Title: Strong dependence of demographic stochasticity on a small effective number of breeders in iteroparous species

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Abstract:

We provided a theoretical basis for integrating the effective number of breeders (N_b) into the stochastic dynamics of the number of adults (N) for iteroparous species based on individual relationships between adult females and their offspring. Recruitment variation was partitioned into i) parental, ii) nonparental, and iii) environmental processes (including density-dependent effects). The first two processes, summarized by N_b, magnified the contribution of the last process to recruitment variation. Assuming that there were no sex differences and an equal sex ratio, the relationship between N_b and the factor amplifying recruitment variation when N_b/N <0.1 was approximated to provide quantitative guidance for using only N_b. For example, N_b <42 would have a non-negligible impact on population stochasticity in terms of amplifying the environmental impact by over 5%. The advantage of assessing recruitment variation using N_b alone is that only genetic information on samples from the same cohort is sufficient. Thus, the proposed method is applicable in data-limited situations (e.g. endangered species), where there is typically insufficient information on life-history parameters or current age/size structure. The study findings reveal the usefulness of N_b in the field of conservation biology and wildlife management.

Keywords:

Population viability analysis, effective population size, age-structured population, recruitment variation, demographic heterogeneity, data-limited population.

1. Introduction

Stochasticity in population dynamics is one of the most fundamental challenges faced in conservation and wildlife management because it is linked to population persistence and extinction risk. Such stochasticity can be divided into two categories, apart from observation error: demographic and environmental stochasticity [1]. Demographic stochasticity is due to individual-level events that occur within a reproductive period, such as births and deaths [2]. Environmental stochasticity is due to events that affect the population-level or mean individual fitness and occur between reproductive periods, such as temperature changes, exploitation, density-dependent regulatory processes, competitive interactions, and other external factors [3]. In sufficiently large populations, environmental stochasticity dominates population stochasticity, and demographic stochasticity can be neglected. However, in small populations, such as threatened species or subdivided populations, demographic stochasticity can affect population persistence even when the external environment is suitable for survival and reproduction, potentially leading to a greater chance of extinction. Thus, estimating the relative impact of demographic and environmental factors on overall stochasticity is essential in population viability analysis (PVA).

The magnitude of variance in recruitment to the next generation, influenced by demographic and environmental factors, is an indicator of stochastic extinction risk [4, 5]. Thus, the specification of stochastic mechanisms is important in the PVA context. Melbourne et al. [6] theoretically derived the variance in recruitment by incorporating several stochastic factors. They showed that overlooked demographic factors, such as sex determination and fertility heterogeneity, significantly impacted the magnitude of the variance and, thus, stochastic extinction risk. Furthermore, they assessed the extinction risk for a laboratory population of semelparous species (i.e. a generation not overlapped) by incorporating the overlooked factors and estimating several parameters from experimental data. However, a situation in which parameters relevant to demographic stochasticity are available for a wild population is not realistic, particularly for threatened species. In addition, demographic heterogeneity is expected to be more influential on iteroparous species (i.e., a generation overlapped by multiple reproductive cycles during life) than on semelparous species because of age structure (e.g. age-specific survival and/or fecundity). However, collecting such data is more difficult [7].

The effective number of breeders (N_b) [8] is a metric for a population of iteroparous species that is converted from parental size (or census size, N) into effective size in a single breeding season. It is analogous to the effective population size (N_e), which is a metric per generation and determines the rates of genetic drift (e.g. [9]). The N_b is defined by known pedigree [10, 11] or life-history information [12, 13] and is estimated from a single cohort sample using pedigree or life-history data or linkage disequilibrium (LD) information from genetic analyses [14]. N_b (or N_b/N) reflects the reproductive variance among parents due to parental and nonparental factors [15–17]. A small N_b/N indicates overdispersed reproduction, which is an additional component of demographic stochasticity. Thus, it is natural to consider that N_b/N provides information on demographic stochasticity and can assess population persistence and extinction risk. However, there is little theoretical basis for interpreting the demographic stochasticity from N_b.

In this study, we propose a method for assessing demographic stochasticity using only N_b, which can be estimated from genetic data sampled from a population. The recruitment process was theoretically partitioned into three stochastic steps to derive an equation for recruitment variation as follows. i) Each adult female produces eggs according to parental fecundity (parental process); ii) each egg hatches and overcomes an initial reduction due to family-correlated survival (nonparental process); and iii) each offspring survives owing to external factors (environmental process). Theoretically, we show that the first two processes magnify the contribution of the last process to recruitment variation. Thus, N_b, which summarizes the first two processes [15], provides information on the relative importance of demographic stochasticity. The present modeling framework can be applied to diverse diploid species with semelparity or iteroparity. For semelparous species, a change from N_b to N_e maintains the consistency of the result. However, the description of the model focuses on iteroparous fish species, which are currently one of the best candidates for application of the proposed method.

2. Theory

Herein, the theoretical basis for integrating N_b into stochastic population dynamics is presented. The main contribution of this paper to the existing literature is the equation for recruitment variation presented in Equations 9–10. These equations were used for a new index of demographic stochasticity that indicates the degree of magnification of

environmental stochasticity (Equation 14). Details of the derivation are provided in S**upplementary Material**; the description herein focuses on model settings and assumptions. **Table 1** summarizes the main symbols used herein.

Table 1. List of mathematical symbols used in the main text.

R	Numbers of recruitment after initial survival
N	Census population size that is matured
N_{f}	Census female population size that is matured
N_{m}	Census male population size that is matured
N_{b}	Effective number of breeders
$N_{\mathrm{b,f}}$	Effective number of female breeders
$N_{\mathrm{b,m}}$	Effective number of male breeders
$\boldsymbol{k_{fi}}$	Number of surviving offspring born to adult female i before affecting population-level stochasticity
$\boldsymbol{\lambda_{\mathrm{f}i}}$	Expected number of surviving offspring of adult female i
$\boldsymbol{f(\lambda_{\mathrm{f}})}$	Frequency of λ_{f} for all adult females
$\boldsymbol{\phi_{\mathrm{f}}}$	Overdispersion parameter under negative binomial reproduction
$\boldsymbol{c_{\mathrm{f}}}$	Combined effect of deviation from the Poisson [15]
Y	Total number of offspring $(= \sum_{i=1}^{N_{\mathrm{f}}} k_{\mathrm{f}i})$
P	Survival probability of offspring to recruitment
r	Sex ratio of adults $(= N_m/N)$
$\boldsymbol{\sigma_{\mathrm{E}}}$	Environmental standard deviation of recruitment variability
$\boldsymbol{\sigma_{\mathrm{D}}}$	Non-Poisson demographic standard deviation of recruitment variability
$\boldsymbol{\Delta_{\mathbb{V}}}$	Magnitude of difference in $\mathbb{V}[R\|N_{\mathrm{f}}]$ when including and excluding $\exp[\sigma_{\mathrm{D}}^2]$
$\boldsymbol{P_{\mathrm{E/ED}}}$	Ratio of environmental stochasticity factor to total factor

(a) Overview

Presumably, there is a hypothetical population of semelparous species with N parents without any population subdivision or spatial structure. Here, a mature individual is referred to as a parent or adult, even if it does not produce offspring. The total number of parents is referred to as the census size, following standard usage in conservation biology. We considered the stochastic process of how the recruitment number (R) is generated from N parents during a reproductive season. The common equation in fisheries science [18] is

$$R = g(SSB)\exp[\varepsilon_R], \#(1)$$

where SSB is the spawning stock biomass ($= \sum_a N_a W_a$, where N_a and W_a are the number of parents at age and weight at age, respectively). The function, $g()$, indicates the parent–recruitment relationship, including the density-dependent effect, such as the Beverton–Holt relationship or Ricker relationship. ε_{R} indicates Gaussian noise with a mean and variance of $-\sigma_{\mathrm{R}}^2/2$ and σ_{R}^2, respectively, where the expectation of R is $g(SSB)$ (denoted by $\bar{R}_{SSB}$). σ_R^2 determines the degree of stochasticity of the process. The variance of R is

$$\mathbb{V}[R|SSB] = \bar{R}_{SSB}^2(\exp[\sigma_{\mathrm{R}}^2] - 1). \#(2)$$

σ_{R}^2 summarizes events that affect the population-level and is considered environmental stochasticity. However, such a top-down approach based on population dynamics (Equation 1) does not include the demographic stochasticity that summarizes individual events. If σ_{R}^2 is zero, then $\mathbb{V}[R|SSB]$ is also zero, indicating the deterministic process in recruitment dynamics.

We theoretically investigated the variance in recruitment by focusing on the family-based relationship between an adult female, eggs, offspring, and recruitment. Of N parents, N_{f} adult females exist in the population before spawning. Each adult female produces eggs according to its reproductive potential (λ_{f}), and heterogeneity among adult females is allowed, expressed by the distribution of λ_{f}, $f(\lambda_{\mathrm{f}})$ (subscript "f" denotes female). Using these notations, we derived the equation of $\mathbb{V}[R|N_{\mathrm{f}}, f(\lambda_{\mathrm{f}})]$ including demographic and environmental stochasticity. It should be noted that $\mathbb{V}[R|N_{\mathrm{f}}, f(\lambda_{\mathrm{f}})]$ corresponds to $\mathbb{V}[R|SSB]$ if SSB in males and demographic stochasticity are ignored and if $f(\lambda_{\mathrm{f}})$ is the weight distribution. For conciseness, $\mathbb{V}[R|N_{\mathrm{f}}, f(\lambda_{\mathrm{f}})]$ is denoted hereinafter by $\mathbb{V}[R|N_{\mathrm{f}}]$.

In addition, we investigated how the effective number of female breeders ($N_{\mathrm{b,f}}$) affects $\mathbb{V}[R|N_{\mathrm{f}}]$. Assuming that the degree of environmental stochasticity is arbitrary information, we theoretically demonstrated how a small $N_{\mathrm{b,f}}$ (and N_{b}) magnifies the contribution of environmental stochasticity to $\mathbb{V}[R|N_{\mathrm{f}}]$.

(b) Bottom-up approach

To incorporate individual events into recruitment variation, a bottom-up approach is proposed using an individual-based model, similar to previous studies (e.g. [6, 19–23]). The proposed model involves three processes. The first is the parental process by which parental individuals leave eggs according to their reproductive potential (such as age or size). The

second is the nonparental process by which early egg survival is influenced by parental individual differences, such as family-correlated survival after egg hatching. The third is the environmental process of recruitment success with equal survival probability among offspring in the absence of parental or family influence. The environmental process is driven by population-based events that include density-dependent effects (such as the Beverton–Holt/Ricker-type survival rate). **Figure 1** shows a schematic representation of the entire process based on the initial survival and recruitment of fish. Here, the first two processes are defined as demographic processes.

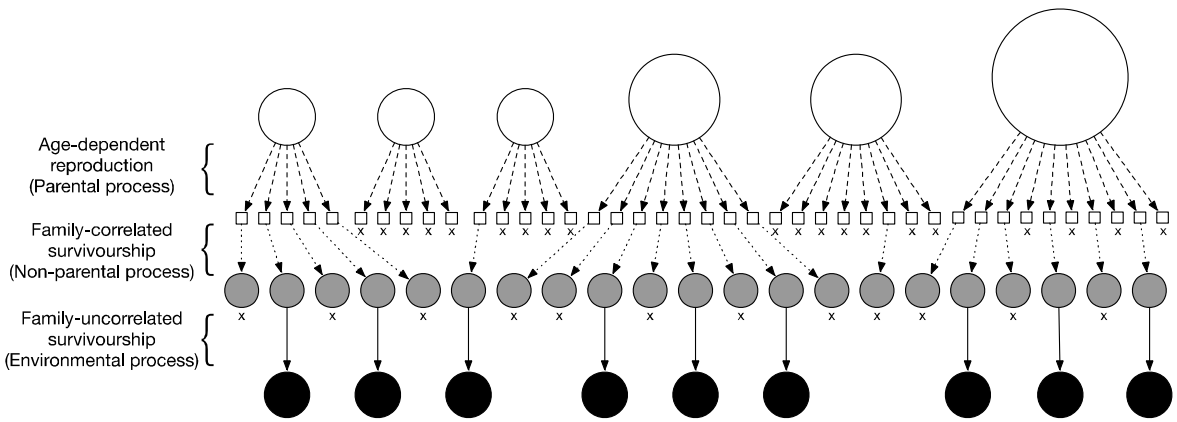

Figure 1. Relationships among adult females, eggs, offspring, and recruitments. The open circles, open squares, gray circles, and filled circles represent adult females, eggs, offspring, and recruitment respectively. The area of an open circle indicates the degree of reproductive potential of an adult female (i.e. $\lambda_{\mathrm{f}i}$). The dashed, dotted, and thin arrows indicate parent–egg, egg–offspring, and offspring–recruitment relationships, respectively. The symbol "×" indicates failure to survive till the recruitment stage.

(c) Reproductive variance governed by parental and nonparental factors

We showed how the demographic process affects the variation in the number of offspring of each parent. To formulate the process, only adult females were considered, and the offspring were not identified by sex. Let $k_{\mathrm{f}i}$ denote the total number of surviving offspring of an adult female i (i = 1, 2,..., N_{f}) prior to recruitment (gray circles, **Figure 1**). Following Akita [15, 16], $k_{\mathrm{f}i}$ was assumed to follow a negative binomial distribution with a mean of $\lambda_{\mathrm{f}i}$, given by

$$\Pr[k_{\mathrm{f}i}|\lambda_{\mathrm{f}i}] = \frac{\Gamma[k_{\mathrm{f}i}+\phi_{\mathrm{f}}]}{k_{\mathrm{f}i}!\,\Gamma[\phi_{\mathrm{f}}]}\left(\frac{\lambda_{\mathrm{f}i}}{\phi_{\mathrm{f}}+\lambda_{\mathrm{f}i}}\right)^{k_{\mathrm{f}i}}\left(\frac{\phi_{\mathrm{f}}}{\phi_{\mathrm{f}}+\lambda_{\mathrm{f}i}}\right)^{\phi_{\mathrm{f}}}. \#(3)$$

It was assumed that $\lambda_{\mathrm{f}i}$ is independent and identically distributed with a density function

$f(\lambda_{\mathrm{f}})$ that generates parental variation. $\lambda_{\mathrm{f}i}$ can be interpreted as reproductive potential, and $f(\lambda_{\mathrm{f}})$ may be described by information, such as maternal weight or size composition in the population. ϕ_{f} (>0) is the overdispersion parameter that describes the degree of nonparental variation and is assumed to be constant among adult females.

Akita [15, 16] derived the variance of the total number of surviving offspring from an adult female as

$$\mathbb{V}[k_{\mathrm{f}}] = \mathbb{E}[\lambda_{\mathrm{f}}] + \mathbb{E}[\lambda_{\mathrm{f}}]^2(c_{\mathrm{f}} - 1), \#(4)$$

where

$$c_{\mathrm{f}} = \left(1 + \phi_{\mathrm{f}}^{-1}\right) \times \left(\frac{\mathbb{E}\left[\lambda_{\mathrm{f}}^2\right]}{\mathbb{E}[\lambda_{\mathrm{f}}]^2}\right). \#(5)$$

c_{f} (≥ 1) indicates the combined effect of parental and nonparental variation. In the absence of parental or nonparental variation (i.e. $c_{\mathrm{f}} \to 1$), $\mathbb{V}[k_{\mathrm{f}}]$ converges to $\mathbb{E}[\lambda_{\mathrm{f}}]$, which corresponds to the Poisson variance in reproduction for all adult females.

By defining $N_{\mathrm{b,f}}$ as the inverse of the probability that two offspring share a maternal sibling relationship with any adult female (denoted by π_{f}), Akita [15] derived the following relationship:

$$\begin{aligned} N_{\mathrm{b,f}} &= \frac{1}{\pi_{\mathrm{f}}} \\ &= \frac{N_{\mathrm{f}} - 1}{c_{\mathrm{f}}} + 1. \#(6) \end{aligned}$$

$N_{\mathrm{b,f}}$ is not influenced by the value of the mean reproductive potential ($\mathbb{E}[\lambda_{\mathrm{f}}]$) but by ϕ_{f} and the coefficient variation ($\mathbb{CV}[\lambda_{\mathrm{f}}]$), since $\mathbb{E}\left[\lambda_{\mathrm{f}}^2\right]/\mathbb{E}[\lambda_{\mathrm{f}}]^2 = \mathbb{CV}[\lambda_{\mathrm{f}}] + 1$, indicating that $N_{\mathrm{b,f}}$ is characterized by the degree of non-Poisson reproductive variation. In the present modeling, it was assumed that $N_{\mathrm{f}} \geq N_{\mathrm{b,f}} \geq 2$.

(d) Survival process leading to recruitment governed by environmental factor

Next, we showed how the environmental process affects the variation in recruitment numbers (thin arrows, **Figure 1)**. After initial survival through demographic processes, an equal probability of offspring survival to recruitment was assumed in the absence of (individual) parental influence. The recruitment number (R) can be described by a binomial process:

$$R \sim \mathrm{Bin}[Y, P], \#(7)$$

where Y is the total number of offspring ($Y = \sum_{i=1}^{N_\mathrm{f}} k_{\mathrm{f}i}$), and P is the density-dependent survival probability. It is natural to assume that Y and P can be independently determined because the present modeling separates a density-dependent phase, where population-level stochasticity is dominant, from the initial survival phase, which is based on individual-level events. To incorporate environmental stochasticity, P was considered as a random variable following a log-normal distribution:

$$P = p(N_\mathrm{f}) \exp[\varepsilon_\mathrm{E}], \#(8)$$

where ε_E is a random noise expressing the degree of environmental stochasticity following a normal distribution with a mean and variance of $-\sigma_\mathrm{E}^2/2$ and σ_E^2, respectively. This equation ensures that $\mathbb{E}[P|N_\mathrm{f}] = p(N_\mathrm{f})$, and $p(N_\mathrm{f})$ indicates the density-dependent term. For conciseness, $\mathbb{E}[P|N_\mathrm{f}]$, $\mathbb{E}[Y|N_\mathrm{f}]$, and $\mathbb{E}[R|N_\mathrm{f}]$ are denoted hereinafter by $\bar{P}, \bar{Y}$, and $\bar{R}$, respectively. $\bar{R} = \bar{P}\bar{Y}$ since Y and P are independent.

3. Results

(a) Partitioning of recruitment variations

Given the functional relationship between N_f and $\bar{R}$, the recruitment variation was obtained through demographic and environmental processes as follows:

$$\mathbb{V}[R|N_\mathrm{f}] = \bar{R} + \bar{R}^2(\exp[\sigma_\mathrm{E}^2 + \sigma_\mathrm{D}^2] - 1), \#(9)$$

where

$$\exp[\sigma_\mathrm{D}^2] = 1 + \frac{1 - \frac{N_\mathrm{b,f}}{N_\mathrm{f}}}{N_\mathrm{b,f} - 1}. \#(10)$$

The interpretation of σ_D^2 is subsequently provided, and the details of the derivation (Equations 9–10) are provided in **Supplementary Material**. This variance equation implies that, given N_f, R follows a Poisson log-normal distribution with a mean of $\bar{R}$.

If σ_E^2 and σ_D^2 are zero, then $\mathbb{V}[R|N_\mathrm{f}]$ is equal to $\bar{R}$, corresponding to the Poisson variance in the recruitment process. Contrarily, when $\sigma_\mathrm{E}^2 + \sigma_\mathrm{D}^2 > 0$, most of the variance is dominated by the second term in Equation 9; $\exp[\sigma_\mathrm{E}^2]$ and $\exp[\sigma_\mathrm{D}^2]$ synergistically amplify the second term. The degree of amplification holds even in the absence of the environmental factor (i.e. $\exp[\sigma_\mathrm{E}^2] = 1$).

In Equation 10, $\exp[\sigma_\mathrm{D}^2]$ monotonically decreases with an increase in $N_\mathrm{b,f}$; as $N_\mathrm{b,f}$

approaches N_{f}, $\exp[\sigma_{\mathrm{D}}^2]$ becomes unity, indicating that the variance is only dominated by the Poisson variance and environmental factor. The case in which $N_{\mathrm{b,f}} < N_{\mathrm{f}}$ corresponds to the non-Poisson reproductive process, driven by parental and/or nonparental factors. Thus, $\exp[\sigma_{\mathrm{D}}^2]$ can be interpreted as a non-Poisson demographic factor. It should be noted that the formulation (Equation 9) was similar to that of the top-down approach (Equation 2) when the terms relevant to the demographic factor were removed, as expected.

Summarily, the recruitment variation (Equation 9) was partitioned into (i) the Poisson demographic factor (first term) and (ii) the combination of non-Poisson demographic and environmental factors (second term). In addition, the degree of the non-Poisson demographic factor can be characterized by the effective number of female breeders and census adult female size.

If most of the variance is dominated by the second term, the coefficient of variation of recruitment can be approximated as follows:

$$\mathbb{CV}[R|N_{\mathrm{f}}] \approx \sqrt{\exp[\sigma_{\mathrm{E}}^2 + \sigma_{\mathrm{D}}^2] - 1}. \#(11)$$

In this equation, $\bar{R}$ has been omitted. This implies that the value of CV is approximately independent of the functional relationship between N_{f} and $\bar{R}$, including density-dependent effects.

(b) Integration of two sexes (assuming no sex differences and equal sex ratio)

The effective number of breeders is obtained by combining the effective number of female breeders and effective-breeding father size (denoted by $N_{\mathrm{b,m}}$) [24, 25]:

$$\frac{1}{N_{\mathrm{b}}} = \frac{1}{N_{\mathrm{b,m}}} + \frac{1}{N_{\mathrm{b,f}}}. \#(12)$$

If $N_{\mathrm{b,m}} = N_{\mathrm{b,f}}$ and $N_{\mathrm{b,m}}$ is removed from Equation 12, then $N_{\mathrm{b,f}} = N_{\mathrm{b}}/2$. Furthermore, assuming an equal sex ratio, $N_{\mathrm{f}} = N/2$. Incorporating $N_{\mathrm{b,f}}$ and N_{f} into Equation 10, the following relationship was obtained:

$$\exp[\sigma_{\mathrm{D}}^2] = 1 + \frac{1 - \frac{N_{\mathrm{b}}}{N}}{\frac{N_{\mathrm{b}}}{2} - 1}. \#(13)$$

This equation substitution is satisfied if (i) the maternal and paternal sibling probabilities within any two sampled offspring are equal and (ii) the sex ratio is 0.5. This equation is

useful for estimating $\exp[\sigma_{\mathrm{D}}^2]$ because the distinction between maternal and paternal relationships is not very easy and is an additional source of uncertainty. Here, $N \geq N_{\mathrm{b}} \geq 4$.

(c) N_{b}, an indicator of the non-Poisson demographic factor that magnifies the recruitment variation due to the environmental factor

Following the relationship in Equation 13, the degree of the non-Poisson demographic factor ($\exp[\sigma_{\mathrm{D}}^2]$) was expressed by N_{b} and N. **Figure 2a** shows the relationship between N_{b} and $\exp[\sigma_{\mathrm{D}}^2]$ at different N values. Here, $\exp[\sigma_{\mathrm{D}}^2]$ decreased with an increase in N_{b} and asymptotically converged to unity when $N_{\mathrm{b}}/N = 1$, indicating that the non-Poisson factor had a relatively small effect on the degree of recruitment variation at large N_{b}, such as $N_{\mathrm{b}} > 100$, or when N_{b}/N was practically unity. However, when $N_{\mathrm{b}} < 50$ and N_{b}/N was small, the effect of the non-Poisson factor could not be ignored.

If N_{b}/N was sufficiently small, $\exp[\sigma_{\mathrm{D}}^2]$ was approximated as follows:

$$\exp[\sigma_{\mathrm{D}}^2] \approx 1 + \frac{1}{\frac{N_{\mathrm{b}}}{2} - 1}. \#(14)$$

Figure 2b shows the contour plot for the relative approximation error. As expected, the error decreased with a decrease in N_{b}/N. The region where $N_{\mathrm{b}}/N < 0.1$ (above the dotted line in **Figure 2b**) almost corresponds to the region where the relative approximation error is below 10%. In this region, the approximation would be acceptable for practical use, and the information of N is not required to estimate $\exp[\sigma_{\mathrm{D}}^2]$. Therefore, if N_{b} is available and $N_{\mathrm{b}}/N < 0.1$ is likely, Equation 14 can provide the degree of the non-Poisson demographic factor (gray line, **Figure 2a**). It should be noted that the approximation of $\exp[\sigma_{\mathrm{D}}^2]$ is always biased upward; therefore, the resulting estimate of the contribution to recruitment variation would be overestimated if N_{b} were available without bias.

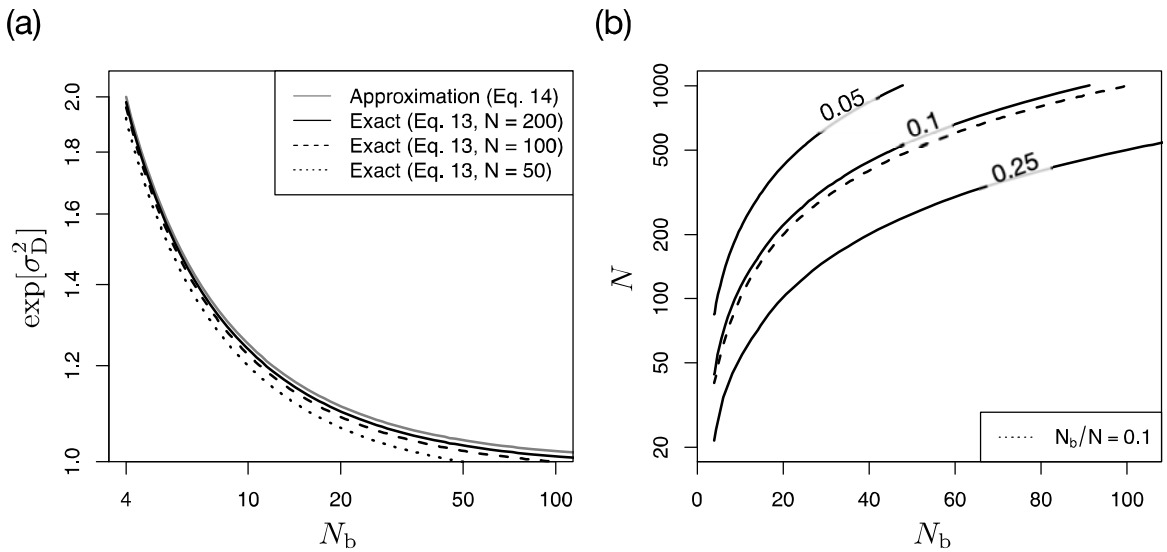

Figure 2. (a) Relationship between the effective number of breeders (N_b) and non-Poisson demographic factor ($\exp[\sigma_D^2]$). The bold, dashed, and dotted lines indicate the exact relationship in Equation 13 at N = 200, 100, and 50 respectively. The gray line indicates the approximated relationship in Equation 14. The x- and y-axes are presented in the logarithmic scale. (b) Contour plot of the approximation accuracy in Equation 14 as a function of N_b and N. The contour labels in the plot indicate the value of a relative approximation error, which is defined as (approximated value − exact value)/exact value. The dotted line represents the relationship that satisfies N_b/N = 0.1. The y-axis is presented in the logarithmic scale.

We provide qualitative guidance for the effect of the non-Poisson factor on recruitment variation. First, the magnitude of the difference in recruitment variation was examined when the non-Poisson demographic factor was included and excluded.

$$\Delta_{\mathbb{V}} = \bar{R}^2 \exp[\sigma_E^2]\,(\exp[\sigma_D^2] - 1), \#(15)$$

The aforementioned relationship indicates that $\Delta_{\mathbb{V}}$ increases in proportion to $(\exp[\sigma_D^2] - 1)$ since $\bar{R}^2 \exp[\sigma_E^2]$ and $(\exp[\sigma_D^2] - 1)$ are independently determined, given N. For example, using Equation 14, when N_b = 4, 8, 22, and 42, $\Delta_{\mathbb{V}}$ increased by 100%, 33%, 10%, and 5%, respectively (gray line, **Figure 2a**).

Second, we evaluated the extent to which the variance in recruitment is underestimated when the non-Poisson factor is ignored. To achieve this, the ratio, $P_{E/ED}$, was introduced.

$$P_{E/ED} = \frac{\exp[\sigma_E^2] - 1}{\exp[\sigma_E^2 + \sigma_D^2] - 1}. \#(16)$$

The denominator indicates the factor involved with $\bar{R}^2$ in Equation 9, and the numerator indicates the same except for the non-Poisson factor. **Figure 3a** illustrates the relationships

between N_b and $P_{E/ED}$ at different levels of environmental stochasticity (i.e. σ_E = 0.6, 0.4, and 0.2) using Equation 14. As expected, $P_{E/ED}$ approached unity with an increase in N_b, and this trend became more pronounced with an increase in environmental stochasticity. Conversely, for a relatively small N_b, the effect of the non-Poisson factor on the variance in recruitment could not be ignored. For example, **Figure 3a** shows that at N_b = 50 with low environmental stochasticity (i.e. σ_E = 0.2), $P_{E/ED}$ equaled 48%, indicating that more than half of the total stochasticity was due to the non-Poisson factor. However, with strong environmental stochasticity (i.e. σ_E = 0.6), $P_{E/ED}$ equaled 88%, indicating that the contribution of the non-Poisson factor was relatively weak but probably not negligible. The aforementioned qualitative relationships are based on the assumption that N_b/N was sufficiently small (e.g. $N_b/N < 0.1$). However, Equation 13 can also provide such qualitative relationships without the approximation when N_b and N are provided (**Figures 3b–d**, corresponding to N = 50, 100, and 200 respectively).

Furthermore, if the aforementioned approximation was appropriate, then by replacing $\exp[\sigma_D^2]$ in Equation 11, the CV was approximately affected by only N_b and $\exp[\sigma_E^2]$.

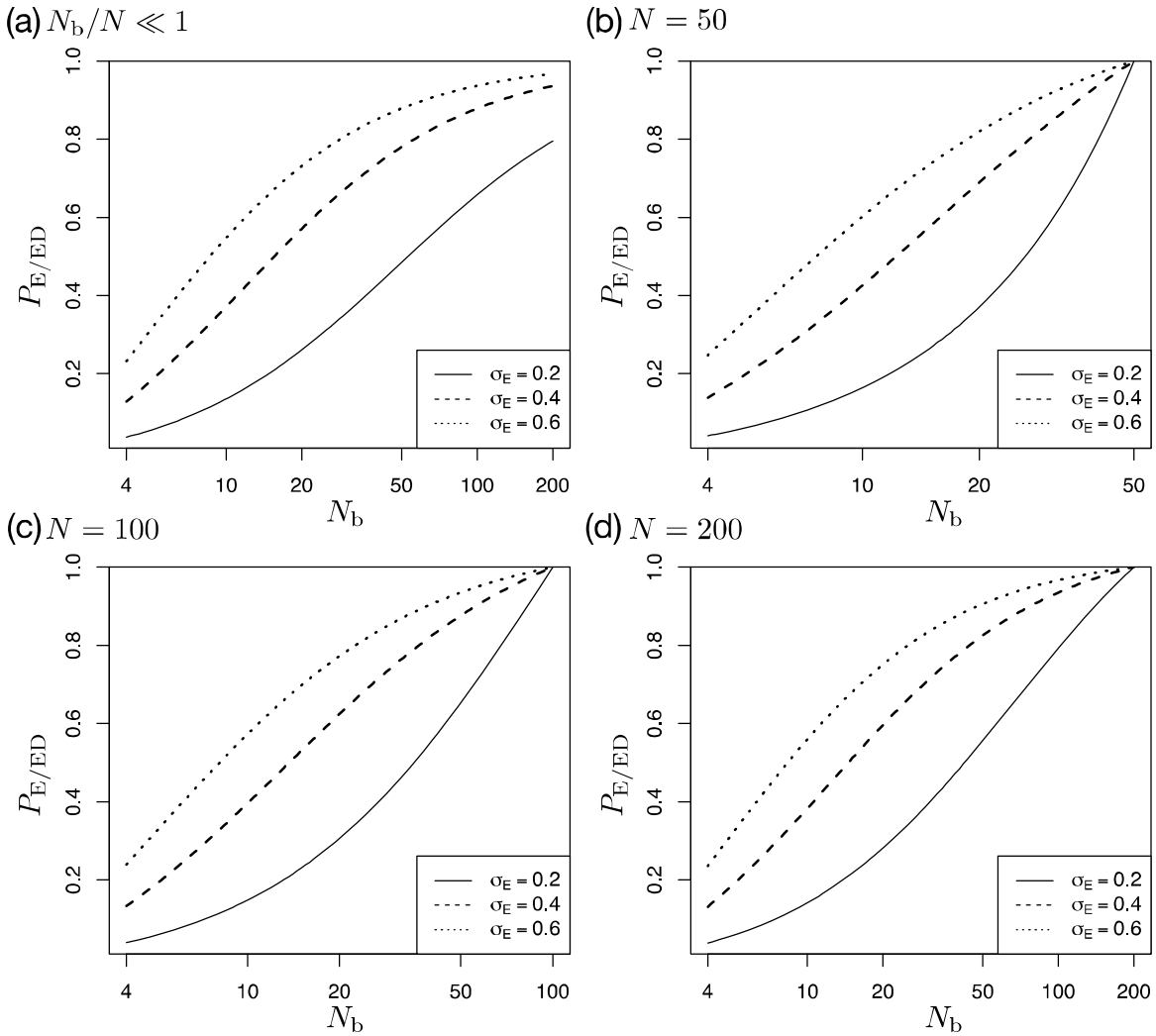

Figure 3. Relationship between the effective number of breeders (N_b) and the ratio indicating the extent to which the variance in recruitment is underestimated when non-Poisson effects are ignored ($P_{E/ED}$). The bold, dashed, and dotted lines correspond to σ_E = 0.2, 0.4, and 0.6 respectively. The x-axis is presented in the logarithmic scale. (a) Approximate relationship using Equation 14 (N is not specified). (b–d) Exact relationship using Equation 14 (N is specified).

4. Discussion

In this study, we provided a theoretical basis for integrating the effective number of breeders (N_b) into stochastic population dynamics for iteroparous species based on individual relationships between an adult female and their offspring. To achieve this, the recruitment variation was derived by partitioning the recruitment process into the parental,

nonparental, and environmental processes. The parental and nonparental processes correspond to the demographic process, which generates stochasticity in population dynamics due to individual events. The equation for recruitment variation (Equation 9) comprises two terms, the Poisson factor term and the synergy term between the non-Poisson (i.e. overdispersed reproduction) factor ($\exp[\sigma_{\mathrm{D}}^2]$) and environmental factor ($\exp[\sigma_{\mathrm{E}}^2]$). Most of the recruitment variation is dominated by the second term. Assuming no sex differences with a sex ratio of 0.5, the magnitude of the non-Poisson factor was characterized by N_{b} and N_{b}/N (Equation 13), and the theoretical relationship between N_{b} and the non-Poisson factors can be approximated when $N_{\mathrm{b}}/N \ll 1$ (Equation 14) (**Figure 2b**). Regardless of whether the approximation was available, we provide qualitative guidance for the effect of the non-Poisson factor on recruitment variation (**Figures 2a** and **3a–d**).

To the best of our knowledge, this is the first report that theoretically links N_{b} to demographic stochasticity. The advantage of this link is that the degree of the non-Poisson demographic factor on overall stochasticity is characterized by N_{b} and N_{b}/N. To obtain recruitment variation for iteroparous species without using N_{b}, the theoretical findings indicate that the current age/size distribution of adult females ($f(\lambda_{\mathrm{f}})$), maternal overdispersion parameter (ϕ_{f}), degree of environmental stochasticity (σ_{E}), parent–recruitment relationship ($\bar{R}$), and N are required. The present approach attributes the effect of parental/nonparental factors to N_{b} and N_{b}/N, where environmental stochasticity and the parent–recruitment relationship, including a density-dependent effect, are arbitrary. In addition, when the approximation was appropriate ($N_{\mathrm{b}}/N \ll 1$), the degree of the non-Poisson demographic factor was characterized by only N_{b}, indicating the possibility of assessing the demographic stochasticity using only genetic data. Although a 10% approximation accuracy threshold was used here, which roughly corresponds to $N_{\mathrm{b}}/N < 0.1$ (**Figure 2b**), the acceptable margin of error was situation-dependent.

The present theoretical results provide guidance regarding the extent to which overdispersed reproduction, i.e. the source of non-Poisson demographic effects, needs to be considered in population dynamics. For example, for a population with the prior information of $N_{\mathrm{b}}/N < 0.1$ and N_{b} estimated as 42, the magnitude of the difference in recruitment variation when including and excluding the non-Poisson factor ($\Delta_{\mathbb{V}}$) was 5% of $\bar{R}^2 \exp[\sigma_{\mathrm{E}}^2]$. This indicates that $N_{\mathrm{b}} < 42$ and that a small N_{b}/N would have a non-negligible impact on population stochasticity in terms of amplifying the environmental impact by over

5%. Conversely, for N_b >100, the impact will be below 1% at best, indicating that the effect of overdispersion can be practically negligible. From the perspective of the level at which non-Poisson demographic stochasticity becomes important, the obtained results may provide a rationale for setting N_b = 50–100 as the threshold. This consideration is not dependent on the life-history strategy of the target species (e.g. long- or short-lived), which implies that the effective number of breeders may function as a universal measure, which is another advantage of the proposed method.

The practical advantage of assessing N_b alone is that only genetic information on samples from the same cohort is sufficient. This showed that the proposed method is applicable in data-limited situations, such as endangered species, where there is typically insufficient information on life-history parameters or current age/size structure. To estimate N_b, it is sufficient to sample offspring from a single cohort, which is also advantageous when parent individuals are difficult to sample. Once genetic information is available for the sample, the sibship frequency [10] or LD [14] methods can be used to estimate the N_b for the parental generation or for averaging over previous generations, respectively [26]. The estimation of N_b in a large population with a realistic sample size is difficult because of the very weak signal for inbreeding [27] or genetic drift [28]. However, in a case where N_b is less than a few hundred, which is the focus of the present study, a relatively small bias in an estimate is expected. A caveat is the sampling time if the cohort is constituted by young-of-year (YOY) individuals. Sampling YOY individuals prior to sufficient mixing with the entire cohort in a population may overestimate the effect of overdispersed reproduction due to temporally or spatially biased sampling. Thus, the sampling activity should be carefully planned to ensure that the sample is as random as possible.

Finally, we discuss two future directions for the theoretical development of this study. The first is to investigate the generality of the results derived from the proposed model. Melbourne et al. [6] derived several equations for recruitment variation assuming different settings of demographic and environmental variation for iteroparous species, which may lead to different relationships between N_b and the non-Poisson factors. For example, although the proposed model assumed no sex differences and an equal sex ratio, they incorporated heterogeneity in sex determination into the recruitment variation. Thus, sensitivity analyses will be performed in the future. The second future direction is to investigate the CV (Equation 11) through overdispersed reproduction. For example, if there are certain ecological or environmental mechanisms such that an increase in CV causes a

decrease in N_b/N in the next year, this indicates that N_b/N is shrinking through positive feedback from non-Poisson factors over the year. This consequence can be placed in the context of the extinction vortex [29]. Furthermore, the proposed theoretical framework may facilitate a future analysis of the theoretical condition of what kind of ecological or environmental mechanisms decrease N_b/N through parental and/or nonparental processes.

Ethics

This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility

Supplementary material is available online.

Declaration of AI use

We have not used AI-assisted technologies in creating this article.

Authors' contributions

T.A.: conceptualization, formal analysis, methodology, writing—original draft, writing—review and editing.

Conflict of interest declaration

We declare we have no competing interests.

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Footnotes

Electronic supplementary material is available online.

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