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1   **Socially induced reproductive synchrony in a salmonid: an approximate Bayesian**

2   **computation approach**

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5   **Running title: Socially induced reproductive synchrony**

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Abstract

Reproductive synchrony is a widespread phenomenon found in many taxa, including plants and corals. However, compared to synchrony caused by environmental cues, knowledge of socially induced reproductive synchrony is limited, partly due to the difficulty of experimentally manipulating and/or making detailed behavioral observations of populations in the wild. In this study, we developed a novel modeling framework combining an individual-based model, a hierarchical Bayesian model, and an approximate Bayesian computation (ABC) to elucidate socially induced reproductive synchrony. This method was applied to time-series redd (i.e., spawning nests) count data in 30 wild populations of stream-dwelling Dolly Varden charr. The model with reproductive synchrony explained all the redd count data, whereas the null model, which did not include the synchrony, failed to reproduce the observed data in several populations. In addition, our models suggest that Dolly Varden should be able to adjust spawning by up to a week following other females to produce synchrony. No significant correlation was observed between reproductive timing and environmental factors, suggesting that the major cue for the synchrony was social rather than environmental. The presence of reproductive synchrony within but not among local populations suggests that predator satiation is not the main driver of the synchrony; rather, other mechanisms must exist in the Dolly Varden, such as induced monogamy or polygamy, or avoidance of nest superimposition. This study has demonstrated the effectiveness of using individual-based and hierarchical modeling together with an ABC parameter estimation method in behavioral ecological studies.

Introduction

Most organisms in temperate or arctic regions exhibit reproductive seasonality so that offspring are born when food resources are most abundant (Munro et al. 1990). Reproduction, however, is often more aggregated in time than would be expected from seasonality alone, a phenomenon called reproductive synchrony (Ims 1990a). Prominent examples include mass spawning of corals, mast seeding of plants, and outbreaks of cicadas (Hoppensteadt and Keller 1976; Harrison et al. 1984; Kelly and Sork 2002). The adaptive significance of such large-scale synchrony is generally considered to be predation satiation, which occurs so predators cannot consume all prey because vast amounts of prey have emerged at the same time (Darling 1938; Janzen 1971). Proximate cues include environmental factors, such as temperature, precipitation, and lunar cycles (Hoppensteadt and Keller 1976; Harrison et al. 1984; Kelly and Sork 2002). At smaller scales, reproductive synchrony caused by social interactions is also of particular interest because internal factors, such as social or pheromonal cues, may influence the reproduction of conspecific individuals (French and Stribley 1987; Jovani and Grimm 2008). Reproductive synchrony could have significant ecological and evolutionary consequences, for example, by mediating population dynamics or mating behavior (Ims 1990a; Mendoza-Cuenca and Macías-Ordóñez 2010; Plot et al. 2012). However, many important aspects of reproductive synchrony are not fully understood, such as the relative importance of internal and external factors and the adaptive significance and its consequences. Furthermore, most knowledge of reproductive synchrony comes from a relatively small number of animal and plant species, such as tropical reef species (e.g., corals, fishes, crabs), masting plants, and some primates (Kelly and Sork 2002; Craydon

75   2004; Baird et al. 2009; Clark et al. 2012).

76

77   Compared to environmentally induced synchrony, socially induced reproductive

78   synchrony has been demonstrated much less in wild populations. Because experimental

79   manipulation and determination of social cues are generally difficult, inductive analyses

80   from observed patterns have often been used (Ims 1990a). For example, when

81   individuals who are in close proximity reproduce more synchronously than those who

82   are further apart, socially induced synchrony will be inferred (Sillero-Zubiri et al. 1998;

83   Evans et al. 2009). However, this can be applied only to sedentary species or species

84   with breeding nests, such as birds and some mammals. In addition, spatial analysis

85   cannot separate social cues from local environmental cues (spatial autocorrelation).

86   Another inductive method is to show the lack of correlation between candidate

87   environmental factors and reproductive timing (Ims 1990a), but this rather passive

88   approach has the potential to be misleading because it overlooks unmeasured

89   environments. Inductive analyses are also generally challenging because socially

90   induced synchrony has a tendency to result in weak patterns. Unlike mast seeding or

91   coral spawning, patterns of socially mediated reproduction are often ambiguous because

92   the effects of social stimuli narrowly focus around a focal individual rather than an

93   entire population. Such weak temporal clusters of reproduction could also result from

94   stochasticity alone, especially when the population size is small (e.g., Henson et al.

95   2010; see also a simulation result below).

96

97   As an alternative to inductive analyses, individual-based models can be used to

98   investigate underlying mechanisms for observed patterns (Grimm and Railsback 2005).

99   In fact, this approach has been used successfully to model individual-based synchronous

100 behaviors, such as flocks of birds, schools of fishes, and swarm of solider crabs (Wood

101 and Acland 2007; Gunji et al. 2012; Attanasi et al. 2014; Murakami et al. 2014; Calovi

102 et al. 2015), as well as reproduction (Jovani and Grimm 2008). In these studies,

103 individuals are given a kind of autonomy, where they are assumed to choose each

104 behavior depending on social interactions with other individuals (e.g., follow the leader

105 or neighbor(s)) with stochastic variability. Even in such simple models, however, global

106 patterns formed by the models are often not directly compared with observational data,

107 or statistical techniques have not been fully utilized. For example, optimization of

108 unknown parameters is frequently overlooked, and the degree of fit of the proposed

109 models is not quantitatively evaluated. This is primarily because the data on individual

110 behavior are not independent due to synchronicity, meaning that statistical models

111 requiring independence of observations (e.g., generalized linear models) are not directly

112 applicable. In addition, including social interactions makes the derivation of the

113 likelihood function, one of the most essential parts in statistical modeling, exceedingly

114 difficult.

115

116 The approximate Bayesian computation (ABC) is a promising tool for linking statistical

117 models to real data in such situations (Beaumont et al. 2002; Beaumont 2010; Sunnåker

118 et al. 2013). Instead of calculating the exact likelihood, the ABC method approximates

119 it by numerical simulations and comparisons with the observed data. Thus, ABC has the

120 potential to be applied to a broad range of complex models (Sunnåker et al. 2013).

121 However, until recently, ABC has been used primarily in population genetics studies

122 (Beaumont et al. 2002; Beaumont 2010). In recent years, its use has been expanded to

123   other disciplines, such as ecology (e.g., Jabot and Chave 2009), but not yet to behavioral

124   ecology. Despite the considerable potential and solid mathematical foundations of ABC,

125   there still remain some challenges, such as choosing appropriate models and summary

126   statistics (Sunnåker et al. 2013). Further applications and improvements of the

127   technique are therefore needed.

128

129   The aims of the present study are (1) to investigate whether socially induced

130   reproductive synchrony exists in a stream fish; (2) to estimate ecologically relevant

131   parameters such as the strength of social interactions; (3) to discuss ultimate factors

132   causing the reproductive synchrony, if any; and (4) to evaluate our new modeling

133   framework, which combines an individual-based model (Grimm and Railsback 2005), a

134   hierarchical Bayesian model (Royle and Drazio 2008), and the approximate Bayesian

135   computation (Beaumont 2010), for behavioral studies. To this end, we first conducted

136   intensive field studies and obtained detailed reproductive datasets for a stream-dwelling

137   salmonid in northern Japan. We then developed individual-based reproductive models

138   with social interactions (i.e., the synchrony model) and without them (i.e., the null

139   model), which also incorporated stochasticity, non-uniform reproductive schedules, and

140   observation processes. Simulated patterns from the alternative models were compared

141   with the observational data and the parameters were estimated by the modified version

142   of the ABC method proposed by Nakagome et al. (2013).

143

144

145   **Materials and methods**

146

147   Study system

148   We investigated reproductive synchrony in the metapopulation of Dolly Varden charr

149   *Salvelinus malma* in the upper Sorachi River system, central Hokkaido, Japan (Koizumi

150   2011). The upper Sorachi River (470 km^2 watershed area above the Kanayama

151   Reservoir) consists of more than a hundred small tributaries (< 500 m in length, 0.5-3.0

152   m in width, 0.01-0.5 m^{3}s^{-1} in water discharge) that directly flow into the larger

153   mainstem (5-30 m in width, 1.0-10 m^{3}s^{-1} in discharge), generating significant habitat

154   heterogeneity between tributaries and the mainstem (Koizumi and Maekawa 2004).

155   Dolly Varden spawn only in small tributaries and the uppermost reaches of large

156   tributaries or the mainstem (Koizumi et al. 2006a). They form a metapopulation

157   structure with each tributary used as a local habitat. Genetic composition and

158   demography are partially independent in each tributary (Koizumi and Maekawa 2004;

159   Koizumi et al. 2006b, 2008). Therefore, local tributary populations are considered as

160   good spatial replicates. There are several fish species inhabiting the Sorachi River, such

161   as white-spotted charr *Salvelinus leucomaenis* and freshwater sculpin *Cottus nozawae*

162   (Koizumi et al. 2012). However, Dolly Varden dominate small tributaries (Koizumi et al.

163   2006a, 2012) and, thus, spawning nests (called "redds" in salmonid literature) in

164   tributaries are unambiguously determined as Dolly Varden redds.

165

166   Redd counts survey

167   Of the more than a hundred small tributaries, we chose 30 (Supplementary Fig. S1 and

168   Table S1) for the breeding survey based on the following criteria: relatively easy to

169   access, whole tributary survey possible (i.e., from the headwater to the junction with the

170   mainstem), and easy to observe spawning redds due to shallow depth, low velocity, and

171   low cover habitat. Only one tributary (T54) had a small erosion control dam, which was

172   106 m upstream from the junction, and we surveyed this reach. In three long tributaries

173   (IK, T51, T59.5) and in one branch of a tributary (T13b), we surveyed only core

174   spawning sites in the uppermost reaches.

175

176   To evaluate reproductive timing we conducted a standard redd count procedure in

177   salmonids (Gallagher et al. 2007) from late August to the end of December 2007,

178   covering the entire spawning season. Surveys were conducted every 3-5 days for most

179   of the breeding period in each tributary until two weeks after the final redd was

180   observed. Occasional visits in a reference tributary confirmed that no spawning

181   occurred after January. Since identifying spawning redds can sometimes be difficult

182   (Gallagher et al. 2007), we carefully evaluated the procedure in advance

183   (Supplementary Appendix A). When we observed spawning behavior (i.e., construction

184   of redds, often accompanied with multiple males), we recorded them as redds on the

185   same day.

186

187

188   Modeling procedures

189   Our modeling combined individual-based modeling (Grimm and Railsback 2005),

190   hierarchical Bayesian modeling (Royle and Drazio 2008), and approximate Bayesian

191   computation (Sunnåker et al. 2013) approaches. Hierarchical Bayesian modeling

192   integrates different levels of models into a single statistical framework by constructing a

193   system model and observation model: the former represents a biological process we are

194   interested in, whereas the latter represents a sampling process. These models are

195   integrated into a hierarchy under the Bayesian framework to jointly estimate each of the

196   parameters (Royle and Drazio 2008). We used an individual-based model for the system

197   model and an ABC technique for parameter estimation.

198

199   We developed two alternative system models: reproduction models with synchrony (i.e.,

200   with social interaction) and without synchrony (i.e., null models). We examined the

201   evidence of socially induced reproductive synchrony by testing which model better

202   explained the observed patterns in 30 local populations of Dolly Varden. Both models

203   have the following breeding parameters, i.e., the number of spawning females (N), the

204   mean spawning date (μ), and its variance (σ) in each population, whereas the synchrony

205   model has another main parameter, a synchrony coefficient (α) that determines the

206   strength of social interactions. We also constructed observation models for redd counts

207   to deal with stochasticity and incomplete field data (i.e., variations in the number of

208   redds a female produces and unequal intervals of field surveys).

209

210   *Reproduction schedule and null model*

211   Suppose that in population k ($k = 1, \ldots, K = 30$) there are N_k females and that the best

212   spawning date of female i, d_i, ($i = 1, \ldots, N_k$) is a random sample from the normal

213   distribution of mean μ_k and variance σ_k^2;

214    $d_i \sim N(\mu_k, \sigma_k^2)$.   (1)

215   The assumption of a normal distribution reflects both physiological and environmental

216   effects on reproductive schedules. This was supported by the redd counts summed over

217   all the tributaries, which fit the normal distribution well. The best spawning date is the

218   most appropriate timing of oviposition in terms of egg ripeness. Intensive hatchery

219   programs for salmonids (i.e., artificial breeding) revealed that fertilization success

220   quickly drops 1-2 weeks after ovulation (Craik and Harvey 1984; Brooks et al. 1997).

221   This also indicates that females can flexibly change the spawning date for a week or two,

222   which we modeled as a result of social interactions in the synchrony model described

223   below.

224

225   Female i is assumed to construct b_i redds according to the categorical distribution,

226    $b_i \sim Categorical(B_1, B_2, B_3,)$,   (2)

227   in which B_h (h = 1, 2, 3) refers to the probability that a female produces h redds. Based

228   on a detailed observational study of stream Dolly Varden (Kitano 1995), we set $B_1 = 0.1$,

229    $B_2 = 0.6$, and $B_3 = 0.3$. Thus, one female produced $1 \times 0.1 + 2 \times 0.6 + 3 \times 0.3 = 1.8$ redds

230   on average. This system model was used as a null model.

231

232   *Reproduction model with synchrony*

233   In order to add socially induced synchrony in spawning behaviors, we assumed that in

234   day d, all females in population k with $d_i = d$ spawn (if they have not spawned yet); after

235   that, female j with later d_j ($d_i < d_j$) may spawn synchronously with probability

236    $\exp(-(d_i - d_j)^2 / 2a_k^2)$.   (3)

237   In other words, if the best spawning dates are close, female j tends to go to spawn with

238   other females. Therefore, the adjustment of spawning timing can be considered to be

239   socially induced synchrony. In this paper, we called a_k the "synchrony coefficient." This

240   system model contains four parameters ($N_k, \mu_k, \sigma_k, a_k$) for each population.

241

242   Figure 1 illustrates examples of redd count data simulated by the synchrony model and

243   the null model with different population sizes (i.e., 300 females vs. 20 females). In the

244   null model, redd counts nearly follow the normal distribution when the population size

245   is large (Fig. 1a). This smooth fitting is deformed to a heavily fluctuating pattern when

246   synchrony is included (Fig. 1b). Similar patterns are often observed in natural

247   populations (Petersen and Hess 1991; Plot et al. 2012). However, even in the null model,

248   random sampling from the normal distribution, together with the variation caused by the

249   number of redds produced by each female, often exhibits fluctuation when the

250   population size is small (Fig. 1c). Thus, although the synchrony amplifies fluctuations

251   (Fig. 1d), such patterns can be produced without synchrony.

252

253   *Observation model for redd counts*

254   Suppose that in population k redd counts were conducted on day $D_1^k, ..., D_{T_k}^k$. On day

255   D_t^k ($t = 1, …, T_k$) we expect to observe redds produced between D_{t-1}^k and D_t^k. Let d_i' be

256   the actual spawning date of female i ($d_i' \leq d_i$ because of synchrony). The observed

257   number of redds, O_t^k, can be written as

258    $$O_t^k = \sum_{i=1}^{N_k} b_i \cdot 1(D_{t-1}^k < d_i' \leq D_t^k), \quad (4)$$

259   in which 1( ) is the indicator function; = 1 if the inside parenthesis is true or = 0 if false.

260   Since we did not know the actual start dates of spawning, we set $D_0^k = D_1^k - 5$.

261   Although arbitrary, few individuals spawn in mid-August (I. Koizumi, personal

262   observation), few redds were found on the initial dates, and this setting affected the

263   results little.

264

265   *Parameter estimation for null model*

266   For simplicity, because the expected redd counts is given by $1.8N_k$, we estimated the

267   number of females (N_k) by

268   {the observed redd counts in population k}/1.8

269   and rounded to an integer. For the other parameters (μ_k, σ_k), denoting as

270    $P_t^k = \int_{D_{t-1}}^{D_t} f_N(x; \mu_k, \sigma_k^2)dx \quad (t = 1, \ldots, T_k),$ (5)

271   and assuming that $\{O_t^k\}$ are random samples from the multinomial distribution

272    $(N_k, P_1^k, \ldots, P_{T_k}^k)$, we conducted the maximum likelihood method. This simplified

273   estimation did not reflect the stochasticity caused by equation (2), but practically, this

274   estimation provided almost equal results to those when the ABC method described

275   below was applied to the null model. Hence, we show only the results using the

276   likelihood estimation.

277

278   *Approximate Bayesian computation (ABC) and approximate kernel Bayesian (AKB)*

279   *algorithm*

280   Because the derivation of a likelihood equation is difficult for the synchrony model, we

281   applied the ABC method for estimating parameters (i.e., N_k, μ_k, σ_k, a_k). In general, the

282   algorithm of the ABC method is summarized as follows (Sunnåker et al. 2013):

283   (1)   Calculate summary statistic(s) from observational (real) data.

284   (2)   Given a certain model (synchrony model in the present case), perform simulations

285   many times, each with a set of parameter(s) drawn from the prior distribution(s)

286   arbitrary assumed (e.g. uniform distribution).

287   (3)   Calculate summary statistic(s) for each simulation.

288   (4)   Decide for each simulation whether its summary statistic(s) is sufficiently close to

289   that of the observed data.

290   (5) Approximate the posterior distribution(s) of parameter(s) associate with accepted

291   simulations.

292

293   Summary statistics are generally used for comparing simulated and observational data

294   because simulated data consists of time-series vectors and are rarely "sufficiently close"

295   to the observed data. Thus, the choice of summary statistics is the first problem with the

296   ABC method (Sunnåker et al. 2013). The second problem is that, in general, even when

297   summarized, most of the simulated data are far from the real data, and most of the

298   parameter values are discarded. Therefore, we need a huge number of simulations (e.g.,

299   100,000 or greater), which constrains calculations. The third problem is that there is no

300   established criterion for determining what is "sufficiently close."

301

302   To overcome these problems, Fukumizu et al. (2013) introduced a new method, and

303   Nakagome et al. (2013) applied this to a population genetics study. The method is called

304   the kernel-ABC algorithm, or the approximate kernel Bayesian algorithm; hereafter, we

305   call it the AKB algorithm. In this method, weights are given to sampled parameters

306   depending on the closeness between the real and simulated data, with adjustment by the

307   ridge regression. Fukumizu et al. (2013) proved that the weighted sum over all the

308   sampled parameters converges to the posterior mean when the number of simulations

309   increases. Unlike most of the ABC methods, the AKB algorithm uses all the sampled

310   parameters from the prior distribution and, therefore, does not necessarily require so

311   many simulations. In summary, the AKB algorithm solves the second and the third

312   problems of the ABC method.

313

314 *Summary statistics*

315 We used the following four summary statistics:

316 S_1: Number of redds $\quad S_1^k = \sum_{t=1}^{T_k} O_t^k$. (6)

317 This is primarily used to estimate the number of females (N_k).

318 S_2: The sample mean over spawning dates $\quad S_2^k = \dfrac{\sum_{t=1}^{T_k} D_t^k O_t^k}{S_1^k}$. $\quad$ (7)

319 This is primarily used to estimate the mean spawning dates (μ_k). Because redds were

320 produced between $D_{t-1}{}^k$ and D_t^k, this statistic is expected to be later than the true mean.

321 If synchrony actually occurred, S_2^k becomes earlier.

322 S_3: The standard deviation (SD) of spawning dates $\quad S_3^k = \sqrt{\dfrac{\sum_{t=1}^{T_k} (D_t^k - S_1^k)^2 O_t^k}{S_1^k}}$. $\quad$ (8)

323 This is primarily used to estimate the SD of spawning dates (σ_k).

324 S_4: Auto-covariance of time-lag =1. $\quad S_4^k = \sum_{t=F^k}^{E^k-1} (O_t^k - \overline{O}_t^k)(O_{t+1}^k - \overline{O}_t^k) \}/(E^k - F^k - 2)$

325 (9)

326 This statistic quantifies the degree of fluctuations and is used for estimating the

327 synchrony coefficient (a_k). Because our model is not stationary, and O_t^ks are expected to

328 take large values around μ_k, the auto-covariance formula for stationary time-series

329 (subtract m instead of $\overline{O_t^k}$ where m refers to the overall mean) is not applicable. Instead,

330 equation (9) subtracts the moving average from $t-1$ to $t+2$ for pair (t, $t+1$). F^k and E^k

331 is the first and the last day when non-zero redd count was obtained, respectively. These

332   were for excluding zeros before and after the spawning period, which otherwise

333   decreased the value of S_4 and weakened the power for quantifying the fluctuations

334   produced by the synchrony.

335

336   The quantification of fluctuations by summary statistic S_4 can be seen in the simulated

337   patterns in Figure 1; S_4 decreased from -6.3 (a) to -116.7 (b) if synchronicity operated.

338   On the other hand, if the population size was small, S_4 only slightly decreased from

339   -0.71 (c) to -0.83 (d).

340

341   *Prior distribution and AKB-algorithm*

342   Prior distributions and the details about the AKB-algorithms are summarized in

343   Supplementary Appendix B. Hereafter, the estimate of a parameter derived by the AKB

344   algorithm is called as the AKB estimate. We also performed a conventional

345   ABC-method for comparative purposes, and the method and its results are briefly

346   summarized in Supplementary Appendix C.

347

348   *Goodness-of-fit*

349   In order to check if the model using AKB estimates actually explains the data, we used

350   another summary statistic that was not used in the AKB algorithm. Let

351     $H_t^k = |O_{t+1}^k - O_t^k| \quad (t = 1, \ldots, T_k - 1) \quad\quad (10)$

352   be the difference in the number of redds between two consecutive surveys. We sorted

353   them from largest to the smallest (let the sorted H_t^ks be $(H_{(1)}^k, \ldots, H_{(T_k-1)}^k)$ and

354   accumulated them;

355 $$G_s^k = \sum_{u=1}^{s} H_{(u)}^k . \quad (11)$$

356 We also calculated these statistics for simulated data using AKB estimates and

357 computed their 2.5 and 97.5 percentiles for each u. If G_s^ks for the real data were all

358 inside the percentiles, the model was evaluated as adequately explaining real data. The

359 same goodness-of-fit was conducted for the null model. Note that $G_{T_k-1}^k$ is equal to the

360 descriptive statistics used in Henson et al. (2010) for quantifying synchrony.

361

362 *Accuracy of AKB estimates*

363 In order to check if AKB estimates were close to the true parameter values, we

364 simulated redd counts using given parameter values 100 times and then applied the

365 AKB algorithm and checked if the AKB estimates obtained were close to the true

366 values.

367

368 We also simulated redd count data by the null model (without synchrony) and applied

369 the AKB algorithm. Then, the AKB estimates of a should be close to 0. Thus, this

370 simulation provides the range of synchrony coefficient that can be explained by the null

371 model.

372

373 *Environmental factors and synchrony among populations*

374 Synchronous spawning might also have been triggered by environmental cues. In

375 salmonids, which are stream-dwelling poikilothermic species, the main environmental

376 factors affecting spawning activities are changes in photoperiod, water temperature, and

377 water discharge (Jonsson 1991). Photoperiod changes gradually throughout the breeding

378 season and can affect reproductive seasonality, but this cannot be a proximal factor for

379 reproductive synchrony. Therefore, we examined the effects of temperature and

380 discharge on the daily spawning activities of Dolly Varden in each of 30 local

381 populations.

382

383 We used the data on ambient temperature and precipitation recorded in one of the

384 meteorological stations within the study area as surrogates of water temperature and

385 discharge, respectively. Since the study area is not spatially widespread (< 10-20 km;

386 Supplementary Fig. S1), local differences should be small (e.g., correlation coefficients

387 of daily precipitation among three meteorological stations within the study area were >

388 0.92 ($P < 0.0001$)).

389

390 We first applied the Poisson regression to the number of redds observed (dependent

391 variable) and the accumulated precipitation (mm) and changes in temperature

392 (maximum minus minimum temperature) during the consecutive surveys (independent

393 variables). In addition, since there were many zero data especially in the beginning and

394 end of breeding season, we used the zero-inflated Poisson (ZIP) regression (Zeileis et al.

395 2008) with the same dependent and independent variables. These regression analyses

396 were performed using statistical R software version 2.15.2 (R Development Core Team

397 2012).

398

399 This exploratory analysis did not reflect the normally distributed redd counts with

400 different means and SDs. If an environmental factor influenced the breeding activity,

401 differences between the observed redd counts and the expectations from the null model

402   (residuals) should be correlated with the environmental data. We thus calculated the

403   correlation coefficients between residuals and the precipitation or temperature data

404   described above.

405

406   If some environmental factors affected the breeding activity, synchrony among local

407   populations would be expected. We therefore calculated pairwise cross-correlation

408   coefficients for redd counts over the 30 local populations: the mean value and the 95%

409   confidence interval were calculated with 1000 bootstrap resampling (Bjørnstad et al.

410   1999). Because observation dates differed, we adjusted redd count data to every 5-day

411   interval from September 1 to December 24 and computed correlation coefficients.

412

413   In addition, since only reproductive seasonality should produce a certain level of

414   synchrony, we have checked whether the observed cross-correlations could be produced

415   without taking environmental data into account. For this purpose, we simulated redd

416   count data by the synchrony model using the AKB estimates 1000 times, calculated

417   cross-correlations and compared them with the observed values. If the observed value

418   exceeds the upper 95% over the simulated data, effects of some environmental cues are

419   suggested. We used population pairs for T7-T7.5-T8-T9, T16-T17, and T50-T50.5

420   because these pairs were spatially close and had exactly the same observation dates.

421

422   **Results**

423

424   General description of spawning activity

425 The spawning season of Dolly Varden lasted 3 to 4 months and peaked in mid-October

426 (Fig. 2a; Supplementary Fig. S2). A total of 1206 spawning redds (934 completed redds

427 and 272 direct spawning behavior) were observed from the 30 tributaries. On average,

428 40 redds were observed in each tributary (range: 9-108), which is equivalent to 22 (=

429 40/1.8) females (range: 5-60 females). Spawning periods overlapped widely and

430 continued for long periods (> 3 months) for most of the tributaries (Supplementary Fig.

431 S2). Multiple spawning aggregations were often observed in some tributaries (the left

432 column in Fig. 3; Supplementary Fig. S2), similar with the patterns produced by the

433 synchrony model (Fig. 1b, d). In addition, gathering of mature adults (10-20

434 individuals) were often observed in some pools of the tributaries before such spawning

435 aggregations.

436

437 Synchrony model vs. null model

438 Table 1 summarizes values of the four summary statistics, the estimates of parameters in

439 the null model and the synchrony model for the 12 populations that had relatively large

440 numbers of redds ($\geq$ 40) (those for all the 30 populations are shown in Supplementary

441 Table S2). For mean spawning dates (μ_k), the null model exhibited earlier mean

442 spawning dates than the observed means, and when the synchrony was included, the

443 estimates tended to become later, as mentioned in the *Summary Statistics* section. The

444 AKB estimates for the number of females were almost the same as $S_1/1.8$.

445

446 The goodness-of-fit test revealed that the synchrony model explained all the patterns

447 observed, but the null model failed for four (33%) populations (Table 1, at the 90%

448 level), meaning significantly more aggregation and fluctuations in the reproductive

449 timing. As demonstrated in Fig. 1, the null models often produced fluctuating redd

450 counts that were visually indistinguishable from those simulated by the synchrony

451 models. However, the summary statistic S_4 successfully differentiated the two patterns

452 and G-values in equation (11) showed sufficient fit for the synchrony model but

453 insufficiency for the null model (the top and the middle rows in Fig. 3). In contrast, for

454 the populations where the null models were not rejected, although the observed redd

455 counts looked fluctuated, the values of S_4 were not so low and the null models produced

456 similar patterns (e.g., the bottom row in Fig. 3).

457

458 Accuracy of AKB estimates

459 When we simulated redd count data using the AKB estimates in Table 1 and applied the

460 AKB algorithm to the simulated data 100 times for the above four populations where

461 the null models were rejected, we obtained values around the true value (Supplementary

462 Fig. S3), and the the SDs of these estimates were small, ranging from 1.15 to 1.28.

463

464 When the AKB algorithm was applied to count data simulated by the null model, most

465 of AKB estimates were 1-3 and less than 5% exceeded the AKB estimates for the

466 observed data (Supplementary Fig. S3), except for T20 that had relatively small

467 synchrony coefficient (2.74).

468

469 Degree of spawning synchrony

470 Figure 4 illustrates how the synchrony operated on the breeding activity. The mean over

471 the above four populations (i.e., null models were rejected) was 4.00, and under this

472 degree of synchrony, 50% probability that a female synchronizes spawning was 4-5

473   days before her best spawning date (Fig. 4a), and almost all females went to spawn 3

474   days before the best spawning date (on the assumption that some other females spawned

475   every day). The average over the 30 populations was 2.77 (Supplementary Table S2),

476   and this synchrony coefficient also involves spawning of almost all females before the

477   best spawning date (Fig. 4). If $a < 1.0$, few females go to span before the best spawning

478   date (Fig. 4), although we found only one such population (Supplementary Table S2).

479

480   Environmental factors and synchrony among populations

481   Neither the Poisson nor ZIP regressions showed clear effects of precipitation or

482   temperature on the spawning activity of the 30 local populations of Dolly Varden

483   (Supplementary Table S3). Poisson regression coefficients for precipitation were

484   significantly positive in 2 populations (2/30 = 6.7%), significantly negative in 6

485   populations (20%), and non-significant in 22 populations (73.3%). However, none were

486   significant after Bonferroni correction (i.e., $P = 0.05/30 = 0.0017$). The regression

487   coefficients for temperature were significantly positive in 6 populations (20%),

488   significantly negative in 2 populations (6.7%), and non-significant in 22 populations

489   (73.3%). In this case, only 2 were significant after Bonferroni correction. ZIP regression

490   analysis showed similar results, although the populations showing significance and the

491   directions of the regression coefficients were often different (Supplementary Table S3).

492

493   We further investigated the effects of precipitation and temperature by residual analysis.

494   However, no significant effects were detected in any of the 30 populations, in which

495   some populations showed positive values whereas others showed negative ones (Fig. 5).

496

497   The overall level of synchrony in breeding activity was positive among the 30

498   populations, but relatively low (mean $r = 0.276$, 95% bootstrap CI $= 0.200$-0.357,

499   Supplementary Fig. S4). We further analyzed the data with the synchrony models taking

500   the seasonality into account. For the three groups of spatially adjacent populations with

501   the same observation dates (T7-T7.5-T8-T9, T16-T17, and T50-T50.5), the observed

502   cross-correlations were not high (mean $r = 0.258$) and were all within confidence

503   intervals obtained by 1000 times simulations (Fig. 6).

504

505   These results collectively showed low or non-consistent environmental effects on

506   breeding activity and also low breeding synchrony between and among the populations

507   inhabiting the 30 tributaries studied.

508

509

510   **Discussion**

511

512   Our models suggested the existence of socially induced reproductive synchrony in some

513   local populations of Dolly Varden. Lack of environmental effects and/or synchrony

514   among local populations further supported the notion that synchronous spawning was

515   triggered by social interactions. As far as we know, this is the first study that applies

516   ABC to animal behavior and also that suggests socially induced reproductive synchrony

517   in stream fish. So far, reproductive synchrony by social stimuli has been indicated

518   mostly in mammals and birds from which we can obtain direct evidence of complex

519   social interactions (French and Stribley 1987; Sillero-Zubiri et al. 1998; Jovani and

520   Grimm 2008; Henson et al. 2010, but see Plot et al. 2012). Our approach, using

521   individual-based modeling and statistical techniques that link models with field data,

522   explored a methodological framework that can be applied to a broad range of species,

523   especially when direct observations of social interactions and mating behavior are

524   difficult.

525

526   ABC framework in behavioral ecology

527   We combined three modelling frameworks (i.e., an individual-based model, a

528   hierarchical Bayesian model, and ABC) that are well established in their own fields

529   (Grimm and Railsback 2005; Royle and Drazio 2008; Beaumont 2010). Since socially

530   induced synchrony is triggered by surrounding individuals, individual-based modeling

531   was an appropriate method to use. Hierarchical modelling was also necessary because

532   field data usually contain stochastic processes, which were incorporated in the

533   observation model. The advantage of ABC, then, was to be able to jointly estimate the

534   parameters even though the derivation of the likelihood is practically impossible. These

535   modelling frameworks were highly compatible since many essential ideas are shared

536   with one another, such as simulation techniques and Bayes theorem. Since animal

537   behavior is an individual-level phenomenon, our approach could be effective for a wide

538   range of behavioral studies, especially when a global pattern can be generated by

539   individual behaviors (e.g., Wood and Acland 2007; Jovani and Grimm 2008; Attanasi et

540   al. 2014; Murakami et al. 2014; Calovi et al. 2015).

541

542   We demonstrated the importance of setting an appropriate null model for investigating

543   relatively weak patterns of socially induced reproductive synchrony (see also, Henson et

544   al. 2010). Intermittent breeding patterns are often used as an indication of socially

545   induced synchrony (Petersen and Hess 1991; Plot et al. 2012), but such patterns can be

546   generated by stochasticity alone. Appropriate summary statistics helped us to judge

547   which data required the synchrony and which did not. In addition, a synchrony index is

548   often tested against the null hypothesis that individuals breed randomly in time

549   (Marsden and Evans 2004). Reproductive timing, however, is often normally-distributed

550   (Munro et al. 1990) and, therefore, calculation of deviations from a normal distribution

551   is required.

552

553   Our study showed that the synchrony model was not always necessary to explain the

554   field data and that the degree of synchrony differed over local populations. The

555   sufficient fit of the null model for some populations may be because the presence of

556   breeding synchrony is conditional or environmentally dependent. Obviously, it is

557   difficult to time breeding with other individuals when population density is low (e.g.,

558   less than 10 females spawned in some populations, Supplementary Table S2). Also,

559   breeding synchrony may be beneficial only in certain situations, such as when breeding

560   areas are limited or when the operational sex ratio is high (see below). It is also possible

561   that there simply was not enough statistical power due to the small numbers of redd

562   counts in some tributaries. Note that non-rejection of the null model does not

563   necessarily mean the absence of reproductive synchrony; all the data were also

564   explained by the synchrony model. A more intensive survey, such as everyday census,

565   would increase detection power. However, there is a trade-off between collecting data

566   intensively in fewer populations or collecting that data extensively in multiple

567   populations but with lower quality. Nonetheless, we were able to detect significant

568   synchrony in multiple populations. In addition, the strengths of social interaction could

569   be evaluated by the synchrony coefficients a even when the synchrony models were

570   statistically differentiated from the null models. Importantly, the synchrony coefficients

571   indicate that breeding timing can be adjusted for up to 7 days by the synchrony, which is

572   consistent with known degree of plasticity in reproductive timing in salmonids (Craik

573   and Harvey 1984; Brooks et al. 1997).

574

575   Reproductive synchrony in fishes

576   Synchronous mass spawning is well known in some marine fishes, such as coral reef

577   fishes and intertidal spawners (Yamahira 1996; Craydon 2004; Byrne and Avise 2009).

578   These are mostly associated with lunar or tidal cycles, and the adaptive significance

579   may be predation satiation (several hypotheses in Craydon 2004). Socially induced

580   synchrony is also suggested in a damsel fish based on intermittent spawning patterns

581   similar with Fig. 1 (Petersen and Hess 1991). In this case, the adaptive mechanism is

582   proposed as avoiding filial cannibalism, which we also discuss later.

583

584   Spawning aggregations or group spawning are also reported in many freshwater fishes,

585   such as cyprinids, lampreys, and salmonids (Sakai 1995; Blanchfield and Ridgway

586   1997; Jang and Lucas 2005). However, surprisingly few studies have focused

587   specifically on reproductive synchrony, including the predation satiation hypothesis,

588   which seems particularly possible in sea-run salmonids by bear predation (Quinn et al.

589   2014). In freshwater (not sea-run) salmonids, two studies indicate reproductive

590   synchrony where 60-90% of spawning occurred within a few days or weeks

591   (Blanchfield and Ridgway 1997; Sato and Harada 2008). They do not discuss the

592   possible effects of social interactions; rather an environmental factor (e.g., precipitation,

593   temperature) was proposed as the proximate driver (Blanchfield and Ridgway 1997).

594   Interestingly, however, the gathering of mature individuals in some pools or near

595   spawning sites was also observed before the synchronous spawning (Blanchfield and

596   Ridgway 1997; T. Sato, personal communication; see also White 1930), indicating

597   some social interactions. Overall, it would be fruitful to reexamine the breeding ecology

598   of fishes in terms of reproductive synchrony for better understanding of its evolutionary

599   significance and ecological consequences (Ims 1990a).

600

601   The major adaptive significance of breeding synchrony is generally believed to be

602   predation satiation (Darling 1938; Janzen 1971). However, this is unlikely in the

603   populations of Dolly Varden. Ims (1990b) has demonstrated theoretically that predation

604   satiation would not be achieved when breeding occurs synchronously within but

605   asynchronously among local populations. In such cases, mobile predators efficiently

606   consume local prey appearing at different times in different areas. This may be exactly

607   the case for Dolly Varden in the Sorachi River. Blakiston's fish owls *Bubo blakistoni*

608   were observed at different times and in different tributaries preying on spawning Dolly

609   Varden (I. Koizumi, personal observation).

610

611   Blanchfield and Ridgway (1997) hypothesized that breeding synchrony in salmonids

612   occurs to avoid sexual harassment or egg cannibalism by satellite males. Some males

613   actively urge females to spawn, sometimes by displaying aggressive behavior (Garner et

614   al. 2010). Similarly, some satellite sneaker males eat eggs right after oviposition

615   especially when the density of sneakers is high (Maekawa and Hino 1990). Synchrony

616   generally reduces the operational sex ratio (OSR) so that each spawning female is

617   surrounded by fewer males (Ims 1988). Thus, synchronous breeding may be a female

618   strategy to reduce harassment and/or filial cannibalism by inducing more monogamous

619   mating. Another potential benefit of synchronous breeding in salmonids is to reduce

620   redd superimposition (Blanchfield and Ridgway 1997). When spawning areas are

621   limited within streams, females dig nests where other females have spawned, which can

622   cause egg death in old nests (van den Berghe and Gross 1989). Therefore, by spawning

623   simultaneously with other females, they can avoid redd superimposition.

624

625   We also propose that the breeding synchrony in Dolly Varden may relate to female

626   choice. Synchronous breeding generally decreases OSR but could also result in male

627   monopolization when dominant males access multiple females (Ims 1988). In fact,

628   breeding groups were often formed within limited stream reaches (e.g., less than 50 m, I.

629   Koizumi, personal observation) and also perfect synchronous egg depositions among

630   females seems difficult. On days when we observed synchronous breeding events, many

631   males were active within limited breeding reaches, which could result in strong sexual

632   selection. Among the large number of competing males, females can directly (via

633   female choice) or indirectly (via male-male competition) mate with the best males. This

634   can be referred to as induced polygamy by females, the opposite strategy discussed in

635   the previous paragraph (i.e., induced monogamy). These alternative hypotheses could be

636   separated by genetic parentage analysis to see if dominant males monopolize

637   reproductive success or if subdominants fertilize eggs due to reduced operational sex

638   ratios.

639

640   **Conclusion**

641

642   This study demonstrated the efficiency of combining intensive field data, modeling and

643   parameter estimation for the study of animal behavior. Elementary statistical techniques

644   such as correlations and generalized linear models do not always work because they

645   require the independence of data while synchrony inevitably produces non-independent

646   time-series data. Our results have shown the importance of intensive field studies

647   covering large numbers of populations and frequent surveys: otherwise, we would have

648   missed variations among the populations in rejection/acceptance of the null model,

649   environmental effects, and values of the synchrony coefficients. In addition, our study

650   has demonstrated the importance of adequate setting of a null model; it is not difficult to

651   make a complex model that can explain given data even when a simpler model can

652   explain the data. Feedbacks between field studies and modeling together with finding a

653   suitable null model will advance the studies of behavioral ecology.

654

655

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657

663

664 **References**

665

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817

818

819 **Figure legends**

820

821 Fig. 1

822 Examples of redd count data simulated by the synchrony model (b, d) and the null

823 model without synchrony (a, c) when a population size is large (300 females, a, b) and

824 small (20 females, c, d). Date was calculated taking 1 September as day 1. Observations

825 are made every 3 days. The thin lines indicate a normal distribution of the best

826 spawning dates for this population (mean = 60, SD = 15). The values of summary

827 statistic S_4 (auto-covariance of time-lag = 1, measuring the degree of synchrony) are

828 indicated for each data.

829

830 Fig. 2

831 (a) Daily number of redds (spawning nests) observed during the spawning season of

832 stream-dwelling Dolly Varden in 30 tributaries of the Sorachi River, Hokkaido, Japan,

833 (b) mean (solid line), highest and lowest (dashed lines) daily ambient temperature, and

834 (c) daily precipitation in the study area.

835

836 Fig. 3

837 The observed redd counts (first column), an example of redd counts simulated by the

838 synchrony model (second column) and the null model (third column), and the

839 goodness-of-fit by equation (19) for the synchrony model (fourth column) and the null

840 model (fifth column) for population T7 (the top row), T9 (the middle row) and T10a

841 (the bottom row).

842

843 Fig. 4

844 The synchrony curve (a) and the cumulative probability that the females do not

845 synchronize (b) when $a = 4.00$ (the mean over the four populations where the null

846 model was rejected), $a = 2.77$ (the mean over all the 30 populations) and $a = 1.00$ (an

847 example of very weak synchrony).

848

849 Fig. 5

850 Correlation coefficients of residual redd counts and environmental factors (i.e.,

851 precipitation and temperature).

852

853 Fig. 6

854 Tests of the synchrony for the three groups of eight spatially adjacent populations. Black

855 circles indicate the observed cross-correlation coefficients, and minus symbols indicate

856 the 2.5, 50 and 97.5 percentiles (from the bottom to the top) over 1000 simulations.

857

858

859

860 Table 1. Summary statistics, parameter estimates by null model and synchrony model for 12 local populations.

861

Populations	T7	T7.5	T8	T9	T10a	T10	T11	T20	TS	T25	T28	IK
Summary statistics												
Number of redds S_1	63	58	40	49	108	72	67	46	47	76	101	63
Mean spawning date S_2	10/15	10/13	10/22	10/12	10/5	10/8	10/17	10/11	10/20	10/26	10/24	10/13
SD over spawning date S_3	14.98	15.63	11.28	13.47	21.75	13.63	19.28	19.95	16.55	18.40	18.45	21.12
Auto-covariance S_4	-7.08	-1.58	-2.48	-5.66	-1.47	-0.92	-0.91	-1.41	-1.77	-1.67	-9.58	-0.85
Null model												
$S_1/1.8$	35	32	22	27	60	40	37	26	26	42	56	35
Mean spawning date μ_k	10/13	10/11	10/20	10/10	10/4	10/6	10/17	10/14	10/18	10/23	10/21	10/10
SD σ_k	14.34	15.02	11.09	13.25	25.42	13.58	22.66	27.57	16.03	18.20	17.88	21.79
Synchrony model (AKB-estimate)												
Number of females N_k	34	32	22	27	60	40	37	26	26	42	56	35
Mean spawning date μ_k	10/15	10/12	10/22	10/12	10/3	10/6	10/15	10/9	10/19	10/24	10/24	10/10
SD σ_k	14.78	15.68	11.30	13.41	22.26	13.84	19.06	20.1	16.42	18.23	18.43	21.40
Synchonicity coefficient a_k	4.51	2.26	2.69	4.57	1.97	1.59	0.91	2.74	2.36	1.76	4.19	1.42
Rejection of null model [a]	**			**					*		**	

a) **: 5%, *: 10%

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