed (sampled) numbers of

94 first-spawning and repeat-spawning fish, n_t^F and n_t^R, respectively. Since we are dealing with

95 each cohort separately, the index t can be interpreted as either age or time (both measured in

96 numbers of spawning seasons), whichever is more convenient. An individual is born as a juve-

97 nile (life stage J), then matures and becomes a first-time spawner (F), before turning into a

98 repeat spawner (R) for the rest of its life. Thus, the generalized ontogeny is of type J $\rightarrow \cdots \rightarrow$

99 J $\rightarrow$ F $\rightarrow$ R $\rightarrow \cdots \rightarrow$ R $\rightarrow$ †, with each arrow corresponding to a time step, typically one year. As

100 appropriate, other conventions for naming the successive stages can be adopted, as long as the

101 distinction between juveniles, newly mature individuals, and individuals that were newly ma-

102 ture during earlier observation steps is maintained.

103   Gulland's method is iterative, progressing backward in time. The estimation is started

104 from the earliest age at which a cohort is fully mature. In the absence of data on juveniles, this

105 can be identified as the latest age at which the samples contain first-time spawners. We there-

106 fore take this as the reference time and denote it by T (Fig. 1). At time T, the maturity ogive,

107 by definition, has the value $o_T = 1$. We can then work backward in time by noting that the

108 proportion o_{T-1} of mature individuals among all individuals one time step earlier, i.e., at time

109 $T - 1$, equals the proportion r_T of repeat spawners among all mature individuals at time T,

110 $o_{T-1} = r_T$. The latter proportion is known directly from the sampling, $r_T = n_T^R/(n_T^F + n_T^R)$. For

111 time $T - 2$, the proportion o_{T-2} of mature individuals among all individuals likewise equals

112 the proportion of repeat spawners among all individuals at time $T - 1$ (Fig. 1). This proportion

113   is not known from the outset. However, the proportion o_{T-1} of mature individuals among all

114   individuals in the cohort is known from the previous step, and the proportion r_{T-1} of repeat

115   spawners among all mature individuals is again known from the sampling. We can multiply

116   these two proportions to determine $o_{T-2} = o_{T-1}r_{T-1}$ (Fig. 1). This equation is readily general-

117   ized for any time t. Thus, we obtain the general iterative equation for Gulland's method under

118   uniform survival probabilities,

$$o_{t-1} = o_t r_t, \tag{1a}$$

119   or equivalently, $o_t = o_{t+1}r_{t+1}$. Accumulating all iterations, the maturity ogive can be expressed

120   as an explicit closed-form function of time t,

$$o_t = \prod_{\tau=t+1}^{T} r_\tau. \tag{1b}$$

121   **3. Generalization of Gulland's method**

122   We now derive Gulland's method from first principles. This allows considering the role of

123   survival, and of differences in survival between life stages, in a rigorous way.

124   Changes in the abundances of fish in a cohort over one time step are described as follows,

$$N_{t+1}^{J} = s_t^{JJ}N_t^{J}(1 - m_t), \tag{2a}$$

$$N_{t+1}^{F} = s_t^{JF}N_t^{J}m_t, \tag{2b}$$

$$N_{t+1}^{R} = s_t^{FR}N_t^{F} + s_t^{RR}N_t^{R}, \tag{2c}$$

125   where N_t^{J}, N_t^{F}, and N_t^{R} are the abundances of juvenile, first-spawning, and repeat-spawning fish

126   at time t, s_t^{JJ}, s_t^{JF}, s_t^{FR}, and s_t^{RR} are the survival probabilities for the transitions J → J, J → F,

127   F → R, R → R, respectively, and m_t is the probability of maturation during the next time step.

128   Here we have assumed that, at any time t, the survival probability for transitions R → R is in-

129   dependent of the number of preceding spawning events.

130   The maturity ogive can always be expressed in terms of stage-specific abundances:

$$O_t = \frac{N_t^F + N_t^R}{N_t^J + N_t^F + N_t^R} = \frac{1}{1 + \frac{N_t^J}{N_t^F + N_t^R}}.$$

(3)

131   With expressions derived from Equations 2a–2c, the terms N_t^J and $N_t^F + N_t^R$ can be expressed

132   in terms of the cohort composition at time $t + 1$. First, rearranging Equation 2b gives $N_t^J =$

133    $N_{t+1}^F / s_t^{JF} / m_t$. The maturation probability m_t can be solved from Equations 2a and 2b as

$$m_t = \frac{1}{1 + \frac{s_t^{JF}}{s_t^{JJ}} \frac{N_{t+1}^J}{N_{t+1}^F}}.$$

(4a)

134   Substituting Equation 4a into the expression for N_t^J gives

$$N_t^J = \frac{N_{t+1}^F (1 + \frac{s_t^{JF}}{s_t^{JJ}} \frac{N_{t+1}^J}{N_{t+1}^F})}{s_t^{JF}}.$$

(4b)

135   Second, dividing Equation 2c with $N_t^F + N_t^R$, using the definition $r_t = N_t^R / (N_t^F + N_t^R)$, and

136   rearranging gives

$$N_t^F + N_t^R = \frac{N_{t+1}^R}{s_t^{FR}(1 - r_{t+1}) + s_t^{RR} r_{t+1}}.$$

(4c)

137   Inserting Equations 4b and 4c into Equation 3 gives

$$O_t = \frac{1}{1 + \frac{N_{t+1}^F}{N_{t+1}^R} \left(1 + \frac{s_t^{JF} N_{t+1}^J}{s_t^{JJ} N_{t+1}^F}\right) \frac{s_t^{FR}(1 - r_{t+1}) + s_t^{RR} r_{t+1}}{s_t^{JF}}}.$$

(5a)

138   This equation still contains two unknown ratios of abundances. As ratios, they are independent

139   of total abundance and can instead be expressed solely in terms of parameters o_{t+1} and r_{t+1}.

140   Specifically, $N_{t+1}^F / N_{t+1}^R = o_{t+1}(1 - r_{t+1}) / o_{t+1} r_{t+1}$ and

141    $N_{t+1}^J / N_{t+1}^F = (1 - o_{t+1}) / o_{t+1}(1 - r_{t+1})$. Using these relationships, rearranging, and shifting

142   the time index back by one time step gives

$$o_{t-1} = \frac{o_t r_t}{o_t r_t + \left(o_t(1-r_t) + (1-o_t)\frac{s_{t-1}^{JF}}{s_{t-1}^{JJ}}\right)\left(\frac{s_{t-1}^{FR}}{s_{t-1}^{JF}}(1-r_t) + \frac{s_{t-1}^{RR}}{s_{t-1}^{JF}}r_t\right)}. \tag{5b}$$

143   This iterative equation allows determining the value o_{t-1} of the maturity ogive at time $t-1$

144   from three sources of information: (i) the ratio r_t of repeat spawners among all mature individ-

145   uals, known from (representative) sampling, (ii) three ratios of survival probabilities, possibly

146   known from independent observations, and (iii) the value o_t of the maturity ogive at time t,

147   known from the equation's previous iteration or because the cohort is known to be fully mature

148   at time t. Equation 5b is similar to Equation 1a, but includes a correction in form of the denom-

149   inator, which accounts for differences in survival between the life stages. It is readily seen that

150   Equation 5b reduces to Equation 1a as a special case when all survival probabilities are equal.

151   Equation 5b contains three ratios of survival probabilities that all include s_{t-1}^{JF}, which

152   therefore naturally serves as the reference against which the other survival probabilities can be

153   compared. Sometimes it is more convenient to use another survival probability as the reference:

154   for instance, when we use s_{t-1}^{RR} as the reference, Equation 5b becomes

$$o_{t-1} = \frac{o_t r_t}{o_t r_t + \left(o_t(1-r_t)\frac{s_{t-1}^{RR}}{s_{t-1}^{JF}} + (1-o_t)\frac{s_{t-1}^{RR}}{s_{t-1}^{JJ}}\right)\left(\frac{s_{t-1}^{FR}}{s_{t-1}^{RR}}(1-r_t) + r_t\right)}. \tag{5c}$$

155   Figure 2 illustrates the sensitivity of the estimated maturity ogive to departures from

156   equal age-specific survival between maturity stages. Not surprisingly, the sensitivity is greater

157   when the estimated maturity proportion is near the middle of the possible range (Fig. 2, left

158   panels) compared to when the proportion is near the border of the possible range (Fig. 2, right

159   panels). The general tendency is that assuming equal survival ratios between maturity stages

160   leads to positively biased maturity estimates (red colors in Fig. 2) when juvenile survival is low

161   relative to repeat-spawning survival ($s_{t-1}^{JJ}/s_{t-1}^{RR} < 1$) and/or when juvenile-to-first-spawning

162   survival is low relative to repeat-spawning survival ($s_{t-1}^{JF}/s_{t-1}^{RR} < 1$); the opposite is true when

163   these ratios are high.

4. Example: Northeast Arctic cod

165   We illustrate the generalized Gulland's method for the 1928 cohort of Northeast Arctic cod, the

166   first cohort for which suitable data are available. For this stock, historic samples are available

167   from the spawning grounds, distinguishing first-time spawners and repeat spawners, but no

168   representative data are available for juvenile individuals (e.g., Jørgensen, 1990; Heino et al.,

169   2002). For the 1928 cohort, the proportions of repeat spawners among all mature individuals

170   equals 0 for ages 6 years and younger, equals 0.03, 0.24, 0.47, 0.66, 0.70, 0.85, 0.96, and 0.95

171   for ages 7 to 14 years, respectively, and equals 1 for older individuals. Because only mature

172   fish were subject to fishing in the spawning grounds, it is likely that juveniles experienced a

173   higher age-specific survival (s_t^{JJ}) than fish that entered the spawning grounds (s_t^{JF}, s_t^{FR}, and

174   s_t^{RR}). We therefore let the ratio s_t^{JJ}/s_t^{RR} vary. In addition to considering the case $s_t^{JF}/s_t^{RR} = 1$

175   and $s_t^{FR}/s_t^{RR} = 1$, we examine a scenario in which individuals lacking spawning experience

176   suffer from additional mortality during their spawning migration, by considering the case

177    $s_t^{JF}/s_t^{RR} = 0.7$ and $s_t^{FR}/s_t^{RR} = 0.9$; the particular numbers here are chosen for illustrative pur-

178   poses only.

179   Applying our generalization of Gulland's method reveals that the estimated maturity

180   ogive is potentially sensitive to departures from equal age-specific survival between maturity

181   stages (Fig. 2, 3). For instance, when spawning individuals suffer from higher mortality than

182   those that do not spawn, assuming that no such survival difference exists results in an ogive

183   that is downward biased. If the survival difference is large ($s_t^{JJ}/s_t^{RR} = 2$), the true ogive is up

184   to about 15 percent points higher than the estimated one (Fig. 3a). If we assume that lack of

185   spawning experience reduces survival, the maximal bias when $s_t^{JJ}/s_t^{RR} = 2$ is slightly lower, at

186   about ten percent points (Fig. 3b).

187   A potential source of bias for estimating the maturity ogive of Northeast Arctic cod is

188   skipped spawning (Jørgensen et al., 2006; Skjæraasen et al., 2012). The effect of skipped

189   spawning on spawner demography is that the sampled proportions of repeat spawners among

190   all mature individuals (r_T) are less than their true proportions. The strength of this bias will vary

191   with a cohort's age, because skipped spawning depends on spawning experience. Figure 4a

192   shows that if skipped spawning is very frequent and leads to a serious underrepresentation of

193   repeat spawners, the estimated maturity ogive can be seriously biased downward. However, for

194   the documented levels of skipped spawning (~24 % in 2006–2008, Skjæraasen et al., 2012), the

195   bias is modest, at most seven percent points (Fig. 4a for $x = 0.25$).

196   Another possible source of uncertainty is the misidentification of first-time and repeat

197   spawners. Figure 4b shows that misidentifying first-time spawners as second-time spawners or

198   vice versa at a relatively high rate (20%) results in a modest downward bias in the estimated

199   maturity ogive. The largest error is about seven percent points for ages 10–11 years.

200   **5. Discussion**

201   Here we have presented a derivation of the generalized Gulland's method to estimate maturity

202   ogives in the absence of data on juveniles. The information required instead are age-specific

203   proportions of repeat spawners among spawning individuals, as well as ratios of age-specific

204   survival among juveniles, maturing individuals, first-time spawners, and repeat spawners, all

205   for a given cohort. These survival ratios can be based on independent observations or expert

206   knowledge. This is more practical than the correction proposed by Jørgensen (1990), which

207   requires adjusting the input data before applying the original Gulland's method assuming stage-

208   independent survival (his Equation 3 and our Equation 1a).

209   As underscored by our examples above, assuming the aforementioned survival ratios to

210   equal 1 can greatly bias the estimation of maturity ogives when these ratios in fact significantly

211   differ from 1. While estimating survival in wild populations is always difficult, two mitigating

212   considerations are worth emphasizing. First, it is only the aforementioned survival ratios that

213   enter the generalized Gulland's method, not the absolute values of survival probabilities. Sec-

214   ond, these ratios will deviate from 1 only when maturation stages differentially impact age-

215   specific survival. When such effects of maturation stages within each age class are weak, as-

216   suming the ratios to equal 1 will not cause major biases in the estimated maturity ogives.

217   Because maturity ogives result from maturation dynamics of a cohort of individuals, the

218   most natural biological unit for estimating ogives is a cohort. For this reason, we have presented

219   the derivation here for cohorts, as did Gulland (1964) and Jørgensen (1990). However, Gul-

220   land's method—and estimation of maturity ogives in general—can also be used with data from

221   a single year or with data averaged over a range of years. The implicit assumption is that age-

222   specific changes in maturity observed for concurrently recorded age groups is similar to what

223   would have been observed when following a cohort over time. The situation is analogous to

224   growth curves, which can be estimated either by cohort or by year (Beverton and Holt, 1957, p.

225   282; Gulland, 1969, p. 93; Ricker, 1975, p. 205). The disadvantage of any such estimations by

226   year is that factors that are specific to a cohort will confound the detection of age-specific

227   change, be it in maturity or in size. For example, strong year classes of Norwegian spring-

228   spawning herring show different maturation dynamics compared to weak ones (Engelhard and

229   Heino, 2004b; ICES, 2016). Whether cohort-to-cohort or year-to-year variability leads to prac-

230   tically significant differences between estimations by cohort and by year is probably case-spe-

231   cific.

232   Gulland's method also applies to irreversible life-history transitions other than matura-

233   tion, such as metamorphosis, smolting, other ontogenetic niche shifts, and sex change. Each of

234   these transitions might pose specific challenges, for example, in regard to the identification of

235 newly transitioned individuals. Furthermore, some of these transitions might not be strictly ir-

236 reversible. For example, sex change can be bi-directional in some non-commercial reef fishes

237 (e.g., Sunobe and Nakazono, 1993; Nakashima et al., 1996; Munday et al., 1998).

238 Skipped spawning has been implicated in a number of fish stocks (Rideout et al., 2005),

239 including the stocks for which Gulland's method has been used (Engelhard and Heino, 2005;

240 Skjæraasen et al., 2012). Skipped spawning has the potential to bias maturity ogives downwards,

241 if not accounted for. For the documented levels of skipped spawning, this bias is modest, but

242 may act in the same direction as other sources of bias. Furthermore, when good estimates of

243 skipped spawning are available, the estimation of maturity ogives can readily be adjusted to

244 account for it.

245 A major limitation of Gulland's method is that it requires data that are only seldom

246 recorded: distinguishing first-time spawners from repeat spawners with routine observations is

247 rarely possible. Exceptions mainly come from stocks with long spawning migrations (such as

248 cod and herring) or an anadromous life cycle (such as shortnose sturgeon and steelhead trout).

249 These show a so-called spawning check, a visually detectable change in the zonation pattern of

250 otoliths or scales. Long migrations increase the energetic cost of spawning, making the slowing

251 down of growth upon maturation more marked than it would otherwise be (e.g., Folkvord et al.,

252 2014).

253 For Northeast Arctic cod, the recording of spawning checks is part of routine data col-

254 lection (Mjanger et al., 2010). However, a strict validation of the assumption that the formation

255 of the first spawning check is associated with the first spawning is as yet lacking. Experiments

256 support the notion that substantial energy investments in reproduction are reflected by reduced

257 otolith growth, but leave open the question whether such changes in the otolith growth of wild

258 cod are always associated with reproduction or can originate also from other sources of ener-

259 getic stress. Furthermore, it remains possible that some spawning cod do not develop a corre-

260 sponding spawning check (Irgens, 2018; Arild Folkvord, University of Bergen, pers. comm.).

261 Our numerical tests suggest that Gulland's method is not overly sensitive to moderate error

262 rates in assessing whether a spawning fish is a first-time or second-time spawner.

263   There are a number of possibilities to identify first-time spawners in the absence of

264 visually marked changes in otoliths or scales. First, numerical methods might allow detecting

265 changes in growth that are not visually obvious as spawning checks (Rijnsdorp and Storbeck,

266 1995; Engelhard et al., 2003; Baulier and Heino, 2008; Brunel et al., 2013). This requires back-

267 calculations of growth, which can be based on both archived and fresh materials. The efficiency

268 of such estimates could potentially be improved using automated image analyses. Unfortunately,

269 detecting maturation from growth trajectories suffers from limited accuracy, especially for in-

270 dividuals captured soon after maturation (Baulier and Heino, 2008; Brunel et al., 2013).

271   Second, advances in sclerochronology offer new possibilities for extracting life-history

272 information from otoliths and scales that go far beyond traditional visual examinations. For

273 example, patterns of ontogenetic vertical migrations in deep-sea fish can be deduced from oto-

274 lith microstructures and stable-isotope composition (Lin et al., 2012; Chang et al., 2015). Like-

275 wise, migrations of eel between marine, brackish, and freshwater environments can be deduced

276 from the ratios of strontium and calcium in their otoliths (Jessop et al., 2008). An experimental

277 study with European plaice (*Pleuronectes platessa*) showed that reproduction alters the zinc-

278 to-calcium ratio in the blood plasma and otoliths of females, offering a potential tool for detect-

279 ing both age at first reproduction and skipped spawning seasons (Sturrock et al., 2015). Also

280 these methods apply to archived as well as fresh materials.

281   Third, histological methods offer what is potentially the most precise approach to sepa-

282 rating first-time and repeat-spawning female fish, at least for determinately spawning boreal

283 species: mature females with postovulatory follicles (POFs) are repeat-spawners, whereas those

284 lacking POFs are first-time spawners, provided that POFs persist long enough after spawning

285 relative to the timing of the sample collection (Rideout et al., 2005). This condition is easily

286 fulfilled in cod where POFs persist for more than a year (Witthames et al., 2010; Folkvord et

287 al., 2014). Unfortunately, histological methods require samples that are specifically conserved

288 for such analysis, which makes them unlikely to be applicable to historical materials. Moreover,

289 obtaining age estimates still requires the reading of otoliths or scales.

290   Gulland's method offers the prospect of estimating maturity ogives for species in which

291 it is difficult to obtain representative data on the juvenile part of the population. This will often

292 necessitate collecting new kinds of data, or using existing materials in novel ways, in order to

293 differentiate between first-time and repeat spawners. At the same time, elucidating individual

294 life cycles with such new data will probably be valuable in its own right. The prospect of ob-

295 taining information on a population's demographic composition by applying Gulland's method

296 can add motivation for investing scarce resources in enhanced analyses of otoliths and scales,

297 as well as into histology. Exciting options for future applications of the generalized Gulland's

298 method presented here include obtaining information on the oceanic phase of anadromous it-

299 eroparous salmonids and estimating the maturity ogives of enigmatic deep-sea fishes such as

300 orange roughy.

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Figure captions

448 **Fig. 1.** Schematic illustration of Gulland's method when survival is equal for all individuals at

449 a given age. At any point in time, a cohort is composed of juvenile (J), first-spawning (F), and

450 repeat-spawning (R) individuals. For all ages t, the proportion of repeat spawners among all

451 spawners is known from sampling, $r_t = n_t^R/(n_t^F + n_t^R)$. The maturity ogive o_t is known from

452 sampling to equal 1 down to the latest age T at which first-time spawners are still present in the

453 samples. For earlier ages $t < T$, o_t can be calculated iteratively using the equation $o_{t-1} = o_t r_t$.

454 For understanding Gulland's method, it is important to recognize that the proportions o_t of ma-

455 ture individuals among all individuals and the proportions r_t of repeat spawners among all ma-

456 ture individuals are measured relative to different totals (all individuals vs. all mature individ-

457 uals), as indicated by the gray extensions of the black curly braces.

458 **Fig. 2.** Sensitivity of the estimated proportion of mature individuals to variations in relative

459 survival between maturity stages. The left and right columns correspond to situations that could

460 be encountered when estimating maturity proportions for near median and relatively early ages,

461 respectively, that is, relatively high and low proportions of mature and first-spawning individ-

462 uals. On the left, assuming that all survival ratios are equal, the estimated maturity proportion

463 is $o_{t-1} = o_t r_t \approx 0.56$, whereas on the right, it is much lower, at $o_{t-1} \approx 0.062$. The color bands

464 indicate how much this estimate deviates from the true value (red: overestimation; blue: under-

465 estimation). Each color band has a width of 0.05. The white band is centered on the true value;

466 hence, it covers an area in which the absolute error is smaller than 2.5%. In the top row, all

467 survival ratios are varied, but $s_{t-1}^{JJ} = s_{t-1}^{JF}$ are kept equal, whereas in the middle row, $s_{t-1}^{JF} =$

468 s_{t-1}^{FR} are kept equal. In the bottom row, s_{t-1}^{JJ} and s_{t-1}^{JF} are varied independently, while $s_{t-1}^{FR} = 1$

469 is kept fixed. Notice that all axes are logarithmic.

470 **Fig. 3.** Application of the generalized Gulland's method to the 1928 cohort of Northeast Arctic

471   cod, *Gadus morhua*. In (a), maturing fish and first-time spawners are assumed to have experi-

472   enced the same survival probability as repeat spawners ($s_t^{\text{JF}}/s_t^{\text{RR}} = s_t^{\text{FR}}/s_t^{\text{RR}} = 1$), whereas in

473   (b), they are assumed to suffer from reduced survival during the spawning migration

474   ($s_t^{\text{JF}}/s_t^{\text{RR}} = 0.7$ and $s_t^{\text{FR}}/s_t^{\text{RR}} = 0.9$). In both panels, the ratio of juvenile to repeat spawner sur-

475   vival probability is varied; the size of the circular markers increases with the survival ratios

476    $s_t^{\text{JJ}}/s_t^{\text{RR}}$, which apply to all ages t. Filled circles correspond to the simpler case in which sur-

477   vival is independent of maturation stage, as is assumed when using the original Gulland's

478   method without our generalization. The results show how estimation errors as large as 100%

479   can result when applying the original Gulland's method to situations in which age-specific sur-

480   vival probabilities are affected by maturation stage.

481   **Fig. 4.** Application of the generalized Gulland's method to the 1928 cohort of Northeast Arctic

482   cod when accounting for (a) skipped spawning and (b) errors in assessing an individual's

483   spawning experience. When some mature fish skip the spawning migration, samples from the

484   spawning grounds show too low proportions r_T of repeat spawners among all mature individu-

485   als. In (a), r_T is corrected for this underrepresentation as $r_T' = r_T(1 + x)/[r_T(1 + x) + 1 - r_T]$,

486   where x is the proportion of mature fish skipping spawning. In (b), it is assumed that there is a

487   20% probability of assigning a first-time spawner as a second-time spawner, and vice versa.

488   The thick curve shows the true ogive when spawning experience is assumed to have been cor-

489   rectly estimated. The boxes show the median value together with the interquartile range of 1000

490   Monte-Carlo replicates in which erroneous assignments are present. Whiskers extend to the

491   most extreme data point no more than 1.5 times the interquartile range away from the box, and

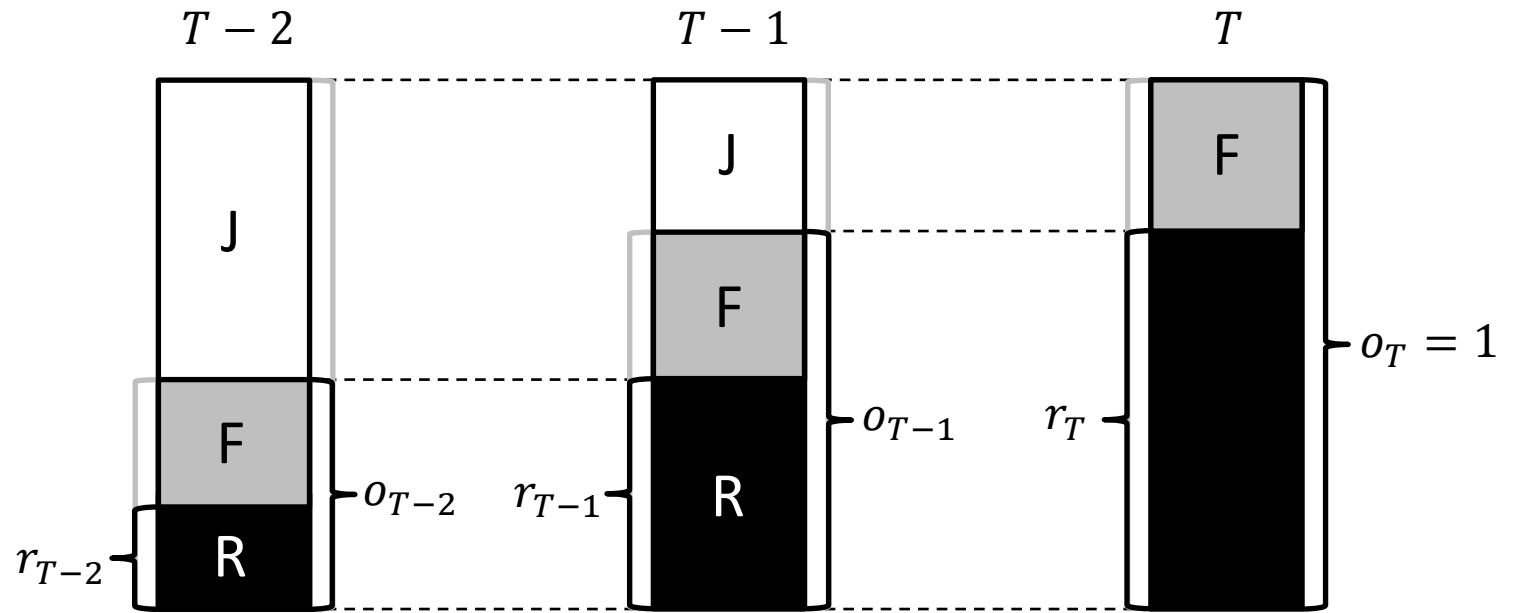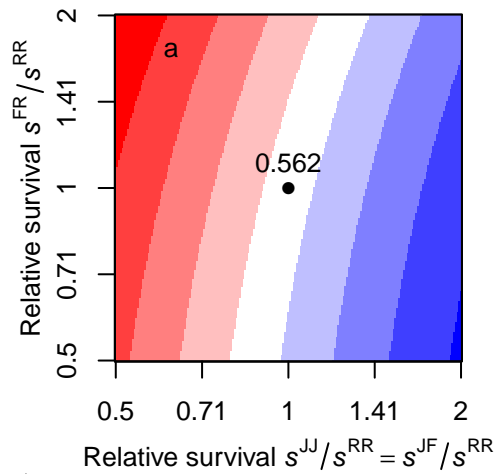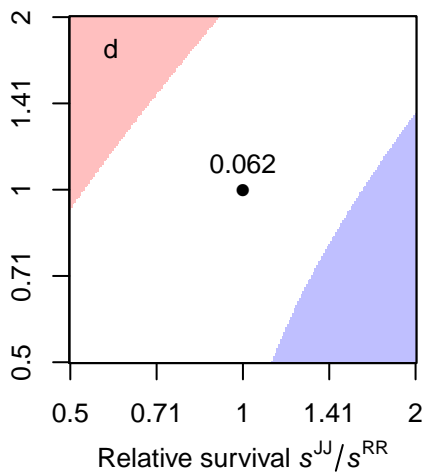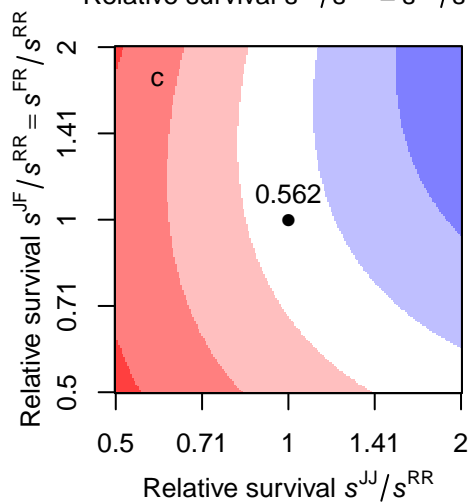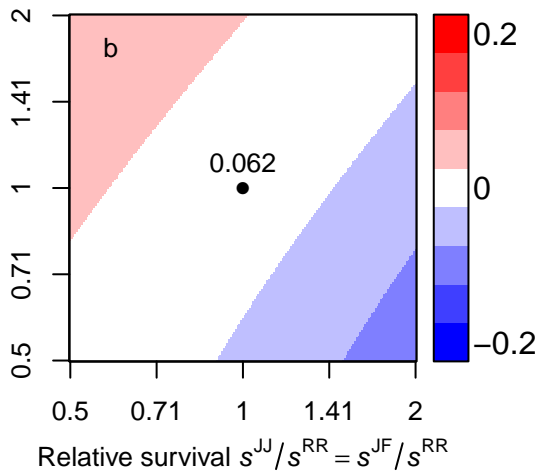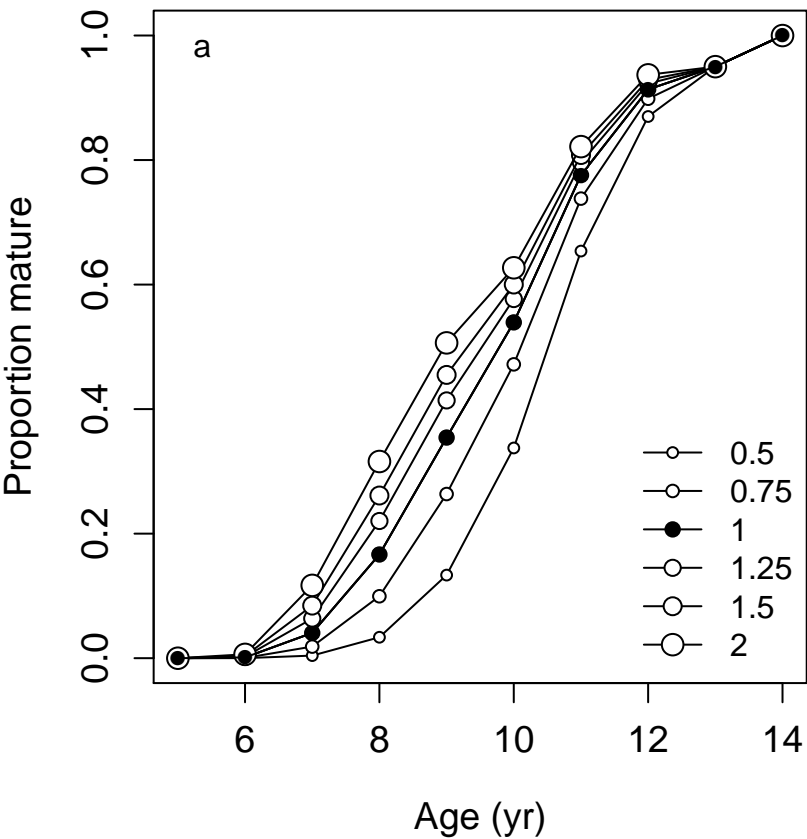492   dots show more extreme data points.

Fig. 1

Fig. 2
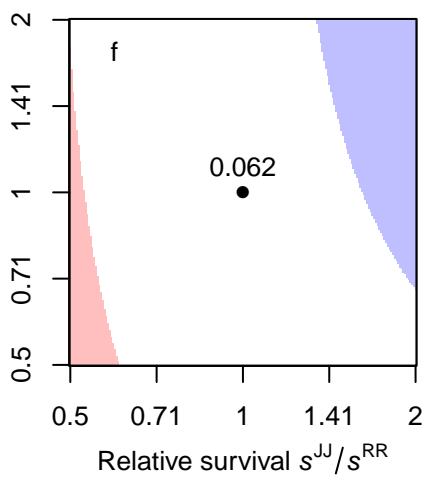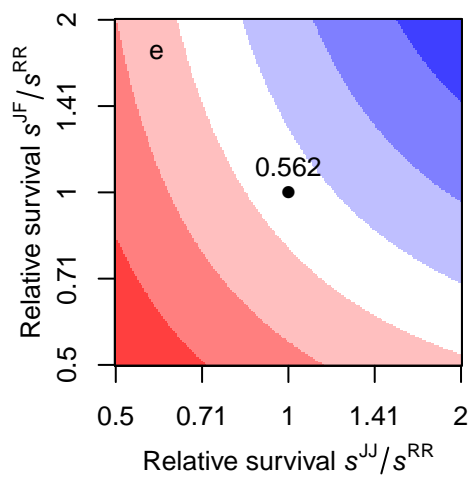
Fig. 3 $s^{JJ}/s^{RR} = 0.5\ldots2$, $s^{JF}/s^{RR} = 1$, $s^{FR}/s^{RR} = 1$ $s^{JJ}/s^{RR} = 0.5\ldots2$, $s^{JF}/s^{RR} = 0.7$, $s^{FR}/s^{RR} = 0.9$
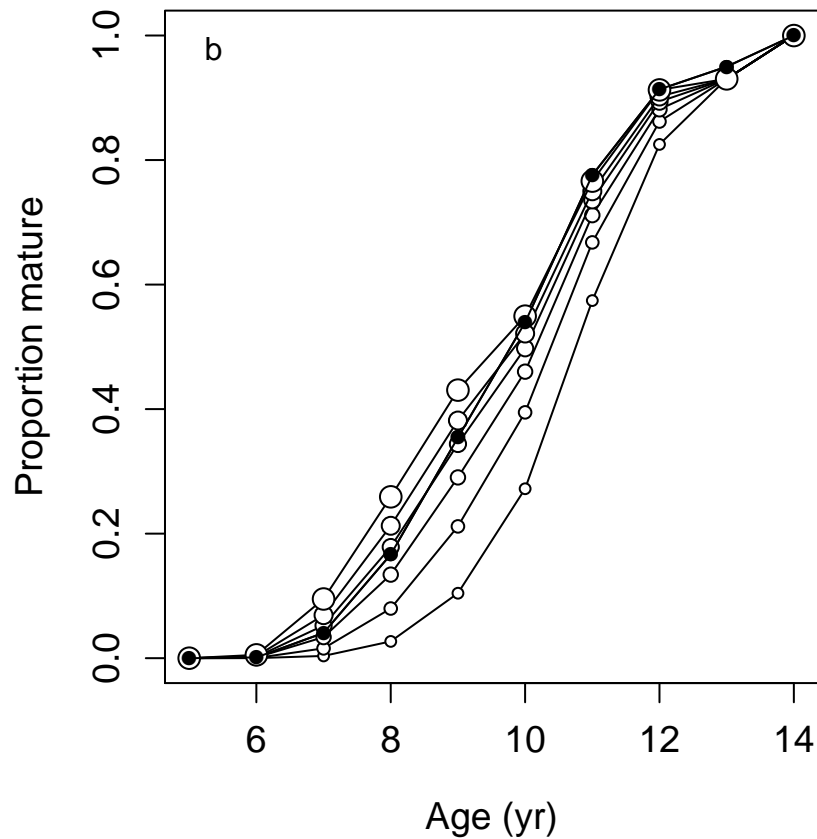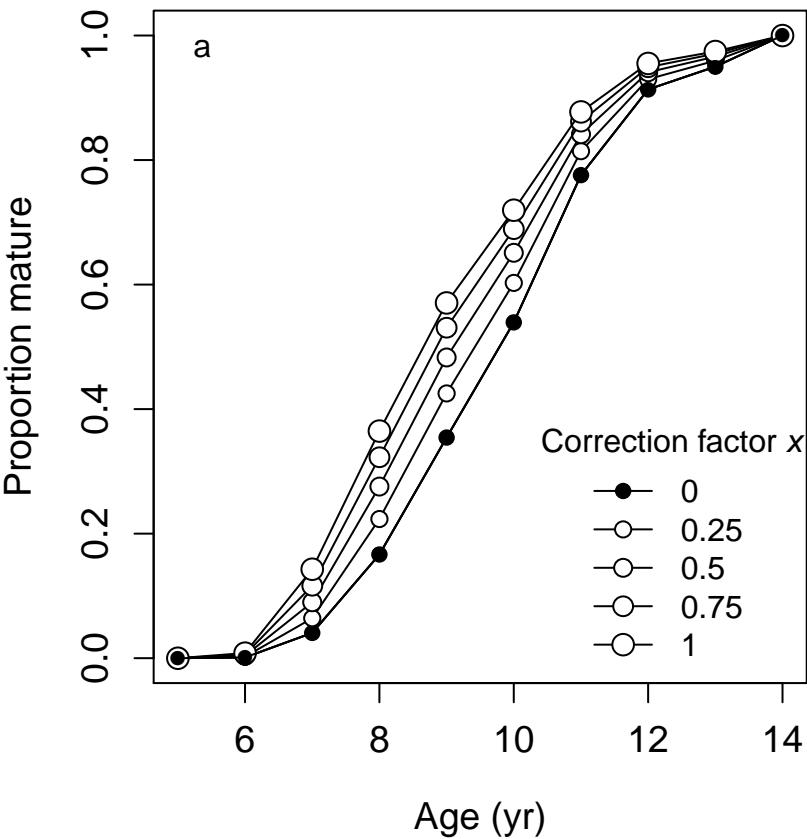
Fig. 4