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ASSESSING DENSITY DEPENDENCE USING INTRA-ANNUAL COUNTS

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Abstract. If causes of population fluctuation vary temporally, then tests that search for density dependence in long time series cannot distinguish, at any given time, how much population change is due to density-dependent or density-independent factors. For some species' dynamics, however, it is possible to determine over a restricted period whether density-dependent factors are involved in reducing population densities. I use a new Return Trajectory Likelihood Ratio Test (RTLRT) to determine whether a population perturbed to high density (e.g., by periodic recruitment) exhibits density dependence by returning to a positive asymptote (or leveling density, L) or is density independent and, through proportional hazards, approaches zero exponentially.

In a series of simulations, declines after recruitment were mimicked by creating sequences that changed due to a combination of density-dependent and density-independent factors. Until the sequence dropped below L , losses due to each mortality type were combined; after that point the density-dependent component was discontinued. The power of the test was assessed over a range of decline rates (e^{-b} , where $b = 0, 0.1, 0.25, 0.5, 0.75, 0.9, 1$) to zero and to L , initial density values (2, 4, and 6 times higher than L), and observation and process errors (e^{σ} where $\sigma = 0.1, 0.25, \text{ and } 0.5$). Test size was assessed by generating trajectories with no density-dependent decline.

These simulations identified four critical parameters that influence the likelihood of detecting density-dependent decline. (1) Detection rates change with the ratio of initial recruitment peak to leveling density: high peaks generally increase detection, although they may decrease detection of slow density-dependent declines. (2) High rates of density-dependent decline relative to density-independent decline also improve detection, except that populations rapidly dropping below L will appear density independent regardless of dynamics governing change prior to that time. (3) Error reduces detection of density dependence, except when declines are shallow and process error is assumed. (4) Slow rates of density-independent decline (to <10% of original value) cause the RTLRT to detect density dependence when it is not present (i.e., size is excessive for slow declines).

As an example of how the RTLRT may be used, I apply it to four years of monthly counts of an intertidal isopod, *Idotea wosnesenskii*, which recruits annually to high densities under boulders. Based on the RTLRT, subsequent declines were density dependent in some years, although detection differed with the assumption of process or observation error, and with the use of separate or averaged samples. In addition to density dependence, selective mortality of one class of individuals or mortality balanced by continuing low immigration could also cause steep declines to L . For isopods, however, densities were higher under boulders with small depressions than under smooth controls, suggesting that declines may occur when densities exceed the number of safe sites available. The postrecruitment decline of *I. wosnesenskii* appears to be at least partially density dependent.

Key words: density dependence; habitat heterogeneity; *Idotea wosnesenskii*; limitation; maximum likelihood; observation error; population dynamics; process error; recruitment; regulation; simulations; time series.

INTRODUCTION

Density dependence, in the sense that per capita rates of population change depend on population size, predicts that populations should decline rapidly from densities exceeding sustainable levels (Pollard et al. 1987, Murdoch and Walde 1989). Experimental tests, which are widely recognized as superior indicators of density dependence because they avoid the complicated causes

of natural population fluctuations (Berryman 1991, Murdoch 1994), often compare trajectories of control populations and those that have been artificially augmented (Harrison and Cappuccino 1995). Higher mortality rates when individuals are abundant imply that some mortality sources act in a density-dependent manner. Natural recruitment, just like an experimental manipulation, can create populations of extremely high densities. Thus, similar comparisons between the dynamics of low- and high-density populations can be carried out on populations that naturally span a wide density range. Numerous organisms in marine environments have periodic pulses of recruitment (fishes:

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Elliot 1984, Pfister 1995; barnacles: Gaines and Roughgarden 1985, Gaines and Bertness 1992; kelps: Paine 1979, Pfister 1992; bivalves: Ayers 1956), as do many terrestrial plants and insects (Gaston and Lawton 1987, Knell 1998). This paper focuses on *Idotea wosnesenskii* (Brandt, 1851), a marine isopod with conspicuous late-summer recruitment into low-mid intertidal areas.

Many techniques already exist for detecting density dependence in annual, univoltine species (Morris 1959, Varley and Gradwell 1960, Smith 1961, Bulmer 1975, Gaston and Lawton 1987, Pollard et al. 1987, Turchin 1990, Crowley 1992, Holyoak 1993, Dennis and Taper 1994, Murdoch 1994, Fox and Ridsdill-Smith 1995, Turchin 1995). Some work particularly well when populations begin far from their equilibrium range (Slade 1977, Pollard et al. 1987), such as after a recruitment peak. However, most of these techniques share three drawbacks. First, they require long time series of annual censuses (>20 yr) because they only achieve reasonable statistical power with large sample sizes (Slade 1977, Hassell et al. 1989, Solow and Steele 1990, Godfray and Hassell 1992, Woiwod and Hanski 1992). Second, sampling error often makes density dependence more likely to be detected regardless of whether density-dependent factors are actually present (Pielou 1974, Dempster and Pollard 1986, Wolda and Dennis 1993). Finally, most tests require that the dynamics governing population change be described by a particular model, which may not accurately reflect actual population dynamics. For instance, the "strength" of density dependence (i.e., the rapidity of a return towards an equilibrium) can be a function of density or its logarithm (Turchin 1995). When different underlying models are explored, sometimes trajectories are essentially indistinguishable (Morris 1990), and in other cases different models differ substantially in whether they create (Solow 1990) or detect (Getz 1996) density dependence.

Relying on long time series presents practical problems because data are difficult to gather, but conceptual problems are still more severe. Traditional tests for density dependence purport to address how much of the numerical variation in populations comes from sources influenced by density (Pollard et al. 1987, Berryman 1991, Vickery and Nudds 1991). However, in practice, these tests cannot quantify density dependence at any given time because they integrate factors affecting population abundances over long time series. At some periods, particularly when the population is near its equilibrium or external perturbations are large, populations may experience primarily density-independent fluctuations. At other times, when populations approach a ceiling or floor (e.g., after a large perturbation), they may experience primarily density-dependent change tending to return them to intermediate abundances. Consequently, the strength of density dependence, and therefore its likelihood of being detected, should change over time.

The existence of density dependence is tautological for every species that does not go extinct (Murdoch 1994), and given sufficient time, densities eventually move away from extreme values. Instead of tests for density dependence, what is really needed is a way to link the pattern of population trajectories to more mechanistic understandings of why and how populations change in abundance (Krebs 1995). Such a link is provided by the new technique presented in this paper. The technique determines the extent to which population change is related to density at particular times, rather than over long periods. Specifically, it distinguishes density-dependent from density-independent decline following recruitment, by using maximum likelihood techniques to compare periodic counts to a model of exponential decline. If a model fits better when the trajectory approaches a positive value rather than zero, then the population shows density-dependent dynamics. In the absence of new recruits, a population experiencing constant proportional (density-independent) mortality inevitably declines to zero. Numbers may be limited by the abundance at the recruitment peak, but not regulated to return to a particular level. In contrast, exponential decline to a positive level is "density-dependent" because per capita mortality rates are higher when population density is above the level than when near it.

First I describe simulations designed to assess the ability of the technique to identify regulated populations, which decline toward a value >0 . The simulations show how power is affected by the height of the initial recruitment peak, the rate of density-dependent relative to density-independent decline, and the amount of error, incorporated as either observation (=sampling, measurement) or process error. When observation error predominates, discrepancies between observed values and a smooth decline stem from mis-measurement (or from an incorrect specification of population dynamics). In creating such sequences, the error in one measurement does not affect subsequent expected values. When process error predominates, the dynamics of the decline vary over time, and each observed value influences the subsequent expected value (see *Methods* section in Pascual and Kareiva 1996). The assumption of error type affects parameter estimation (Walters and Ludwig 1981, Pascual and Kareiva 1996) and detection of density dependence (Slade 1977, Crowley 1992).

I then apply the technique to four years of monthly counts of a marine isopod, *Idotea wosnesenskii*, which shows dramatic annual fluctuations in density. Population counts and life history data are used to: (1) assess whether postrecruitment population decline is density dependent; (2) calculate the amount of error in the counts; and (3) provide corroboration, through changes in isopod size, sex ratio, and stage of reproduction, as well as through habitat manipulation, of causes of the decline.

METHODS

Model of density-dependent vs. density-independent decline

Decline equations.—The population dynamics considered here are restricted to declines after recruitment peaks. Density-independent declines were assumed to be exponential, which describes mortality of a constant proportion of the population in each time interval regardless of population size. Density-dependent mortality can be incorporated in this model with a single additional parameter, a density towards which a population tends to return, which I will call a “leveling density” to avoid the static notion of equilibrium. In these models, N is population size, N_t its value at time t , N_0 the initial recruitment peak, and \hat{N} the expected value in the absence of error. The parameter b represents the rate of decline, and higher values imply faster rates of decline ($b > 0$). If exponential decline is represented as

$$\hat{N}_t = \hat{N}_0 \times e^{-bt} \tag{1}$$

then the model of decline to a positive leveling density (L , where $L < N_0$) is

$$\hat{N}_t = (\hat{N}_0 - L) \times e^{-bt} + L. \tag{2}$$

Eq. 2 represents the full model, whereas Eq. 1 is a reduced version of Eq. 2 in which L is constrained to a value of zero. In order to distinguish the decline rates estimated by the full and reduced models, I will use subscripts: b_z is the decline rate to zero and b_L is the decline rate to a leveling density.

Model justification.—In choosing a model to represent a decline to a leveling density, I had numerous options, including a suite of models of density dependence (Getz 1998). I chose Eq. 2 because it includes a specific parameter for leveling density and requires just one parameter to be added to the reduced model.

Eq. 2 includes only density-dependent decline, whereas actual changes in population abundance might more realistically involve a combination of density-dependent and independent decline. If these processes occur simultaneously, then population change would involve a combination of Eqs. 1 and 2 until N reached L , after which only the density-independent component (Eq. 1) would continue. I employ this strategy to simulate population declines (see Eq. 6), but simply compare Eqs. 1 and 2 when testing for density dependence in any given trajectory, which provides a conservative test involving few variables.

Another possible description of density-dependent decline would involve a rate of decline that acts on the logarithm of the population density, rather than on the actual density (Turchin 1995). In practice, there may be little difference between the trajectories resulting from each assumption, although the same absolute change in abundance can be achieved with a smaller rate of decline applied to ln-transformed density or a

larger rate of decline applied to untransformed density. The model in this paper assumes that populations decline as a function of density. To determine whether detection of density dependence is sensitive to this assumption, I include in my simulations (described in detail below) several cases in which trajectories are generated based on ln-density dependence but are analyzed assuming density dependence.

Test statistic.—I use a likelihood ratio test (Edwards 1972, Hilborn and Mangel 1997) to assess density dependence in species with periodic recruitment. The likelihood ratio test compares the relative fit of full (Eq. 2) and reduced (Eq. 1) models to population counts, given maximum likelihood estimates (MLE) of parameters. For MLE, population abundances are ln-transformed to account for lognormal error structure in count data: variance is expected to increase with mean population density, and densities cannot fall below zero. The Return Trajectory Likelihood Ratio Test (RTLRT) developed here tests whether a population perturbed to high density returns to L or to zero.

The likelihood ratio (R) is equivalent to twice the difference in negative log likelihoods, where the superscripts f and r denote full and reduced models, and n population counts are available:

$$R = 2 \left\{ \left[n \left(\ln \sigma^f + \frac{1}{2} \ln(2\pi) + \sum_{i=1}^n \frac{(\ln N_i - \ln \hat{N}_i^f)^2}{2\sigma^{f2}} \right) \right] - \left[n \left(\ln \sigma^r + \frac{1}{2} \ln(2\pi) + \sum_{i=1}^n \frac{(\ln N_i - \ln \hat{N}_i^r)^2}{2\sigma^{r2}} \right) \right] \right\}.$$

R has a chi-square distribution with 1 degree of freedom (df), because the full and reduced models differ by one fitted parameter (leveling density $L = 0$). Variances of the full and reduced models are unknown but can be approximated by

$$\sigma^{f2} = \sum_{i=1}^n (\ln N_i - \ln \hat{N}_i^f)^2$$

and

$$\sigma^{r2} = \sum_{i=1}^n (\ln N_i - \ln \hat{N}_i^r)^2$$

respectively. Then, the likelihood ratio simplifies to

$$R = 2n[\ln(\sigma^r) - \ln(\sigma^f)] = n \left[\ln \left(\frac{\sigma^f}{\sigma^r} \right)^2 \right] = n \left[\ln \left(\frac{\sum_{i=1}^n (\ln N_i - \ln \hat{N}_i^r)^2}{\sum_{i=1}^n (\ln N_i - \ln \hat{N}_i^f)^2} \right) \right] \tag{3}$$

which is a function of the ratio of the sum of squared deviances from the reduced model relative to the sum of squared deviances from the full model.

Error in models.—Counts of declining populations are unlikely to lie exactly along a trajectory of density-

dependent or density-independent decline. Instead, error shifts samples away from the expected trajectory. This error can have two sources. Observation error (ϵ_v) stems from mismeasurement (Walters and Ludwig 1981, Pascual and Kareiva 1996). The error involved in one measurement is assumed not to affect the next measurement; that is, population dynamics occur independent of sampling noise. Process error (ϵ_w) stems from variation in the processes governing the decline, meaning that rates of decline, leveling densities, or external perturbations change over time. Both types of error likely affect population estimates, but they cannot be fit concurrently without making an assumption about their relative values or the magnitude of one type. The assumption of which error is most important influences both the values of parameter estimates and their certainty (Pascual and Kareiva 1996). Rather than choosing between process and observation error models (e.g., most tests for density dependence invoke only process error [Pollard et al. 1987, Reddingius and den Boer 1989, Holyoak 1993, Dennis and Taper 1994], as do many stock-recruitment models [Walters and Ludwig 1981]), the best strategy is to explore error types separately, to determine how each affects detection of density dependence (Hilborn and Walters 1992).

Observation error was incorporated into simulated population declines as

$$N_t = \hat{N}_t \times e^{\epsilon_{v,t}} \quad (4)$$

where $\epsilon_{v,t}$ is drawn from a normal distribution with standard deviation σ_v . The RTLRT subsequently minimized the sum of squares between simulated observations and the expected decline from N_0 (all ln-transformed) (Fig. 1A). In contrast, process error was simulated as

$$N_t = g(N_{t-1}) \times e^{\epsilon_{w,t}} \quad (5)$$

where g represents the rules governing population decline. Any discrepancy ($\epsilon_{w,t}$) from the underlying model in this case did affect subsequent points. The RTLRT minimized the sum of squares between each observation and the expected decline from the previous observation (all ln-transformed) (Fig. 1B). Consequently, trajectories that were fit with process error could only include a single sample at each time step, whereas observation error allowed multiple samples.

I added process error to simulated declines in a manner that makes no assumption about the parameter most influenced by error, which is similar to Dennis and Taper's (1994) "random shock to population growth rate" and in contrast to Holyoak (1993), who applied error only to the parameter determining the "strength of density dependence." This strategy is the most general approach, making no assumption about whether b or L or both vary among time steps. In my simulations, process error occurred after the action of any density-dependent or density-independent factors, which Crowley (1992) believes applies to some but not all situa-

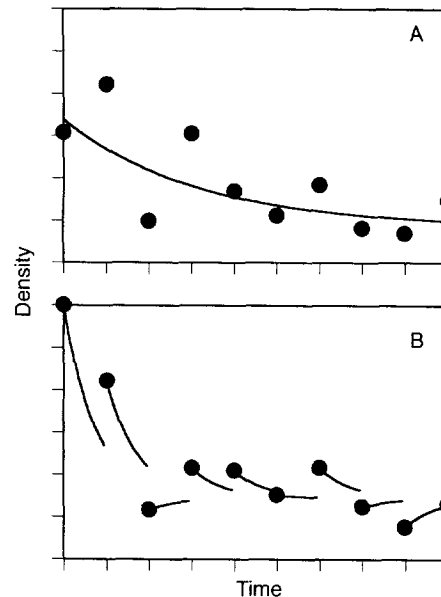


FIG. 1. Schematic representation of (A) observation and (B) process error. The points represent simulated density-dependent declines (Eq. 2), with $N_0 = 6$, $L = 1$, $b_L = 0.75$, and $\sigma_v = \sigma_w = 0.5$. Maximum-likelihood techniques were used to find parameter values that minimize the sum of squares of the difference between expected and actual values (distance between each data point and best-fit line, ln-transformed). In (A), $N_t = (3.39 - 1.77) \times e^{(-0.32t)} + 1.77$, and in (B), $N_t = (N_{t-1} - 1.45) \times e^{(-1.37)} + 1.45$.

tions. In a sense, then, process error acts as an additional source of density-independent fluctuation, which may shift the population above or below the expected abundance.

Assuming observation error only, the full model has three parameters (N_0 [peak], b [decline rate], L [leveling density]), and the reduced model has two ($L = 0$). Assuming process error, N_0 is an irrelevant parameter because the prediction at each time step depends only on the observed value at the previous time. Also, sample size of points used to fit the decline (n) is reduced by one because there is no expected value to compare to N_0 .

Because the likelihood ratio has a chi-square distribution, Eq. 2 provides a better fit than Eq. 1 at the $\alpha = 0.05$ level if $R > 3.84$ in Eq. 3 (Edwards 1972, Stuart and Ord 1991).

Simulations

To evaluate the ability of the RTLRT to detect density dependence, I applied it to data simulated with known underlying dynamics. Simulations with error were run for 10 time steps, corresponding roughly to monthly counts between protracted annual recruitment events characteristic of *I. wosnesenskii*. I explored the behavior of >65%, randomly chosen, of the combinations of the following parameters: ratio of peak height to leveling density (Eqs. 2, 4, 6), rate of ex-

ponential decline to 0 ($b_z = 0, 0.1, 0.25, 0.5, 0.75, 1$), and rate of exponential decline to leveling density L ($b_L = 0, 0.1, 0.25, 0.5, 0.75, 1$). This last parameter was only used in the simulation as long as the current and predicted densities were higher than the leveling density ($N_{i-\tau} > L$ and $N_i > L$), where τ is the time interval between simulated counts. Declines with both density dependence and density independence were simulated with the formula

$$N_i = N_{i-\tau} e^{-b_z \tau} - (N_{i-\tau} - L)(1 - e^{-b_L \tau}) \quad (6)$$

and error was incorporated using Eqs. 4 and/or 5.

The same ratio of peak height to leveling density (N_0/L) provides an identical fit regardless of the absolute values of these parameters (*personal observation*). Identical fits are also achieved for all models with the same product of decline rate and time step ($b \times \tau$) (*personal observation*). Because errors are lognormally distributed, they alter observations by relative, not absolute amounts, and I was able to rescale peak height and decline rate so that $L = 1$ and $\tau = 1$. The rate of decline has a bounded range of interesting parameter values. If overall decline (combining exponential decline to zero and to L) is too slow, populations do not approach their leveling density within the full time of observation; if too high, they pass below the leveling density almost immediately. In either case, a decline to a positive leveling density cannot be distinguished from a decline to zero.

Trajectories were also created in which declines to L affected ln density, while declines to zero continued to affect untransformed density. For these simulations, values of b_L were chosen such that density-dependent trajectories ($b_z = 0$) reached the same final values as in the main simulations.

For each set of parameters, I created 200 separate "population" declines with process error, observation error, or both. Errors ($\varepsilon_{v,i}$ or $\varepsilon_{w,i}$) were randomly drawn, at each of 10 time steps, from a normal distribution of mean = 0 and $\sigma = 0.1, 0.25, \text{ or } 0.5$. The same 200 series of 10 random errors were used with each set of parameters. (To simulate both observation and process error concurrently required 20 random errors, since two were incorporated at each time step.) For some simulations with high error ($\sigma = 0.5$), I added additional samples at each time step of the simulations to explore the influence of sample size on RTLRT results. Using these multiple samples, I also calculated average values at each time step and performed the RTLRT.

For each simulation, I searched for new (MLE) parameters for Eqs. 1 and 2 that best fit the decline. Trajectories generated with observation error were fit assuming observation error; similarly, those generated with process error were fit assuming process error. Trajectories generated with both process and observation error were fit twice, once assuming observation error only, and again assuming process error only. A decline was determined to be density dependent if the RTLRT

indicated that Eq. 2 fit significantly better than Eq. 1. All simulations were run in a visual basic program in Microsoft Excel 5.0.

The estimated power of the RTLRT, for each parameter combination and error level, is the proportion of the 200 runs that results in significantly better fit with than without density dependence. The size, which refers to detection of density dependence when it is not present in the parameters used for the simulation, comes from runs with $b_L = 0$.

Annual declines in Idotea wosnesenskii

The marine isopod *Idotea wosnesenskii* lives on algae, interstitially among mussels, and under rocks in mid-low intertidal areas of rocky shores from Alaska to southern California (Brusca and Wallerstein 1979, Rafi and Laubitz 1990). Males reach lengths of 35 mm, and females are rarely larger than 25 mm. Females become reproductive in December, and brood offspring underneath overlapping oostegites on their ventral surface (marsupium) until the juveniles reach a length of 4 mm (*personal observation*). Many marine isopod species experience annual fluctuations in numbers associated with the release of offspring and their subsequent disappearance (Naylor 1955, Lee 1966, Salemaa 1979).

I counted a population of *I. wosnesenskii* in a boulder field on an east-facing beach of Tatoosh Island, Washington, USA (48°24' N, 124°44' W), a site at which gravel and boulders shifted over time. Unlike other populations of isopods, peak densities occur several months after release of brooded juveniles, when large nonreproductive individuals recruit to the boulder field (*personal observation*). Although I often examined different boulders during each count, I tried to select those where isopods would be most abundant. These tended to be boulders at about +0.5 m above mean lower low water, not buried in gravel, ranging in area from 100 to 2000 cm². At monthly intervals during low tide series from July 1992 to August 1996, I turned over 3–5 boulders and collected all isopods underneath. This sampling regime provided a biased sample of boulder field densities, concentrating on boulders under which isopods were most common. Despite my selectivity, I occasionally chose boulders that were anoxic underneath and harbored few isopods. Any samples with two or fewer individuals were censored, as these represented poor habitat. Isopods were returned to the boulder field after they were recorded.

For each isopod I recorded the following data: length (in millimeters), sex (males with bristles on their legs, females with marsupia), and, for females, developmental stage of brooded offspring. Offspring were categorized as eggs, embryos without legs, embryos with legs, and juveniles. Females with empty marsupia were also noted.

Per capita reproduction was based on the brood sizes of 78 females with eggs or embryos, collected from a beach adjacent to the study site in December 1992 and

March 1993. Based on 18 females kept in the laboratory during spring 1995, developing young took one month to reach the embryo stage, and two months before release. Juvenile growth rate (5–15 mm initial length) was 2.0 ± 0.36 mm/mo (mean ± 1 SE, $n=19$). Thus, each female observed with eggs during monthly field surveys should represent an independent reproductive event, and juveniles should take 6 mo to reach reproductive size.

I applied the RTLRT to each year's recruitment peak and subsequent decline. The RTLRT determined whether a model of exponential decline to a positive leveling density fit the count data significantly better than an exponential decline to zero. The tests were performed assuming either observation or process error. Average densities for these analyses were weighted by boulder area.

Causes of population change

The RTLRT reveals whether count data are consistent with density-dependent decline, but does not indicate causes of population change. I separately examined some potential causes of isopod fluctuations, including class-specific mortality and habitat availability. Immigration could also compensate for on-going population declines, but nonreproductive individuals in the samples >6 mo after the peak were excluded from analyses to eliminate this possible cause of leveling population abundance.

If certain isopod classes contribute disproportionately to the decline, then size structure or sex ratio of the population should change. These data were available from the monthly counts. In particular, I related average size of males to isopod density using a non-parametric test for correlation in ranks (Spearman's r_s), and compared the frequency of females at various stages of brood development with expectations based on the proportion of time they spent at each stage when monitored in the laboratory (G test).

If populations are regulated by habitat availability, then providing additional habitat should increase population densities. Because other marine invertebrates respond to rock microtopography (Emson and Faller-Fritsch 1976), I altered the undersides of artificial "boulders." Holes (1 cm diameter \times 0.5 cm deep) were drilled into five 20 \times 20 cm cement bricks. These bricks were paired with undrilled bricks and added to the boulder field. I monitored isopod densities beneath these bricks four times between July and September 1995. Isopods were removed from the bricks after each count. Because of the presence of several samples without isopods, I analyzed the results using a generalized linear model with Poisson error, where the factors were date, replicate, and treatment (Crawley 1993). Overdispersion was corrected by an empirically derived scale parameter (Crawley 1993).

Error in population estimates

The magnitude of observation or process error in monthly counts of isopods was calculated from

$$\varepsilon_{v,j} = \ln \left[\frac{N_j}{\hat{N}_j} \right] \quad (7)$$

or

$$\varepsilon_{w,j} = \ln \left(\frac{N_j}{g(N_{t-1})} \right) \quad (8)$$

which are simply rearrangements of Eqs. 4 and 5. The magnitude of observation error (ε_v) was calculated from separate samples and from samples averaged by date; process error required average values. I examined these errors for normality and calculated standard deviations.

RESULTS

Simulations

Fig. 2 highlights the results of the simulations, showing how often the RTLRT detected density dependence in 200 simulated postrecruitment declines. Density dependence was generally easier to detect when most of the simulated decline was to L instead of zero (b_L large and b_Z small). Higher initial recruitment peaks also generally increased detection of density dependence. However, when density-dependent declines were slow, higher peak heights resulted in lower detection: for example, when $b_L = 0.25$ and $b_Z = 0$ ($\sigma_v = 0.5$), a rise in peak height from 2 to 6 was associated with a decline in density dependence from 13% to 5%. Increasing the rate of density-independent decline ($b_Z = 0.1$) actually raised detection of density dependence (to 17–32%). The overall faster rate of decline must bring the trajectory more rapidly towards L , so that an early steep and later gradual decline appear to approach a leveling density (less than the actual L).

As the amount of process error or observation error increased, the detection of density dependence declined (Fig. 2). For example, for a given combination of declines to L ($b_L = 0.5$) and to 0 ($b_Z = 0.1$), and for a low peak height ($\hat{N}_0 = 2$), an increase in observation error ($\sigma_v = 0.1$ to 0.5) reduced detection of density dependence from 57% to 22%, and a similar increase in process error reduced detection from 67% to 40%. Using both types of error in the simulations tended to increase overall error levels, and detection of density dependence declined accordingly (Fig. 2). Averaging multiple samples from a single time step tended to reduce error levels, and detection of density dependence in simulations became more common (Fig. 3A). When multiple samples were considered separately rather than averaged, error (negative log likelihood) increased but so did sample size, and detection of density dependence changed little (Fig. 3B).

An obvious exception to the general pattern that error reduced detection of density dependence was that slow

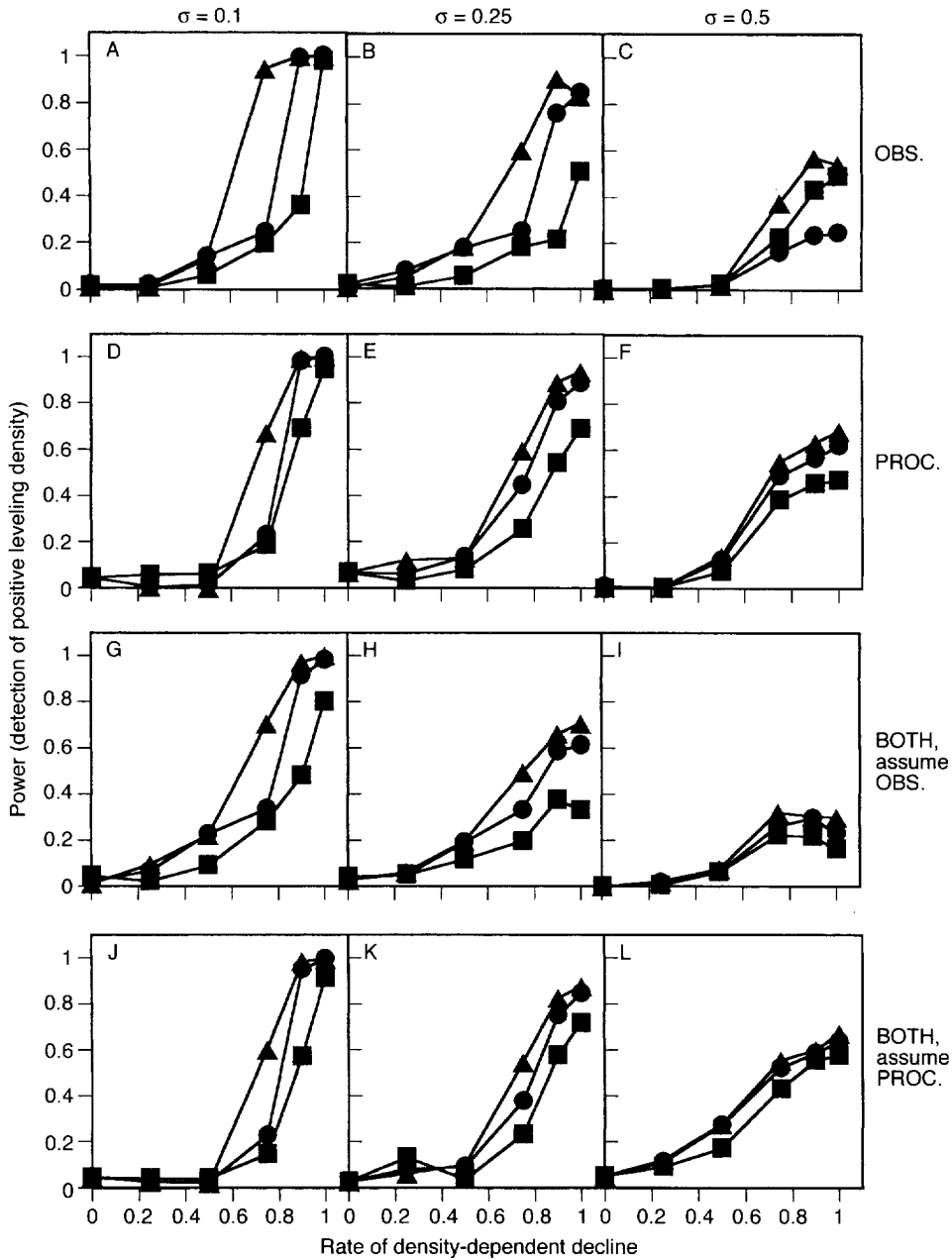


FIG. 2. Power and size of the Return Trajectory Likelihood Ratio Test for different parameter values and levels of error, based on the proportion of 200 simulated trajectories in which density dependence is detected. Error is incorporated as (A–C) observation error (OBS.), (D–F) process error (PROC.), (G–I) both, but assuming only observation error, and (J–L) both, but assuming only process error. Each column of graphs corresponds to power under a different magnitude of error (σ), and each graph shows results for three peak heights (solid square, $N_0 = 2$; solid circle, $N_0 = 4$; solid triangle, $N_0 = 6$). Although numerous combinations of density-dependent and density-independent decline were explored, the graphs show a subset of results for steep declines after recruitment, where $b_z + b_L = 1$.

declines, coupled with high process error, often appeared density dependent (and reduction of error did not necessarily improve detection [Fig. 3C]). In fact, slow density-independent declines ($b_z = 0.1$ – 0.25) appeared density dependent up to 40% of the time according to the RTLRT, even when no density dependence was included in the simulations; that is, test size

could be excessive assuming process error. However, <5% of the simulations appeared density dependent when populations declined at higher density-independent rates. The critical decline rate was $b_z > 0.25$, which would cause a population to decline by one-fourth at each of 10 time steps in the absence of error. Assuming that population declines were density de-

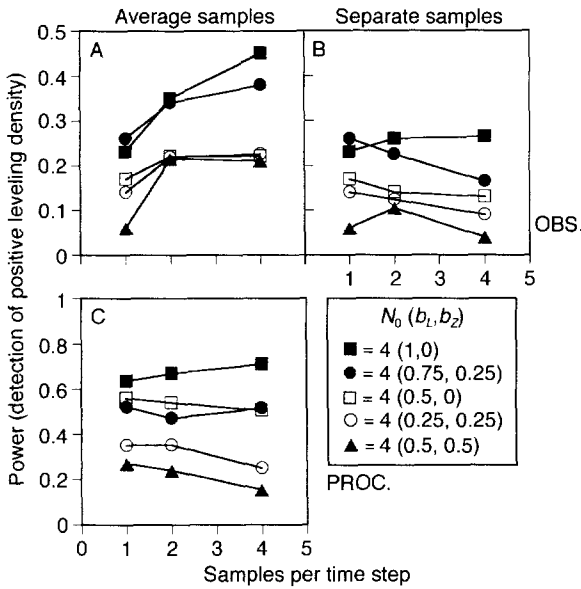


FIG. 3. Power of the Return Trajectory Likelihood Ratio Test (RTLRT) when multiple samples are collected at each time. Both observation ($\sigma_v = 0.5$) and process ($\sigma_w = 0.5$) error were incorporated in the simulations, which were analyzed by (A) averaging samples at each time and assuming only observation error, (B) keeping samples separate and assuming observation error, and (C) averaging samples at each time and assuming only process error. Values for initial peak height (N_0), rate of decline to L (b_1), and rate of decline to zero (b_2) are presented in the key.

pendent when in fact they were ln-density dependent had little effect on detection of a positive leveling density. Ln-density-dependent declines were more concave than their density-dependent counterparts, particularly when declines were rapid. Low peaks and slow declines favored detection of density dependence in trajectories generated with ln-density dependence, whereas high peaks and fast declines favored detection in density-dependent trajectories (Fig. 4).

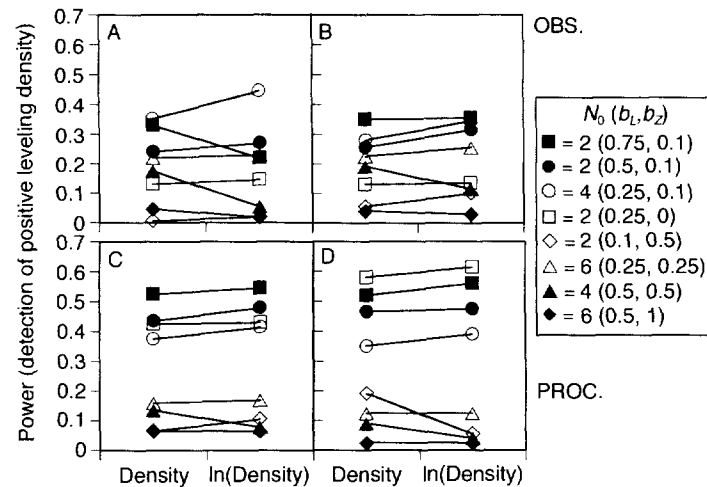


FIG. 4. Comparison of density-dependent and ln-density-dependent declines analyzed using the Return Trajectory Likelihood Ratio Test with decline rate assumed to affect untransformed density. One level of error is considered ($\sigma_v = \sigma_w = 0.25$). The rates for ln-density-dependent decline used in the simulations were chosen so that final densities would equal those reached by density-dependent declines acting on untransformed density (b_1). (A) observation error; (B) both, but assuming observation error; (C) process error; (D) both, but assuming process error. Values for initial peak height (N_0), rate of decline to L (b_1), and rate of decline to zero (b_2) are presented in the key.

Causes of population change in Idotea wosnesenskii

Idotea wosnesenskii showed dramatic annual cycles in population abundance (Fig. 5). New individuals, identifiable by size (<20 mm) and nonreproductive status, began appearing in the boulder field each July. Maximum population densities occurred as late as October. Recruitment peaks significantly exceeded average densities by as much as fivefold (Fig. 5).

Adding microtopography to the underside of cement bricks increased isopod densities relative to smooth controls (Fig. 6). In a generalized linear model, the only significant interaction term was date \times replicate ($\chi^2_{12} = 21.06, P = 0.05$), which suggests that the samples through time were independent. The main effect of treatment was highly significant ($\chi^2_1 = 46.77, P < 0.0001$), with drilled bricks harboring on average 2.60 times more isopods than undrilled bricks (standard error is asymmetric: 2.24–3.01).

In *I. wosnesenskii*, offspring number was correlated with female size, which accounted for 45% of the variation in brood size (Fig. 7). Estimated offspring production could account for the following year's recruitment peak if juveniles suffered mortality rates of 0.6–0.75 mo^{-1} outside the boulder field (Table 1). These juvenile mortality rates fell within estimates for benthic invertebrates (Strathmann 1985) and, surprisingly, were similar to estimates for adult isopods (Table 1).

Detection of density dependence in Idotea wosnesenskii

Declines from peak recruitment indicated a significant contribution from density-dependent sources in only one of four years, assuming observation error and considering each boulder as a separate sample (Table 1). When counts were combined by date, density dependence was detected in two of four years assuming observation error and three of four years assuming process error. The detection of density dependence in these

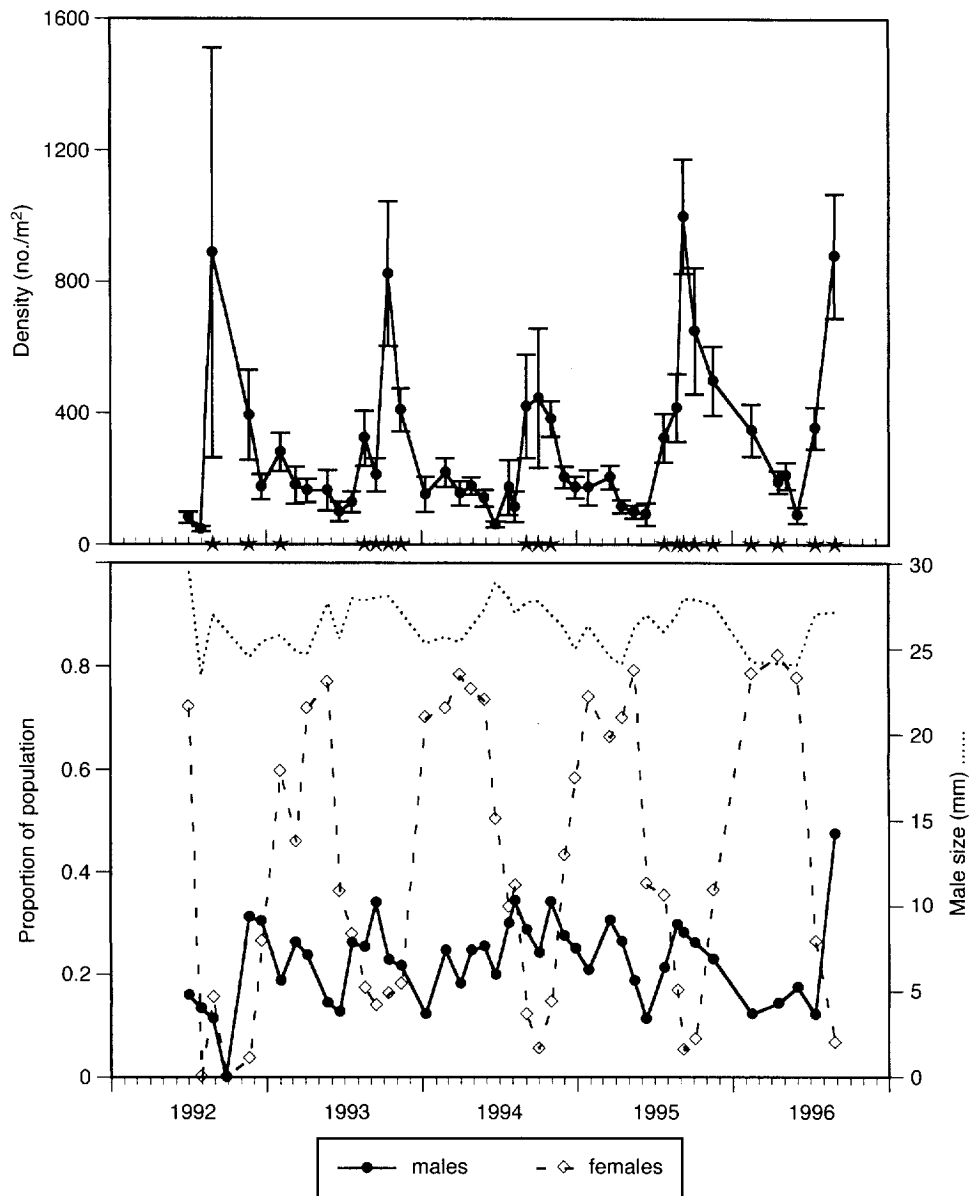


FIG. 5. Counts of *Idotea vosnesenskii* in the boulder field on Tatoosh Island. Samples came from 3–5 boulders each month. Mean density (± 1 SE) is reported in the upper panel. Stars indicate dates on which at least half of the samples are outliers (exceed 224 isopods/m², which is the upper 95% confidence limit [CL] of average density based on all samples). Confidence limits (CL) were calculated from ln-transformed abundances, because variance increases with the mean. The lower panel shows the proportions of males and females (which do not sum to 1 because some individuals were of indeterminate sex) and average male size.

cases is unlikely to be due to excessive test size, because overall decline rates exceeded $b = 0.5$.

The monthly isopod counts exhibited high error levels. Using Eq. 7 and considering each boulder as a separate sample, I calculated observation error at $\sigma_v = 0.5$ – 0.7 . Combining monthly values reduced sample size and level of error (σ_v and $\sigma_w = 0.25$ – 0.35) (Table 1), which work antagonistically to change the likelihood ratio. The fact that density dependence was more readily detected with combined samples suggests that

reduction of error more than balanced the reduction of sample size, which was also the case in the simulations (Fig. 3).

During the decline, the proportion of females in the population increased, probably because females recruited before I was able to distinguish their sex and then became ovigerous (Fig. 5). The proportion of females at each brooding stage should reflect the time required for offspring to develop through the stage, but females at late stages were underrepresented in the pop-

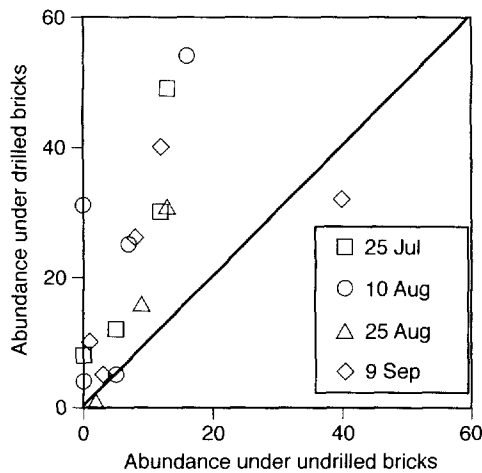


FIG. 6. Isopod response to experimental manipulation of habitat in 1995. Each point represents isopod numbers under a pair of cement bricks, one with and one without holes (1 cm diameter \times 0.5 cm deep); the 45° line shows the expected one-to-one relationship.

ulation relative to those at less advanced stages (Fig. 8; $G_4 = 113.2$, $P \ll 0.001$). Males made up less than a third of the population throughout the year, but average size of males became smaller during the popu-

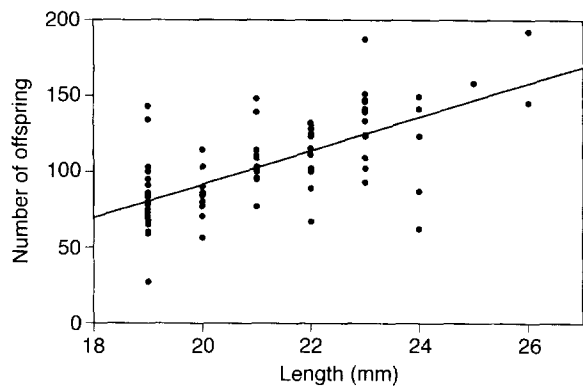


FIG. 7. Relationship between female length and brood size in *Idotea wosnesenskii*. Only females brooding eggs or embryos were used in the analysis. Simple linear regression: Number of offspring = $11 \times (\text{length of female}) - 129$; $n = 78$, adjusted $r^2 = 0.44$, $F = 61.4$, $P \ll 0.001$.

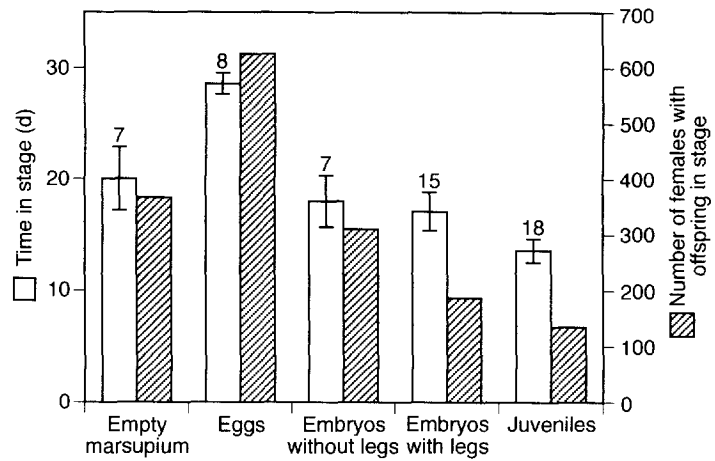
lation decline (Fig. 5). Average male size was correlated with population density (Pearson's $\rho = 0.46$, $P < 0.01$, $n = 41$ samples from August 1992 to August 1996). This pattern suggests a disappearance of large males initially recruiting into the population, while newly maturing males were small.

TABLE 1. Maximum-likelihood parameter estimates and outcome of Return Trajectory Likelihood Ratio Tests (RTLRT) for four years of population declines following recruitment in *Idotea wosnesenskii*.

Parameter	1992-1993 (28 Aug-20 Jul)	1993-1994 (14 Oct-25 Jul)	1994-1995 (3 Oct-25 Jul)	1995-1996 (9 Sep-14 Jul)
Process error, each date as a separate sample				
RTLRT	3.96	9.08	6.51	2.09
N_0 (N_0/L)	997 (8.0)	835 (5.7)	456 (3.3)	1042 (7.4)
L	125	147	138	141
b_L	0.55	1.19	0.78	0.38
n	8	8	9	7
Error (σ_w)	0.33	0.34	0.28	0.29
Observation error, each date as a separate sample				
RTLRT	1.95	4.89	6.21	0.08
N_0 (N_0/L)	846 (9.4)	814 (6.2)	480 (4.0)	867 (41.3)
L	90	132	119	21
b_L	0.37	0.89	0.61	0.22
n	9	9	10	8
Error (σ_w)	0.29	0.32	0.25	0.23
Observation error, each boulder as a separate sample				
RTLRT	0	3.99	1.87	0.11
N_0 (N_0/L)	447	658 (5.4)	339 (3.6)	803 (26.8)
L	0	122	93	30
b_L	0.17	0.83	0.12	0.23
n	44	42	49	40
Error (σ_w)	0.71	0.60	0.60	0.52
Prerecruitment dynamics				
N_F	422	399	363	
b_j	0.66	0.75	0.60	

Notes: Boldface numbers indicate that the full model (exponential decline to leveling density) fit significantly better than the reduced model (exponential decline to zero). N_0 is the estimated recruitment peak (=actual density given process error), L is the estimated leveling density, b_L is the monthly rate of decline from peak to leveling density (sometimes $L = 0$), and n is sample size. Rocks hosting two or fewer isopods and juveniles appearing >6 mo after the peak were censored from the analysis. Error in the counts was estimated from Eqs. 7 and 8 in *Methods: Error in population estimates*. The table also shows cumulative densities of females with eggs throughout each year's decline (N_F), and the juvenile (exponential) mortality rate (b_j) assuming average production of 104 offspring per female and 6 mo between release and the following recruitment peak.

FIG. 8. Developmental sequence of brooded offspring of *Idotea wosnesenskii*. The length of time spent at each stage of development comes from laboratory observations (left axis). Error bars represent standard errors, and sample sizes are given above each bar. Total numbers of females observed with offspring at each developmental stage include all records over four years (right axis).



DISCUSSION

The argument advanced in this paper is that patterns of population decline after recruitment contain information about causes of mortality. Density-independent factors should cause populations to decline to zero (exponentially if mortality is proportional), whereas density dependence should result in a decline to a positive leveling density (L). The ability of the RTLRT to detect this density dependence generally improves as: (1) error (observation, process, or both) declines, (2) peak height rises relative to L ; (3) rate of decline to L becomes more rapid; or (4) rate of decline to zero becomes shallower (Fig. 2). The test fails to detect density dependence when the population does not approach L over the time of observation. Conversely, slow density-independent declines can appear density dependent.

The isopod *I. wosnesenskii* recruited to boulder beaches on Tatoosh Island in late summer. When declines from recruitment peaks were significantly density dependent according to the RTLRT, decline rates were 0.6–1.2 mo^{-1} and peaks were 3–8 times higher than L . Error levels were higher when boulders were analyzed separately than when densities were averaged by date. Given these parameter values, simulations demonstrated that the RTLRT would detect density-dependent trajectories about half the time. Indeed, density dependence was only detected in two (observation error) or three (process error) of four years of isopod counts. The RTLRT suggests that isopods often declined after recruitment due to density-dependent factors, and may even have been experiencing density dependence in years when it was not detected, because the power of the test was low at observed error levels.

The RTLRT can accommodate a number of modifications of sampling regime and population dynamics. (1) If several counts are available for each time period, then counts may be tested for density dependence separately (for observation error only) or as an average (for observation or process error). Averaging increased test power, apparently by reducing error levels. Mul-

iple samples, considered separately, were less likely to be recognized as density dependent, since minimizing squared deviances in density tended to flatten the trajectory. (2) Density-dependent factors have traditionally been modeled either as a function of density or as a function of its logarithm, although nothing is known about when each model is more accurate. If density dependence is a function of \ln -density, but the RTLRT assumes it is a function of density, then test power changes only slightly. However, density-dependent declines could be described by numerous other models (Getz 1998), and the power of the RTLRT to detect such density dependence is currently unknown. (3) I have not examined the consequences of incorporating process error into the parameters b or L , although, in other density-dependence tests, the way in which error, even of a single type, is incorporated can have substantial effects on power (Fox and Ridsdill-Smith 1995). (4) Uneven time steps between samples may alter the power of the RTLRT, but this issue has not been explored, nor have the effects of temporally correlated errors (Solow 1990).

The issues mentioned above concern details of the RTLRT; there are, in addition, restrictions on using the test at all. The RTLRT requires populations with periodic recruitment, and it detects density dependence poorly when population densities stay above or below L for most of the samples. In addition, mechanisms other than density dependence generate apparently density-dependent trajectories. The first mechanism is immigration, which could arrest a density-independent decline by the continual addition of new individuals. Fig. 1B provides an indication of the problem, because process error, like immigration, can displace the actual density of a population in a positive direction. High process error and shallow declines create an illusion of density dependence even when it is weak or non-existent if the population appears to move toward an intermediate level ($L > 0$). Thus, individuals arriving after the recruitment peak should be censored. For I .

wosnesenskii, possible immigrants were easily eliminated by censoring nonreproductive individuals counted >6 mo after the peak.

The second mechanism that may result in spurious detection of density dependence is the disappearance of one class of individuals while other classes survive. For instance, in *I. wosnesenskii*, portions of each sex disappear during the decline: large males apparently disappear (Fig. 5; see also Jormalainen and Tuomi 1989), and females at later brooding stages are underrepresented (Fig. 8), even though females adjust reproductive output to size (Fig. 7, see also Tuomi et al. 1988a, b). However, because sex ratio does not change consistently during the postrecruitment decline (Fig. 5), class-specific mortality is unlikely to cause apparent density dependence.

Because the RTLRT analyzes patterns, not mechanisms of decline, it gives no guidance on the causes of population dynamics, even when other evidence can eliminate spurious causes of apparently density-dependent declines such as continued immigration or class-specific mortality. On the other hand, the detection of density dependence should be a prompt to look for mechanistic explanations of density-dependent dynamics. In this case, detection of density dependence using the RTLRT prompted a study of habitat refuges. A crack or depression in a boulder may protect isopods from fish or birds known to eat them (Pfister 1995, Wootton 1997), but these safe sites may also be limited in number. Because isopod densities were higher under bricks with microtopography in comparison to smooth ones, it appears that physical attributes of the habitat can help determine densities (Fig. 6). However, it is still unclear if isopods were attracted to microtopography, or died at higher rates when holes were unavailable.

After more than 50 years of debate (Smith 1935, Andrewartha and Birch 1954), the importance of density dependence is still contested (Berryman 1991, Hanski et al. 1993, Holyoak and Lawton 1993, Wolda and Dennis 1993, Wolda et al. 1994). One way to resolve the debate over density dependence is to look for its prevalence in natural populations, but this has spawned another layer of argument concerning appropriate statistical tests (Holyoak 1993, Fox and Ridsdill-Smith 1995, Turchin 1995). Tests using actual or simulated data generate results that differ widely, depending on assumptions about underlying dynamics, error structure, time lags, spatial structure, and trends (initial value close to or far from equilibrium) (Stiling 1988, Hassell et al. 1989, Turchin 1990, Ray and Hastings 1996). Some have excessive size (Holyoak 1993, Wolda and Dennis 1993); others have low power to detect density dependence when it is present. But almost inevitably, density dependence is detected as time series increase in length (Hassell et al. 1989, Solow and Steele 1990, Godfray and Hassell 1992, Woiwod and Hanski 1992). The major conceptual problem with using long

time series to detect density dependence is that most tests do not actually answer the question of how much population change is due to density-dependent sources. They indicate only that at some times populations reach extreme densities that tend to move toward an equilibrium range rather than away.

The RTLRT synthesizes two growing realizations in the study of density dependence. (1) Experimental manipulations provide immediate evidence of how population growth rate changes with density. The nonexperimental density perturbations experienced naturally by many organisms echo these experiments, although they suffer from a lack of "controls." Observing actual population dynamics does have the advantage, however, of assuring that density manipulations occur within a natural range. (2) Regulated populations, regardless of underlying dynamics, should exhibit stationarity, maintaining a constant mean and variance over time. Perturbations away from this mean value are used by Turchin (1995) to exemplify the advantages of density-dependence tests based on stationarity. He posits a situation in which a population is always censused just after a random perturbation away from equilibrium. In this case, there would be no relationship between population density sampled at one time, and population change to the next, because abundance would have shifted randomly. However, the sequence should, after sufficient time, be stationary. The RTLRT shows that there may be more to learn from following short-term population changes, as populations return from their perturbed densities towards a sustainable level, than from waiting for these random perturbations to accumulate. Applying the test is not limited by time (waiting until densities reach levels where density-dependent factors prevail), but by error, which can obscure a positive asymptote.

The controversy surrounding population regulation has remained a central focus of ecology because of its implications for how and why populations fluctuate. Increasingly, the issues have been cast in a conservation context, as providing insight into how to reduce population outbreaks or avoid extinctions. For conservation, detailed case-by-case information about proximal factors influencing population change is more relevant than a general sense of whether density dependence is common or rare among species. In fact, what is needed are tools like the RTLRT that demonstrate, within a species, when density-dependent processes are likely to have large effects on abundance relative to other causes of population change. These tools help direct attention to times and conditions when it may be possible to identify density-dependent mechanisms of population change.

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