

Density-vague dynamics of biological populations

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1 Introduction

Biological populations fluctuate in abundance over time. These fluctuations are affected both by external environmental factors independent of population density, and by density-dependent factors. The long-term average about which a population fluctuates will ultimately be set by the density-dependent factors. The nature of the negative feedback relationship between population growth rate and density is at the heart of population ecology. The existence and detection of density dependence in real data sets has been, however, the subject of much controversy for several decades. The consensus emerging from this prolonged debate is now that, when sufficiently long runs of data are available, ecologists should be able to detect density dependence from population time-series [1–9]. The duration of a time series necessary to distinguish a regulated population trajectory from a random walk is still uncertain [8, 10, 11]; how long of a time series is required to be able to disentangle deterministic (density-dependent) signals from external noise in the ecological systems? When plotting data on the form of the density-dependent relationship, ecologists have been confounded by considerable noise around each relationship, i.e. “density vagueness” [12]; explaining this bivariate scatter has remained a largely unrealized goal [13, 14]. The vagueness in the density-dependent relationship concerns uncertainty in locating the population equilibrium. The issue of indeterminacy of the density-dependent relationship, which has not been analyzed quantitatively [15], is set in a formal mathematical framework associated with the number of years in the census. I analyze the population renewal process of marine exploited fishes in the North Atlantic. Data are extracted from the 2008 working group reports of the International Council for the Exploration of the Sea (ICES) prepared for advice on living resources and their harvesting provided by the ICES Advisory Committee [16]. The analysis is based on the 38 commercial stocks, which are the same as the fish stocks analyzed by Sparholt et al. [17].

2 Stochastic population dynamics

For most fish species the breeding population consists of several age groups, and the most useful measure is usually the spawner abundance (biomass S in tonnes). During year t an amount $Y(t)$ is harvested with a fraction to the harvestable adult population, $1 - e^{-F(t)}$, where $F(t) = \ln[1 + Y(t)/S(t)]$ denotes the fishing mortality. Harvesting leaves a population size $S(t)$, i.e. the escapement of adults from the harvest. The biomass grows as a result of, not only growth of escapees in body weight, but also of recruitment of offspring; $\Xi(t)$ is designated the

recruits to the adult population (counts of surviving progeny) in year t . All density dependence is assumed to be exerted by the adult population density [18]; this would apply if juveniles do not compete with adults. The system is described by a discrete difference equation

$$S(t+1) = \Lambda(S(t)) S(t) + w_0 \Xi(t+1) - Y(t+1) \quad (1)$$

with a growth-survival factor Λ dependent on S , where w_0 is body weight at entry to the harvestable adult population. Choose as geometric means, the equilibrium escapement S_* , recruitment Ξ_* and yield Y_* . In a stationary state, Eq.(1), log-transformed, gives $\ln(1-w) + F_* = \ln \Lambda(S_*)$ with the stationary fishing mortality $F_* = \ln(1 + Y_*/S_*)$, where $w = w_0 \Xi_*/(S_* + Y_*)$ is the stationary ratio of each year's recruitment (in biomass) to the harvestable adult population. Denoting the relative deviations from equilibrium point as $n(t) = \ln(S(t)/S_*)$, $\xi(t) = \ln(\Xi(t)/\Xi_*)$, and $f(t) = F(t)/F_* - 1$, linearizing the (log-transformed) equation (1) yields

$$n(t+1) - n(t) = -\gamma n(t) + w\xi(t+1) - F_* f(t+1) \quad (2)$$

with constant coefficient $\gamma = 1 - (1-w)(1 + d \ln \Lambda / d \ln S)_*$ evaluated at equilibrium. The successive difference $r(t) = n(t+1) - n(t)$ approximates the annual rate of increase of a population, i.e. the per-unit-abundance growth rate. Stochasticity enters the population dynamics in two ways [19], both as environmental variation mirrored by recruitment variability $\xi(t)$ and as variation in the fishing mortality $f(t)$. These natural and human-caused forces $(t) = w\xi(t) - F_* f(t)$ are considered as external disturbances.

3 Population-dynamic equilibrium

Figure 1A shows the empirical variance trajectories of fish populations in the North Atlantic, demonstrating the increase in temporal population variability over time scales as long as decades, which are often used to describe temporal patterns of population fluctuations [20–23]. Recruitment and fishing rate are presumed to track population fluctuations. Adjacent values in the time series of recruitment and catches-to-escapement ratio are correlated [24]; as the consequence the delayed effect of density dependence appears in population dynamics [25]. For generating temporally structured noise, $\xi(t)$ and $f(t)$ are both assumed to be described as a first-order autoregressive, AR(1), process [19, 21, 25, 26] with serial correlation coefficients β_ξ and β_f . The AR(1) coefficients are estimated for the examined time-series of length L years, giving $|\beta_\xi|$ and $\beta_f < e^{-1/L}$ which implies that both the processes of $\xi(t)$ and $f(t)$ contain constant means, i.e. there exist stationary equilibrium values for recruitment Ξ_* and fishing mortality F_* . Consequently, the population is anticipated to exhibit a return tendency to the equilibrium point S_* . The population process with multiple decay-time constants $(-1/\ln(1-\gamma))$, $-1/\ln|\beta_\xi|$, and $-1/\ln\beta_f$ is considered to determine the total decay-time constant, i.e. the asymptotic equilibration time T_{eq} .

The necessary calculations of the variance of a population with autocorrelated environment were done more than three decades ago [26]; the result is generalized to connect the three parameters γ , β_ξ and β_f to the population fluctuations, the mean square successive difference $\frac{2}{r}$ and the variance $\frac{2}{n}$ in population size n , the variances $\frac{2}{\xi}$ and $\frac{2}{f}$ of recruitment ξ and fishing rate f . On the assumption that ξ and f are inter-independent, the impact of fishing on the population

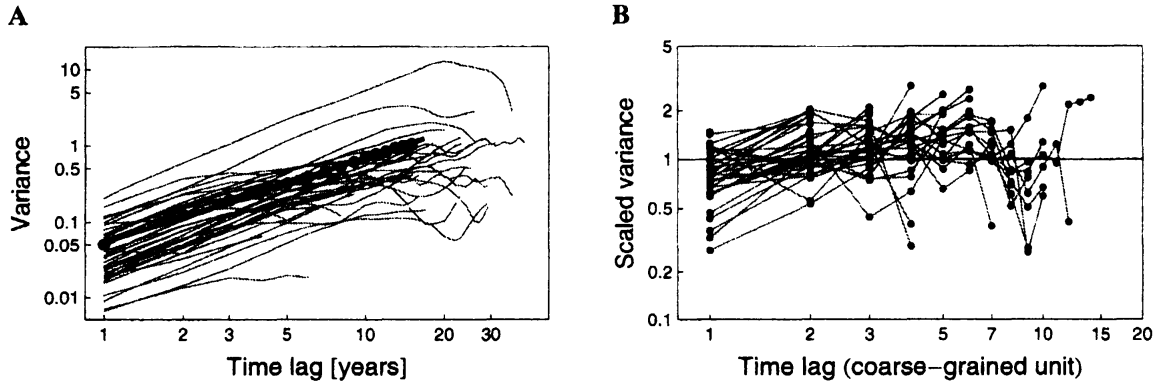


Fig. 1: Variance trajectories. (A) The mean square t -year difference of population size, $\sigma^2(t) = E[\{n(t+t) - n(t)\}^2]$, increases with the census period. The solid circles are the average for the examined populations, which, fitted to a power law (black line), increases as $(t)^{2H}$ with $H = 0.55 \pm 0.01$. The spawning biomass is walking a geometric random-walk [23] at short periods $t < 10$ years. (B) The coarse-grained plots of variance trajectories (the same as the data in panel A). The mean square $j[T_{eq}]$ -year difference $\sigma^2(j[T_{eq}])/2\sigma_n^2$ is plotted at $j = 1, 2, \dots$

dynamics is separable from the effects of environmental variability. Let $\hat{\xi}^2 = w^2 \xi^2 / (1 - \lambda\beta_\xi)$ and $\hat{f}^2 = F_\star^2 f^2 / (1 - \lambda\beta_f)$ with $\lambda = 1 - \gamma$. Taking the mean squares over Eq.(2) and the Δt -year difference of population size, $n(t + \Delta t) - n(t)$, with AR(1) disturbance terms mediates the following two relations, respectively,

$$\frac{\sigma^2}{r} \frac{2}{n} = \gamma - \sum_{k \in \{\xi, f\}} \hat{k}^2 \beta_k / \frac{2}{n} \quad (3)$$

with subscript k representing ξ or f , and

$$\gamma \sum_{\Delta t=0}^{\infty} \rho(\Delta t) = 1 + \frac{2}{n} \sum_{k \in \{\xi, f\}} \hat{k}^2 \beta_k / (1 - \beta_k) \quad (4)$$

with the autocorrelation function $\rho(\Delta t) = (1 - \gamma)^{\Delta t} + \rho_1(\Delta t)$, where the correction term

$$\rho_1(\Delta t) = \frac{2}{n} \sum_{k \in \{\xi, f\}} \hat{k}^2 \beta_k \frac{\lambda^{\Delta t} - \beta_k^{\Delta t}}{\lambda - \beta_k} \quad (5)$$

is due to memory effects in the variable recruitment and fishing mortality. From the recursion, $n(t) = \sum_{j=0}^{\infty} \lambda^j (t - j)$, a corollary to Eq.(4) is obtained:

$$\frac{2}{n} = \sum_{k \in \{\xi, f\}} (1 + \lambda\beta_k) \hat{k}^2 / (1 - \lambda^2). \quad (6)$$

Eqs.(3) and (6) yield the equation for γ

$$\gamma^2 \frac{2}{n} + (1 - \gamma) \frac{2}{r} = \frac{2}{\eta} \quad (7)$$

with $\frac{2}{\eta} = w^2 \xi^2 + F_\star^2 f^2$. According to the relation (Eq.7) connecting γ with population fluctuations, Eq.(2) yields

$$\frac{n(t+1) - n(t)}{r} = -\gamma \frac{n(t)}{r} + \sqrt{1 - \gamma + \gamma^2 \frac{2}{r}} \frac{(t+1)}{\eta}, \quad (8)$$

implying that, if these populations are governed by undercompensatory dynamics, external noises mask signals for evidence of deterministic behavior of the systems. Unless the population exhibits perfect- or over-compensation ($\gamma \geq 1$), the relationship between $r(t) [= n(t+1) - n(t)]$ and $n(t)$ is plagued by large variance in growth rate; most of the changes in population size occur in a density-independent manner.

The average relaxation time of population fluctuations defines the equilibration time T_{eq} :

$$\sum_{\Delta t=0}^{\infty} \rho(\Delta t) = \sum_{\Delta t=0}^{\infty} \exp(-\Delta t/T_{eq}), \quad (9)$$

where T_{eq} is estimated with Eq.(4). After the time T_{eq} memory of the initial conditions is lost: the population unbalance (i.e. deviation from the equilibrium size) is expected to decay away in an exponential fashion with a time constant given by the equilibration time T_{eq} . The asymptotic elasticity with respect to change in population size measures the strength D of total density dependence [18]:

$$E[n(t+1) - n(t)|n(t) = n] = -Dn, \quad (10)$$

i.e. the expectation of change in population size given $n(t) = n$ is equal to 100 D percent negative feedback. Since the total density dependence is the asymptotic multiple growth rate of population per year, $-\ln(1 - D)$ reads the asymptotic decay constant. Therefore, the total density dependence is estimated as

$$D = 1 - e^{-1/T_{eq}}. \quad (11)$$

Accordingly, Eq.(10) is iterated to give the conditional mean of T_{eq} -year difference:

$$E[n(t + T_{eq}) - n(t)|n(t) = n] = -(1 - e^{-1})n. \quad (12)$$

I now apply the above theory to examine the density dependence by using the fish population time-series in the North Atlantic. Since the length of each time-series data is longer than the equilibration time, $L > T_{eq}$, the examined populations fluctuate about the time-series average; the population changes in the T_{eq} -year interval level out (Fig.1B). The relationship of $r(t)/D$ to $n(t)$ contains much noise in population growth (Fig.2A). There is no or negligible correlation between $r(t)$ and $n(t)$. On the other hand, at large temporal scales $\Delta t > T_{eq}$, it is expected that the time series is mean-reverting and that the negative relationship (Eq.12) is testable. These are indeed found: when $y = n(t + T_{eq}) - n(t)$ are plotted against $x = n(t)$, the data fall around the line $y = -x$ as shown in Fig.2B. The result quantifies the fact that the number of years monitored has a strong positive influence on the evidence for density dependence.

4 Indeterminacy

When one performs some observations for actual years L , the uncertainty in locating the population equilibrium, $\Delta\bar{n} = SD[\bar{n}]$, i.e. the standard deviation of the empirical mean $\bar{n} = L^{-1} \sum_{t=1}^L n(t)$, propagates into the density dependence. The variance of $\bar{n}$ is written as [18, 21],

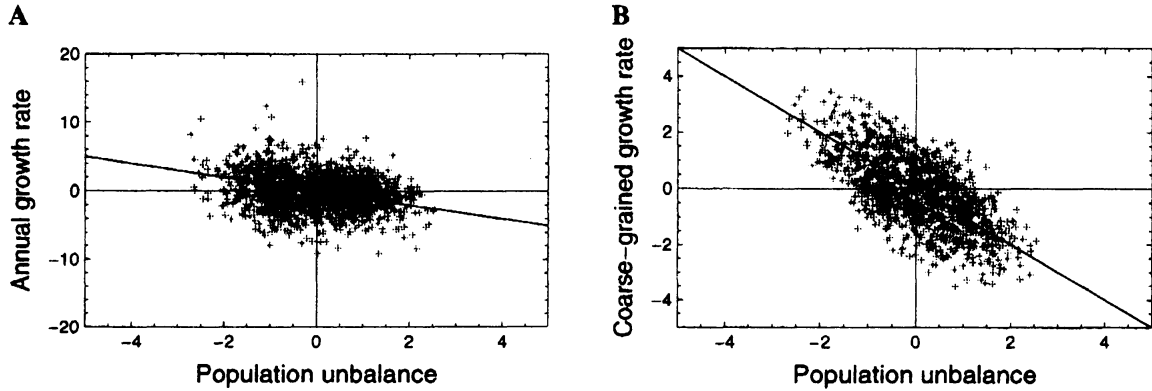


Fig. 2: Population growth diagram on fine- and coarse-grained scales. (A) Aggregated plots of annual growth rate (divided by D) against population abundance. The coefficient of determination $R^2 = 0.05$. x - and y -axes are scaled by σ_n . The solid line represents $y = -x$. (B) Relationship between $[T_{\text{eq}}]$ -year growth rate and population unbalance from equilibrium. $R^2 = 0.44$.

$\text{Var}[\bar{n}] = \frac{2}{n} L^{-2} \sum_{i,j=1}^L \rho(i-j)$. Making use of the explicit form for the autocorrelation function yields $\text{Var}[\bar{n}] = [2 \sum_{\Delta t=0}^{\infty} \rho(\Delta t) - 1] \frac{2}{n} L^{-1} + \mathcal{O}(L^{-2})$, giving, by virtue of Eq.(9), a time-equilibrium uncertainty relation

$$\Delta \bar{n} / n = \sqrt{L_c / L \pi} + \mathcal{O}(L^{-3/2}) \quad (13)$$

with $L_c = 1 + 2 / (e^{1/T_{\text{eq}}} - 1) \pi$, where $\mathcal{O}(L^{-3/2})$ denotes a remainder term of order $L^{-3/2}$ given by $\varepsilon L^{-3/2} \sqrt{\pi / 4 L_c}$ with

$$\varepsilon = -\frac{2\lambda(1-\lambda^L)}{(1-\lambda)^2} \left(1 + \sum_{k \in \{\xi, f\}} \frac{\beta_k}{\lambda - \beta_k} \frac{\hat{\alpha}_k^2}{n} \right) - \sum_{k \in \{\xi, f\}} \frac{2\beta_k(1-\beta_k^L)}{(1-\beta_k)^2} \frac{\beta_k}{\lambda - \beta_k} \frac{\hat{\alpha}_k^2}{n}. \quad (14)$$

Any observation over a short duration is associated with large indeterminacy. The population equilibrium $\ln S_*$ chosen as the sample mean and the number of years in the census are complementary: the uncertainty of population equilibrium is decreased by increasing the duration of observation.

For normally distributed n with $E[n|n \geq 0] = \pm n \sqrt{2/\pi}$, the inequality $L_c < L$ is translated into $\Delta \bar{n} < \pm E[n|n \geq 0] / \sqrt{\pi}$. It is then expected that the negative relationship between mean growth rate and mean abundance, conditioned on a current population size that is larger (or smaller) than the equilibrium size, is visible. It is difficult to judge whether the system is heading toward the equilibrium point in the time series of length less than the complementary time $L_c [= 2\pi T_{\text{eq}} + \mathcal{O}(T_{\text{eq}}^{-1})]$; then $E[n|n \geq 0]$ are in the uncertain range of $\pm \sqrt{2} \Delta \bar{n}$. Though, when plotting annual growth rate against population size, the relationship well looks like a shotgun pattern (Fig.2A), the negative relationship with marked correlation can be seen as an average in the time-series data over $L > L_c$ years (Fig.3A); after averaged over sizes $n > 0$ (or $n < 0$) in the data comprising $L < L_c$ years, the dependence of $E[r|n \geq 0]$ on $E[n|n \geq 0]$ remains vague (Fig.3B).

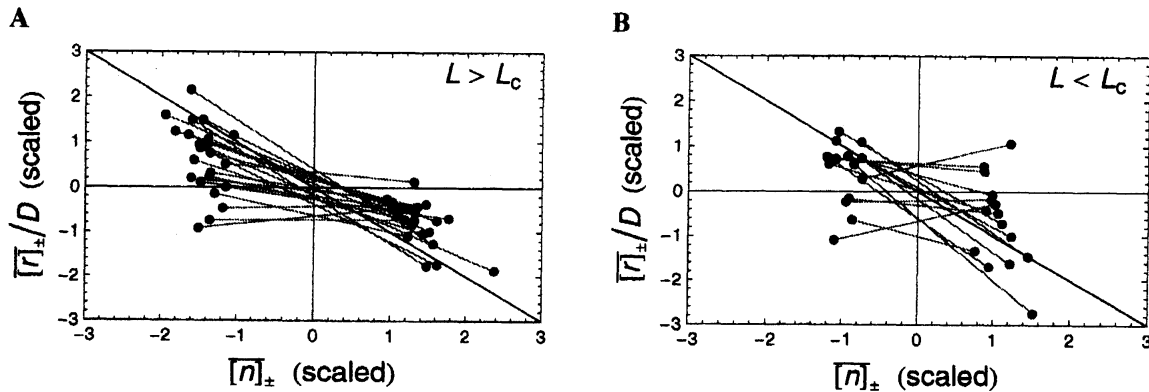


Fig. 3: Diagrams (scaled by $\sqrt{2/\bar{n}}$) of mean growth rate $\bar{r}_{\pm}$ (divided by D) versus mean abundance $\bar{n}_{\pm}$, conditioned on a current population unbalance $n \geq 0$. The negative feedback only becomes statistically visible with an observation series of length $L > L_c$ years (panel A; $R^2 = 0.62$): the bivariate plots fall around the black line $y = -x$. For $L < L_c$, the diagrams are plagued by much scatter (panel B; $R^2 = 0.35$).

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