Socially induced reproductive synchrony in a salmonid: an approximate Bayesian computation approach

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.

Keywords: breeding synchrony, individual-based modelling, hierarchical Bayesian modeling, time-series count data, spawning aggregation, synchronous spawning

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

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

Compared to environmentally induced synchrony, socially induced reproductive synchrony has been demonstrated much less in wild populations. Because experimental manipulation and determination of social cues are generally difficult, inductive analyses from observed patterns have often been used (Ims 1990a). For example, when individuals who are in close proximity reproduce more synchronously than those who are further apart, socially induced synchrony will be inferred (Sillero-Zubiri et al. 1998; Evans et al. 2009). However, this can be applied only to sedentary species or species with breeding nests, such as birds and some mammals. In addition, spatial analysis cannot separate social cues from local environmental cues (spatial autocorrelation). Another inductive method is to show the lack of correlation between candidate environmental factors and reproductive timing (Ims 1990a), but this rather passive approach has the potential to be misleading because it overlooks unmeasured environments. Inductive analyses are also generally challenging because socially induced synchrony has a tendency to result in weak patterns. Unlike mast seeding or coral spawning, patterns of socially mediated reproduction are often ambiguous because the effects of social stimuli narrowly focus around a focal individual rather than an entire population. Such weak temporal clusters of reproduction could also result from stochasticity alone, especially when the population size is small (e.g., Henson et al. 2010; see also a simulation result below).

As an alternative to inductive analyses, individual-based models can be used to investigate underlying mechanisms for observed patterns (Grimm and Railsback 2005).

In fact, this approach has been used successfully to model individual-based synchronous behaviors, such as flocks of birds, schools of fishes, and swarm of solider crabs (Wood and Acland 2007; Gunji et al. 2012; Attanasi et al. 2014; Murakami et al. 2014; Calovi et al. 2015), as well as reproduction (Jovani and Grimm 2008). In these studies, individuals are given a kind of autonomy, where they are assumed to choose each behavior depending on social interactions with other individuals (e.g., follow the leader or neighbor(s)) with stochastic variability. Even in such simple models, however, global patterns formed by the models are often not directly compared with observational data, or statistical techniques have not been fully utilized. For example, optimization of unknown parameters is frequently overlooked, and the degree of fit of the proposed models is not quantitatively evaluated. This is primarily because the data on individual behavior are not independent due to synchronicity, meaning that statistical models requiring independence of observations (e.g., generalized linear models) are not directly applicable. In addition, including social interactions makes the derivation of the likelihood function, one of the most essential parts in statistical modeling, exceedingly difficult.

The approximate Bayesian computation (ABC) is a promising tool for linking statistical models to real data in such situations (Beaumont et al. 2002; Beaumont 2010; Sunnåker et al. 2013). Instead of calculating the exact likelihood, the ABC method approximates it by numerical simulations and comparisons with the observed data. Thus, ABC has the potential to be applied to a broad range of complex models (Sunnåker et al. 2013). However, until recently, ABC has been used primarily in population genetics studies (Beaumont et al. 2002; Beaumont 2010). In recent years, its use has been expanded to

other disciplines, such as ecology (e.g., Jabot and Chave 2009), but not yet to behavioral ecology. Despite the considerable potential and solid mathematical foundations of ABC, there still remain some challenges, such as choosing appropriate models and summary statistics (Sunnåker et al. 2013). Further applications and improvements of the technique are therefore needed.

The aims of the present study are (1) to investigate whether socially induced reproductive synchrony exists in a stream fish; (2) to estimate ecologically relevant parameters such as the strength of social interactions; (3) to discuss ultimate factors causing the reproductive synchrony, if any; and (4) to evaluate our new modeling framework, which combines an individual-based model (Grimm and Railsback 2005), a hierarchical Bayesian model (Royle and Drazio 2008), and the approximate Bayesian computation (Beaumont 2010), for behavioral studies. To this end, we first conducted intensive field studies and obtained detailed reproductive datasets for a stream-dwelling salmonid in northern Japan. We then developed individual-based reproductive models with social interactions (i.e., the synchrony model) and without them (i.e., the null model), which also incorporated stochasticity, non-uniform reproductive schedules, and observation processes. Simulated patterns from the alternative models were compared with the observational data and the parameters were estimated by the modified version of the ABC method proposed by Nakagome et al. (2013).

Materials and methods

Study system

We investigated reproductive synchrony in the metapopulation of Dolly Varden charr *Salvelinus malma* in the upper Sorachi River system, central Hokkaido, Japan (Koizumi 2011). The upper Sorachi River (470 km^2 watershed area above the Kanayama Reservoir) consists of more than a hundred small tributaries (< 500 m in length, 0.5-3.0 m in width, 0.01-0.5 m^3s^{-1} in water discharge) that directly flow into the larger mainstem (5-30 m in width, 1.0-10 m^3s^{-1} in discharge), generating significant habitat heterogeneity between tributaries and the mainstem (Koizumi and Maekawa 2004). Dolly Varden spawn only in small tributaries and the uppermost reaches of large tributaries or the mainstem (Koizumi et al. 2006a). They form a metapopulation structure with each tributary used as a local habitat. Genetic composition and demography are partially independent in each tributary (Koizumi and Maekawa 2004; Koizumi et al. 2006b, 2008). Therefore, local tributary populations are considered as good spatial replicates. There are several fish species inhabiting the Sorachi River, such as white-spotted charr *Salvelinus leucomaenis* and freshwater sculpin *Cottus nozawae* (Koizumi et al. 2012). However, Dolly Varden dominate small tributaries (Koizumi et al. 2006a, 2012) and, thus, spawning nests (called “redds” in salmonid literature) in tributaries are unambiguously determined as Dolly Varden redds.

Redd counts survey

Of the more than a hundred small tributaries, we chose 30 (Supplementary Fig. S1 and Table S1) for the breeding survey based on the following criteria: relatively easy to access, whole tributary survey possible (i.e., from the headwater to the junction with the mainstem), and easy to observe spawning redds due to shallow depth, low velocity, and

low cover habitat. Only one tributary (T54) had a small erosion control dam, which was 106 m upstream from the junction, and we surveyed this reach. In three long tributaries (IK, T51, T59.5) and in one branch of a tributary (T13b), we surveyed only core spawning sites in the uppermost reaches.

To evaluate reproductive timing we conducted a standard redd count procedure in salmonids (Gallagher et al. 2007) from late August to the end of December 2007, covering the entire spawning season. Surveys were conducted every 3-5 days for most of the breeding period in each tributary until two weeks after the final redd was observed. Occasional visits in a reference tributary confirmed that no spawning occurred after January. Since identifying spawning redds can sometimes be difficult (Gallagher et al. 2007), we carefully evaluated the procedure in advance (Supplementary Appendix A). When we observed spawning behavior (i.e., construction of redds, often accompanied with multiple males), we recorded them as redds on the same day.

Modeling procedures

Our modeling combined individual-based modeling (Grimm and Railsback 2005), hierarchical Bayesian modeling (Royle and Drazio 2008), and approximate Bayesian computation (Sunnåker et al. 2013) approaches. Hierarchical Bayesian modeling integrates different levels of models into a single statistical framework by constructing a system model and observation model: the former represents a biological process we are interested in, whereas the latter represents a sampling process. These models are

integrated into a hierarchy under the Bayesian framework to jointly estimate each of the parameters (Royle and Drazio 2008). We used an individual-based model for the system model and an ABC technique for parameter estimation.

We developed two alternative system models: reproduction models with synchrony (i.e., with social interaction) and without synchrony (i.e., null models). We examined the evidence of socially induced reproductive synchrony by testing which model better explained the observed patterns in 30 local populations of Dolly Varden. Both models have the following breeding parameters, i.e., the number of spawning females (N), the mean spawning date (μ), and its variance (σ) in each population, whereas the synchrony model has another main parameter, a synchrony coefficient (α) that determines the strength of social interactions. We also constructed observation models for redd counts to deal with stochasticity and incomplete field data (i.e., variations in the number of redds a female produces and unequal intervals of field surveys).

Reproduction schedule and null model

Suppose that in population k ($k = 1, \ldots, K = 30$) there are N_k females and that the best spawning date of female i, d_i, ($i = 1, \ldots, N_k$) is a random sample from the normal distribution of mean μ_k and variance σ_k^2;

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

The assumption of a normal distribution reflects both physiological and environmental effects on reproductive schedules. This was supported by the redd counts summed over all the tributaries, which fit the normal distribution well. The best spawning date is the most appropriate timing of oviposition in terms of egg ripeness. Intensive hatchery

programs for salmonids (i.e., artificial breeding) revealed that fertilization success quickly drops 1-2 weeks after ovulation (Craik and Harvey 1984; Brooks et al. 1997). This also indicates that females can flexibly change the spawning date for a week or two, which we modeled as a result of social interactions in the synchrony model described below.

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

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

in which B_h (h = 1, 2, 3) refers to the probability that a female produces h redds. Based on a detailed observational study of stream Dolly Varden (Kitano 1995), we set $B_1 = 0.1$, $B_2 = 0.6$, and $B_3 = 0.3$. Thus, one female produced $1\times 0.1 + 2 \times 0.6 + 3 \times 0.3 = 1.8$ redds on average. This system model was used as a null model.

Reproduction model with synchrony

In order to add socially induced synchrony in spawning behaviors, we assumed that in day d, all females in population k with $d_i = d$ spawn (if they have not spawned yet); after that, female j with later d_j ($d_i < d_j$) may spawn synchronously with probability

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

In other words, if the best spawning dates are close, female j tends to go to spawn with other females. Therefore, the adjustment of spawning timing can be considered to be socially induced synchrony. In this paper, we called a_k the "synchrony coefficient." This system model contains four parameters (N_k, μ_k, σ_k, a_k) for each population.

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

the null model with different population sizes (i.e., 300 females vs. 20 females). In the null model, redd counts nearly follow the normal distribution when the population size is large (Fig. 1a). This smooth fitting is deformed to a heavily fluctuating pattern when synchrony is included (Fig. 1b). Similar patterns are often observed in natural populations (Petersen and Hess 1991; Plot et al. 2012). However, even in the null model, random sampling from the normal distribution, together with the variation caused by the number of redds produced by each female, often exhibits fluctuation when the population size is small (Fig. 1c). Thus, although the synchrony amplifies fluctuations (Fig. 1d), such patterns can be produced without synchrony.

Observation model for redd counts

Suppose that in population k redd counts were conducted on day $D_1^k, \ldots, D_{T_k}^k$. On day D_t^k ($t = 1, \ldots, T_k$) we expect to observe redds produced between D_{t-1}^k and D_t^k. Let d_i' be the actual spawning date of female i ($d_i' \leq d_i$ because of synchrony). The observed number of redds, O_t^k, can be written as

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

in which 1( ) is the indicator function; = 1 if the inside parenthesis is true or = 0 if false. Since we did not know the actual start dates of spawning, we set $D_0^k = D_1^k - 5$. Although arbitrary, few individuals spawn in mid-August (I. Koizumi, personal observation), few redds were found on the initial dates, and this setting affected the results little.

Parameter estimation for null model

For simplicity, because the expected redd counts is given by $1.8N_k$, we estimated the number of females (N_k) by

{the observed redd counts in population k}/1.8

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

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

and assuming that $\{O_t^k\}$ are random samples from the multinomial distribution $(N_k, P_1^k, \ldots, P_{T_k}^k)$, we conducted the maximum likelihood method. This simplified estimation did not reflect the stochasticity caused by equation (2), but practically, this estimation provided almost equal results to those when the ABC method described below was applied to the null model. Hence, we show only the results using the likelihood estimation.

Approximate Bayesian computation (ABC) and approximate kernel Bayesian (AKB) algorithm

Because the derivation of a likelihood equation is difficult for the synchrony model, we applied the ABC method for estimating parameters (i.e., N_k, μ_k, σ_k, a_k). In general, the algorithm of the ABC method is summarized as follows (Sunnåker et al. 2013):

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

(2) Given a certain model (synchrony model in the present case), perform simulations many times, each with a set of parameter(s) drawn from the prior distribution(s) arbitrary assumed (e.g. uniform distribution).

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

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

that of the observed data.

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

Summary statistics are generally used for comparing simulated and observational data because simulated data consists of time-series vectors and are rarely “sufficiently close” to the observed data. Thus, the choice of summary statistics is the first problem with the ABC method (Sunnåker et al. 2013). The second problem is that, in general, even when summarized, most of the simulated data are far from the real data, and most of the parameter values are discarded. Therefore, we need a huge number of simulations (e.g., 100,000 or greater), which constrains calculations. The third problem is that there is no established criterion for determining what is “sufficiently close.”

To overcome these problems, Fukumizu et al. (2013) introduced a new method, and Nakagome et al. (2013) applied this to a population genetics study. The method is called the kernel-ABC algorithm, or the approximate kernel Bayesian algorithm; hereafter, we call it the AKB algorithm. In this method, weights are given to sampled parameters depending on the closeness between the real and simulated data, with adjustment by the ridge regression. Fukumizu et al. (2013) proved that the weighted sum over all the sampled parameters converges to the posterior mean when the number of simulations increases. Unlike most of the ABC methods, the AKB algorithm uses all the sampled parameters from the prior distribution and, therefore, does not necessarily require so many simulations. In summary, the AKB algorithm solves the second and the third problems of the ABC method.

Summary statistics

We used the following four summary statistics:

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

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

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

This is primarily used to estimate the mean spawning dates (μ_k). Because redds were produced between $D_{t\text{-}1}{}^k$ and D_t^k, this statistic is expected to be later than the true mean. If synchrony actually occurred, $S_2{}^k$ becomes earlier.

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

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

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

(9)

This statistic quantifies the degree of fluctuations and is used for estimating the synchrony coefficient (a_k). Because our model is not stationary, and O_t^ks are expected to take large values around μ_k, the auto-covariance formula for stationary time-series (subtract m instead of $\overline{O_t^k}$ where m refers to the overall mean) is not applicable. Instead, equation (9) subtracts the moving average from $t - 1$ to $t + 2$ for pair (t, $t + 1$). F^k and E^k is the first and the last day when non-zero redd count was obtained, respectively. These

were for excluding zeros before and after the spawning period, which otherwise decreased the value of S_4 and weakened the power for quantifying the fluctuations produced by the synchrony.

The quantification of fluctuations by summary statistic S_4 can be seen in the simulated patterns in Figure 1; S_4 decreased from -6.3 (a) to -116.7 (b) if synchronicity operated. On the other hand, if the population size was small, S_4 only slightly decreased from -0.71 (c) to -0.83 (d).

Prior distribution and AKB-algorithm

Prior distributions and the details about the AKB-algorithms are summarized in Supplementary Appendix B. Hereafter, the estimate of a parameter derived by the AKB algorithm is called as the AKB estimate. We also performed a conventional ABC-method for comparative purposes, and the method and its results are briefly summarized in Supplementary Appendix C.

Goodness-of-fit

In order to check if the model using AKB estimates actually explains the data, we used another summary statistic that was not used in the AKB algorithm. Let

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

be the difference in the number of redds between two consecutive surveys. We sorted them from largest to the smallest (let the sorted H_t^ks be $(H_{(1)}^k, \ldots, H_{(T_k-1)}^k)$ and accumulated them;

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

We also calculated these statistics for simulated data using AKB estimates and computed their 2.5 and 97.5 percentiles for each u. If G_s^ks for the real data were all inside the percentiles, the model was evaluated as adequately explaining real data. The same goodness-of-fit was conducted for the null model. Note that $G_{T_k-1}^k$ is equal to the descriptive statistics used in Henson et al. (2010) for quantifying synchrony.

Accuracy of AKB estimates

In order to check if AKB estimates were close to the true parameter values, we simulated redd counts using given parameter values 100 times and then applied the AKB algorithm and checked if the AKB estimates obtained were close to the true values.

We also simulated redd count data by the null model (without synchrony) and applied the AKB algorithm. Then, the AKB estimates of a should be close to 0. Thus, this simulation provides the range of synchrony coefficient that can be explained by the null model.

Environmental factors and synchrony among populations

Synchronous spawning might also have been triggered by environmental cues. In salmonids, which are stream-dwelling poikilothermic species, the main environmental factors affecting spawning activities are changes in photoperiod, water temperature, and water discharge (Jonsson 1991). Photoperiod changes gradually throughout the breeding

season and can affect reproductive seasonality, but this cannot be a proximal factor for reproductive synchrony. Therefore, we examined the effects of temperature and discharge on the daily spawning activities of Dolly Varden in each of 30 local populations.

We used the data on ambient temperature and precipitation recorded in one of the meteorological stations within the study area as surrogates of water temperature and discharge, respectively. Since the study area is not spatially widespread (< 10-20 km; Supplementary Fig. S1), local differences should be small (e.g., correlation coefficients of daily precipitation among three meteorological stations within the study area were > 0.92 ($P < 0.0001$)).

We first applied the Poisson regression to the number of redds observed (dependent variable) and the accumulated precipitation (mm) and changes in temperature (maximum minus minimum temperature) during the consecutive surveys (independent variables). In addition, since there were many zero data especially in the beginning and end of breeding season, we used the zero-inflated Poisson (ZIP) regression (Zeileis et al. 2008) with the same dependent and independent variables. These regression analyses were performed using statistical R software version 2.15.2 (R Development Core Team 2012).

This exploratory analysis did not reflect the normally distributed redd counts with different means and SDs. If an environmental factor influenced the breeding activity, differences between the observed redd counts and the expectations from the null model

(residuals) should be correlated with the environmental data. We thus calculated the correlation coefficients between residuals and the precipitation or temperature data described above.

If some environmental factors affected the breeding activity, synchrony among local populations would be expected. We therefore calculated pairwise cross-correlation coefficients for redd counts over the 30 local populations: the mean value and the 95% confidence interval were calculated with 1000 bootstrap resampling (Bjørnstad et al. 1999). Because observation dates differed, we adjusted redd count data to every 5-day interval from September 1 to December 24 and computed correlation coefficients.

In addition, since only reproductive seasonality should produce a certain level of synchrony, we have checked whether the observed cross-correlations could be produced without taking environmental data into account. For this purpose, we simulated redd count data by the synchrony model using the AKB estimates 1000 times, calculated cross-correlations and compared them with the observed values. If the observed value exceeds the upper 95% over the simulated data, effects of some environmental cues are suggested. We used population pairs for T7-T7.5-T8-T9, T16-T17, and T50-T50.5 because these pairs were spatially close and had exactly the same observation dates.

Results

General description of spawning activity

The spawning season of Dolly Varden lasted 3 to 4 months and peaked in mid-October (Fig. 2a; Supplementary Fig. S2). A total of 1206 spawning redds (934 completed redds and 272 direct spawning behavior) were observed from the 30 tributaries. On average, 40 redds were observed in each tributary (range: 9-108), which is equivalent to 22 (= 40/1.8) females (range: 5-60 females). Spawning periods overlapped widely and continued for long periods (> 3 months) for most of the tributaries (Supplementary Fig. S2). Multiple spawning aggregations were often observed in some tributaries (the left column in Fig. 3; Supplementary Fig. S2), similar with the patterns produced by the synchrony model (Fig. 1b, d). In addition, gathering of mature adults (10-20 individuals) were often observed in some pools of the tributaries before such spawning aggregations.

Synchrony model vs. null model

Table 1 summarizes values of the four summary statistics, the estimates of parameters in the null model and the synchrony model for the 12 populations that had relatively large numbers of redds ($\geq$ 40) (those for all the 30 populations are shown in Supplementary Table S2). For mean spawning dates (μ_k), the null model exhibited earlier mean spawning dates than the observed means, and when the synchrony was included, the estimates tended to become later, as mentioned in the *Summary Statistics* section. The AKB estimates for the number of females were almost the same as S_1/1.8.

The goodness-of-fit test revealed that the synchrony model explained all the patterns observed, but the null model failed for four (33%) populations (Table 1, at the 90% level), meaning significantly more aggregation and fluctuations in the reproductive

timing. As demonstrated in Fig. 1, the null models often produced fluctuating redd counts that were visually indistinguishable from those simulated by the synchrony models. However, the summary statistic S_4 successfully differentiated the two patterns and G-values in equation (11) showed sufficient fit for the synchrony model but insufficiency for the null model (the top and the middle rows in Fig. 3). In contrast, for the populations where the null models were not rejected, although the observed redd counts looked fluctuated, the values of S_4 were not so low and the null models produced similar patterns (e.g., the bottom row in Fig. 3).

Accuracy of AKB estimates

When we simulated redd count data using the AKB estimates in Table 1 and applied the AKB algorithm to the simulated data 100 times for the above four populations where the null models were rejected, we obtained values around the true value (Supplementary Fig. S3), and the the SDs of these estimates were small, ranging from 1.15 to 1.28.

When the AKB algorithm was applied to count data simulated by the null model, most of AKB estimates were 1-3 and less than 5% exceeded the AKB estimates for the observed data (Supplementary Fig. S3), except for T20 that had relatively small synchrony coefficient (2.74).

Degree of spawning synchrony

Figure 4 illustrates how the synchrony operated on the breeding activity. The mean over the above four populations (i.e., null models were rejected) was 4.00, and under this degree of synchrony, 50% probability that a female synchronizes spawning was 4-5

days before her best spawning date (Fig. 4a), and almost all females went to spawn 3 days before the best spawning date (on the assumption that some other females spawned every day). The average over the 30 populations was 2.77 (Supplementary Table S2), and this synchrony coefficient also involves spawning of almost all females before the best spawning date (Fig. 4). If $a < 1.0$, few females go to span before the best spawning date (Fig. 4), although we found only one such population (Supplementary Table S2).

Environmental factors and synchrony among populations

Neither the Poisson nor ZIP regressions showed clear effects of precipitation or temperature on the spawning activity of the 30 local populations of Dolly Varden (Supplementary Table S3). Poisson regression coefficients for precipitation were significantly positive in 2 populations (2/30 = 6.7%), significantly negative in 6 populations (20%), and non-significant in 22 populations (73.3%). However, none were significant after Bonferroni correction (i.e., $P = 0.05/30 = 0.0017$). The regression coefficients for temperature were significantly positive in 6 populations (20%), significantly negative in 2 populations (6.7%), and non-significant in 22 populations (73.3%). In this case, only 2 were significant after Bonferroni correction. ZIP regression analysis showed similar results, although the populations showing significance and the directions of the regression coefficients were often different (Supplementary Table S3).

We further investigated the effects of precipitation and temperature by residual analysis. However, no significant effects were detected in any of the 30 populations, in which some populations showed positive values whereas others showed negative ones (Fig. 5).

The overall level of synchrony in breeding activity was positive among the 30 populations, but relatively low (mean r = 0.276, 95% bootstrap CI = 0.200-0. 357, Supplementary Fig. S4). We further analyzed the data with the synchrony models taking the seasonality into account. For the three groups of spatially adjacent populations with the same observation dates (T7-T7.5-T8-T9, T16-T17, and T50-T50.5), the observed cross-correlations were not high (mean r = 0.258) and were all within confidence intervals obtained by 1000 times simulations (Fig. 6).

These results collectively showed low or non-consistent environmental effects on breeding activity and also low breeding synchrony between and among the populations inhabiting the 30 tributaries studied.

Discussion

Our models suggested the existence of socially induced reproductive synchrony in some local populations of Dolly Varden. Lack of environmental effects and/or synchrony among local populations further supported the notion that synchronous spawning was triggered by social interactions. As far as we know, this is the first study that applies ABC to animal behavior and also that suggests socially induced reproductive synchrony in stream fish. So far, reproductive synchrony by social stimuli has been indicated mostly in mammals and birds from which we can obtain direct evidence of complex social interactions (French and Stribley 1987; Sillero-Zubiri et al. 1998; Jovani and Grimm 2008; Henson et al. 2010, but see Plot et al. 2012). Our approach, using

individual-based modeling and statistical techniques that link models with field data, explored a methodological framework that can be applied to a broad range of species, especially when direct observations of social interactions and mating behavior are difficult.

ABC framework in behavioral ecology

We combined three modelling frameworks (i.e., an individual-based model, a hierarchical Bayesian model, and ABC) that are well established in their own fields (Grimm and Railsback 2005; Royle and Drazio 2008; Beaumont 2010). Since socially induced synchrony is triggered by surrounding individuals, individual-based modeling was an appropriate method to use. Hierarchical modelling was also necessary because field data usually contain stochastic processes, which were incorporated in the observation model. The advantage of ABC, then, was to be able to jointly estimate the parameters even though the derivation of the likelihood is practically impossible. These modelling frameworks were highly compatible since many essential ideas are shared with one another, such as simulation techniques and Bayes theorem. Since animal behavior is an individual-level phenomenon, our approach could be effective for a wide range of behavioral studies, especially when a global pattern can be generated by individual behaviors (e.g., Wood and Acland 2007; Jovani and Grimm 2008; Attanasi et al. 2014; Murakami et al. 2014; Calovi et al. 2015).

We demonstrated the importance of setting an appropriate null model for investigating relatively weak patterns of socially induced reproductive synchrony (see also, Henson et al. 2010). Intermittent breeding patterns are often used as an indication of socially

induced synchrony (Petersen and Hess 1991; Plot et al. 2012), but such patterns can be generated by stochasticity alone. Appropriate summary statistics helped us to judge which data required the synchrony and which did not. In addition, a synchrony index is often tested against the null hypothesis that individuals breed randomly in time (Marsden and Evans 2004). Reproductive timing, however, is often normally-distributed (Munro et al. 1990) and, therefore, calculation of deviations from a normal distribution is required.

Our study showed that the synchrony model was not always necessary to explain the field data and that the degree of synchrony differed over local populations. The sufficient fit of the null model for some populations may be because the presence of breeding synchrony is conditional or environmentally dependent. Obviously, it is difficult to time breeding with other individuals when population density is low (e.g., less than 10 females spawned in some populations, Supplementary Table S2). Also, breeding synchrony may be beneficial only in certain situations, such as when breeding areas are limited or when the operational sex ratio is high (see below). It is also possible that there simply was not enough statistical power due to the small numbers of redd counts in some tributaries. Note that non-rejection of the null model does not necessarily mean the absence of reproductive synchrony; all the data were also explained by the synchrony model. A more intensive survey, such as everyday census, would increase detection power. However, there is a trade-off between collecting data intensively in fewer populations or collecting that data extensively in multiple populations but with lower quality. Nonetheless, we were able to detect significant synchrony in multiple populations. In addition, the strengths of social interaction could

be evaluated by the synchrony coefficients *a* even when the synchrony models were statistically differentiated from the null models. Importantly, the synchrony coefficients indicate that breeding timing can be adjusted for up to 7 days by the synchrony, which is consistent with known degree of plasticity in reproductive timing in salmonids (Craik and Harvey 1984; Brooks et al. 1997).

Reproductive synchrony in fishes

Synchronous mass spawning is well known in some marine fishes, such as coral reef fishes and intertidal spawners (Yamahira 1996; Craydon 2004; Byrne and Avise 2009). These are mostly associated with lunar or tidal cycles, and the adaptive significance may be predation satiation (several hypotheses in Craydon 2004). Socially induced synchrony is also suggested in a damsel fish based on intermittent spawning patterns similar with Fig. 1 (Petersen and Hess 1991). In this case, the adaptive mechanism is proposed as avoiding filial cannibalism, which we also discuss later.

Spawning aggregations or group spawning are also reported in many freshwater fishes, such as cyprinids, lampreys, and salmonids (Sakai 1995; Blanchfield and Ridgway 1997; Jang and Lucas 2005). However, surprisingly few studies have focused specifically on reproductive synchrony, including the predation satiation hypothesis, which seems particularly possible in sea-run salmonids by bear predation (Quinn et al. 2014). In freshwater (not sea-run) salmonids, two studies indicate reproductive synchrony where 60-90% of spawning occurred within a few days or weeks (Blanchfield and Ridgway 1997; Sato and Harada 2008). They do not discuss the possible effects of social interactions; rather an environmental factor (e.g., precipitation,

temperature) was proposed as the proximate driver (Blanchfield and Ridgway 1997). Interestingly, however, the gathering of mature individuals in some pools or near spawning sites was also observed before the synchronous spawning (Blanchfield and Ridgway 1997; T. Sato, personal communication; see also White 1930), indicating some social interactions. Overall, it would be fruitful to reexamine the breeding ecology of fishes in terms of reproductive synchrony for better understanding of its evolutionary significance and ecological consequences (Ims 1990a).

The major adaptive significance of breeding synchrony is generally believed to be predation satiation (Darling 1938; Janzen 1971). However, this is unlikely in the populations of Dolly Varden. Ims (1990b) has demonstrated theoretically that predation satiation would not be achieved when breeding occurs synchronously within but asynchronously among local populations. In such cases, mobile predators efficiently consume local prey appearing at different times in different areas. This may be exactly the case for Dolly Varden in the Sorachi River. Blakiston's fish owls *Bubo blakistoni* were observed at different times and in different tributaries preying on spawning Dolly Varden (I. Koizumi, personal observation).

Blanchfield and Ridgway (1997) hypothesized that breeding synchrony in salmonids occurs to avoid sexual harassment or egg cannibalism by satellite males. Some males actively urge females to spawn, sometimes by displaying aggressive behavior (Garner et al. 2010). Similarly, some satellite sneaker males eat eggs right after oviposition especially when the density of sneakers is high (Maekawa and Hino 1990). Synchrony generally reduces the operational sex ratio (OSR) so that each spawning female is

surrounded by fewer males (Ims 1988). Thus, synchronous breeding may be a female strategy to reduce harassment and/or filial cannibalism by inducing more monogamous mating. Another potential benefit of synchronous breeding in salmonids is to reduce redd superimposition (Blanchfield and Ridgway 1997). When spawning areas are limited within streams, females dig nests where other females have spawned, which can cause egg death in old nests (van den Berghe and Gross 1989). Therefore, by spawning simultaneously with other females, they can avoid redd superimposition.

We also propose that the breeding synchrony in Dolly Varden may relate to female choice. Synchronous breeding generally decreases OSR but could also result in male monopolization when dominant males access multiple females (Ims 1988). In fact, breeding groups were often formed within limited stream reaches (e.g., less than 50 m, I. Koizumi, personal observation) and also perfect synchronous egg depositions among females seems difficult. On days when we observed synchronous breeding events, many males were active within limited breeding reaches, which could result in strong sexual selection. Among the large number of competing males, females can directly (via female choice) or indirectly (via male-male competition) mate with the best males. This can be referred to as induced polygamy by females, the opposite strategy discussed in the previous paragraph (i.e., induced monogamy). These alternative hypotheses could be separated by genetic parentage analysis to see if dominant males monopolize reproductive success or if subdominants fertilize eggs due to reduced operational sex ratios.

Conclusion

This study demonstrated the efficiency of combining intensive field data, modeling and parameter estimation for the study of animal behavior. Elementary statistical techniques such as correlations and generalized linear models do not always work because they require the independence of data while synchrony inevitably produces non-independent time-series data. Our results have shown the importance of intensive field studies covering large numbers of populations and frequent surveys: otherwise, we would have missed variations among the populations in rejection/acceptance of the null model, environmental effects, and values of the synchrony coefficients. In addition, our study has demonstrated the importance of adequate setting of a null model; it is not difficult to make a complex model that can explain given data even when a simpler model can explain the data. Feedbacks between field studies and modeling together with finding a suitable null model will advance the studies of behavioral ecology.

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Figure legends

Fig. 1

Examples of redd count data simulated by the synchrony model (b, d) and the null model without synchrony (a, c) when a population size is large (300 females, a, b) and small (20 females, c, d). Date was calculated taking 1 September as day 1. Observations are made every 3 days. The thin lines indicate a normal distribution of the best spawning dates for this population (mean = 60, SD = 15). The values of summary statistic S_4 (auto-covariance of time-lag = 1, measuring the degree of synchrony) are indicated for each data.

Fig. 2

(a) Daily number of redds (spawning nests) observed during the spawning season of stream-dwelling Dolly Varden in 30 tributaries of the Sorachi River, Hokkaido, Japan, (b) mean (solid line), highest and lowest (dashed lines) daily ambient temperature, and (c) daily precipitation in the study area.

Fig. 3

The observed redd counts (first column), an example of redd counts simulated by the synchrony model (second column) and the null model (third column), and the goodness-of-fit by equation (19) for the synchrony model (fourth column) and the null model (fifth column) for population T7 (the top row), T9 (the middle row) and T10a (the bottom row).

Fig. 4

The synchrony curve (a) and the cumulative probability that the females do not synchronize (b) when a = 4.00 (the mean over the four populations where the null model was rejected), a = 2.77 (the mean over all the 30 populations) and a = 1.00 (an example of very weak synchrony).

Fig. 5

Correlation coefficients of residual redd counts and environmental factors (i.e., precipitation and temperature).

Fig. 6

Tests of the synchrony for the three groups of eight spatially adjacent populations. Black circles indicate the observed cross-correlation coefficients, and minus symbols indicate the 2.5, 50 and 97.5 percentiles (from the bottom to the top) over 1000 simulations.

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

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%