

Estimation of growth and mortality parameters from size frequency distributions lacking age patterns: the red sea urchin (*Strongylocentrotus franciscanus*) as an example

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Abstract: We present a maximum likelihood procedure for estimating population growth and mortality parameters by simultaneously analysing size frequency and growth increment data. The model uses von Bertalanffy growth with variability among individuals in the two parameters that determine growth rate, and size-dependent mortality. Analyzing growth increments together with size frequencies reduces the statistical confounding of the natural mortality rate with von Bertalanffy's K parameter. We assume steady-state (constant recruitment) conditions for the size distributions; hence the method does not depend on age modes in the distribution. We evaluate the bias and precision of estimates obtained for growth-dominated distributions typical of the red sea urchin (*Strongylocentrotus franciscanus*) in northern California, although the method and its evaluation could be applied as easily to mortality-dominated or bimodal distributions. The method provides good estimates with sample sizes as low as 200 individuals in a size distribution and 30 growth increments. Results are robust to random variability in recruitment, measurement error, and sampling selectivity up to the size where about one third of the distribution is affected. Estimation of the fishing mortality rate could require size distributions from both an unharvested and a harvested population. Estimates of growth and mortality rates depend critically on reliable growth data.

Résumé : Nous présentons une méthode du maximum de vraisemblance servant à estimer les paramètres de croissance et de mortalité d'une population par l'analyse simultanée de données sur les fréquences de taille et les incréments de croissance. Le modèle fait appel à la fonction de croissance de von Bertalanffy avec variabilité entre les individus dans les deux paramètres qui déterminent le taux de croissance, et à la mortalité dépendante de la taille. Le fait d'analyser les incréments de croissance en combinaison avec les fréquences de taille réduit la possibilité de confondre statistiquement le taux de mortalité naturelle avec le paramètre K de von Bertalanffy. Nous supposons des conditions stables (recrutement constant) pour la distribution des tailles, de sorte que la méthode ne dépend pas des modes d'âge dans la distribution. Nous évaluons le biais et la précision des estimations obtenues pour des distributions ayant la croissance comme facteur dominant, typiques de l'oursin rouge (*Strongylocentrotus franciscanus*) dans le nord de la Californie, mais la méthode et son évaluation pourraient être appliquées avec autant de facilité aux distributions dont le facteur dominant est la mortalité ou aux distributions bimodales. La méthode fournit de bonnes estimations avec des échantillons de 200 individus seulement pour la distribution des tailles et avec 30 incréments de croissance. Les résultats sont robustes par rapport à la variabilité aléatoire du recrutement, aux erreurs de mesure et à la sélectivité de l'échantillonnage jusqu'à une taille où environ un tiers de la distribution est touché. Pour avoir une estimation du taux de mortalité par pêche, il faudrait peut-être obtenir des distributions des tailles dans une population non exploitée et dans une population exploitée. Les estimations des taux de croissance et de mortalité dépendent de façon critique de la fiabilité des données sur la croissance.

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Introduction

Estimation of population parameters such as mortality, recruitment, and growth rates from age distributions is common practice. Methods are well developed for analyses of either single cohorts (e.g., Pope 1972) or several cohorts simultaneously (Fournier and Archibald 1982; Deriso et al. 1985; see review in Megrey 1989). A significant component of the cost of those procedures is the determination of age for a large number of individuals. Individual size is easier and less expensive to determine, and measurement of size is a necessary alternative when individuals of a species do not have permanent anatomical structures that record the passage

of time. However, methods for the estimation of population parameters from size distributions are not as completely developed. Most early methods for estimating parameters from a single size distribution were related to Beverton and Holt's (1956) estimate of the ratio of the growth parameter, usually represented by K in the von Bertalanffy equation, to total instantaneous mortality in terms of moments of the size distribution (see Weatherall et al. 1987). Others have estimated mortality rate from a known growth pattern and moments of a size distribution (e.g., Ebert 1981).

Modern methods deal with the structure of the size distribution, rather than just the moments. However, with few exceptions (e.g., Van Sickle 1977; Ebert 1981), these methods are still in part age based in that they depend on the modes in size distributions that result from annual pulses of recruitment (Macdonald and Pitcher 1979; Schnute and Fournier 1980; Pauly and David 1981; Fournier and Breen 1983; Fournier et al. 1990; Smith and McFarlane 1990) or moulting of invertebrate instars (Smith and Jamieson 1989). These methods descend from Petersen's (1892) technique for separating age modes in size distributions (see Grant et al. 1987 for other descendants). They are limited by the fact that age modes are not present in all size distributions, and if they are present, they typically occur only at smaller sizes.

An extant, challenging problem is the estimation of growth and mortality rates from single size frequency distributions that lack age patterns. Such distributions would be typical of species that either do not have annual recruitment pulses or have enough variability in growth patterns to obscure age modes in their size distributions (Barry and Tegner 1990; Ebert et al. 1993; Botsford et al. 1994). Tropical and subtropical species are more likely to be characterized by size frequency distributions lacking age patterns, but such distributions are also characteristic of some temperate species. Here, we present a method for estimating growth and mortality from size distributions that do not exhibit dominant age modes by including an auxiliary source of information, growth increments. Growth increments are the changes in sizes of individuals over a measured time period; hence, they require greater effort to collect than size measurements alone. However, the ages of individuals do not have to be determined. Including growth increment data allows unequivocal estimation of population growth and mortality parameters (e.g., Barry and Tegner 1990).

We use size distributions and growth increments obtained for the red sea urchin (*Strongylocentrotus franciscanus*) population of northern California to demonstrate the use of this method. Red sea urchin frequency distributions of test diameters typically lack the modes at small sizes that would indicate recent recruitment. Size distribution data are available from both harvested and unharvested sites in northern California. Growth increments, on the other hand, are scarce, primarily because urchins are difficult to tag. Here, we use growth increments from individuals held in the laboratory at natural temperatures and fed natural foods to demonstrate the estimation method. Because we use data from laboratory-grown urchins in this demonstration, the estimates obtained will not necessarily represent those of wild red sea urchins. We are in the process of obtaining growth increments for wild urchins using passive integrated transponder (PIT) tags. Our use of laboratory-grown urchins allows us to demonstrate the

importance of having reliable growth data when estimating mortality rates with this method.

Our interest in the red sea urchin results from its commercial exploitation (Tegner 1989) and a concern that recent exploitation rates exceed those necessary for a sustainable fishery. The northern California fishery began in the mid-1980s, with landings peaking at 13.6×10^3 t in 1988 and then declining every year since to a level of 2.6×10^3 t in 1994. We used the method developed here to obtain preliminary estimates of urchin growth and mortality for an analysis of rotating spatial harvest schemes (Botsford et al. 1993). Subsequent investigation of growth and mortality rates indicated the need to characterize bias and precision in these estimates. This provided the motivation for this paper where we (i) derive a method for estimating growth and natural and fishing mortality rates from combinations of size frequency and growth increment data, (ii) evaluate the statistical characteristics of that method and its limitations, and (iii) demonstrate the method using laboratory growth increments and northern California size frequency data from both unharvested and harvested sites. We have used this method to interpret size distributions of other species (Smith and Botsford 1998) and are using it in a comprehensive description of the spatial variability of growth and mortality rates in the red sea urchin in northern California.

Estimation method

Size frequency model

Estimation of growth and mortality parameters from size frequencies and growth increments requires models for size distributions and growth increments that contain those parameters. Such models facilitate the statistical evaluation of parameter estimates with respect to those data using a criterion such as maximum likelihood.

We use the size-structured von Foerster equation

$$(1) \quad \frac{\partial n(l, t)}{\partial t} = -\frac{\partial}{\partial l} [n(l, t)g(l)] - D(l)n(l, t)$$

to describe how the density $n(l, t)$ of individuals in a size frequency distribution changes with size l and time t , when governed by growth and mortality functions $g(l)$ and $D(l)$, respectively (Botsford et al. 1994; Smith and Botsford 1998). If sampled distributions show no modes at small sizes, then we assume that recruitment is constant. This steady-state condition means that a size distribution will not change appreciably in form over time given that growth and mortality rates also do not change. Under steady-state conditions, eq. 1 yields (Botsford et al. 1994)

$$(2) \quad \frac{\partial n(l)}{\partial l} = -\frac{n(l)}{g(l)} \left[\frac{\partial g(l)}{\partial l} + D(l) \right].$$

Integrating this expression over size provides a size distribution corresponding to the specified $g(l)$ and $D(l)$. Van Sickle (1977) noted that if the growth pattern is known, the mortality pattern can be obtained from eq. 2.

We assumed a von Bertalanffy growth function because our observed growth increments for the red sea urchin decline approximately linearly with size:

$$(3) \quad g(l) = K(L - l)$$

where K is the instantaneous rate of change in growth rate and L is asymptotic test diameter. Total mortality is the sum of natural and fishing mortalities:

$$(4) \quad D(l) = Ze^{-bl} + F(l)$$

where Z is the instantaneous natural mortality rate at $l = 0$, $b > 0$ allows the natural mortality rate to decline with size, and $F(l)$ is the instantaneous fishing mortality rate at size l . A positive value for b can result in a bimodal size distribution.

Previous assessments of red sea urchin test diameter frequency distributions indicated that variability in growth was required to produce size frequency distributions similar to those observed from field-collected red sea urchins (Botsford et al. 1994). Variability in individual growth can be described in two ways: (i) as variability in inherent growth patterns among individuals and (ii) as random independent variability in each individual's growth over time (cf. Kirkpatrick 1984; Deriso and Parma 1988). Both growth models can produce the growth increment patterns we see in our urchin data.

We introduced variability in growth rate by admitting random variability in the von Bertalanffy parameters L and K (Sainsbury 1980). Equation 2 with variable growth can describe three generic types of size distributions observed in field collections: growth dominated (a single mode composed of larger individuals), mortality dominated (a single mode composed of smaller individuals), and bimodal (modes of both smaller and larger individuals), each depending on the relative values of K and the mortality rate (Botsford et al. 1994; Smith and Botsford 1998). Sampled distributions typically underrepresent the smallest individuals in a population because they are more difficult to collect. Thus, to complete our model, we chose a cumulative Gaussian selectivity curve defined by its mean (μ_ψ) and SD (σ_ψ).

Growth increment model

Following Sainsbury (1980), we chose L to be Gaussian in distribution and K to be gamma-distributed. We defined the growth parameters to be μ_L (mean of L), σ_L (SD of L), μ_K (mean of K), and σ_K (SD of K). Variability in L produces the mode at large sizes (i.e., the difference between the dashed and the solid lines in fig. 1a of Botsford et al. 1994). Variability in K , on the other hand, has little discernible effect on a steady-state size distribution (Botsford et al. 1994), but can dramatically affect the appearance of growth increment plots (Smith and Botsford 1998).

Sainsbury (1980) derived the mean and variance of the growth increments that would result from von Bertalanffy growth with random L and K . Specifically, the expected value of a growth increment, I_j , conditional on initial size l_j and time interval Δt is

$$(5) \quad \mu_{I_j} = (\mu_L - l_j)(1 - E[e^{-\mu_K \Delta t}])$$

where μ_{I_j} is the expected increment of individual j . When K is gamma-distributed

$$(6) \quad E[e^{-\mu_K \Delta t}] = \left(1 + \frac{\Delta t \sigma_K^2}{\mu_K}\right)^{-\frac{\mu_K^2}{\sigma_K^2}}$$

The variance of the distribution of increments conditional on initial test diameter l and time interval Δt is

$$(7) \quad \sigma_{I_j}^2 = \eta \sigma_L^2 + (\mu_L - l_j)^2 V[e^{-\mu_K \Delta t}] + \sigma_{M,I_j}^2$$

where

$$(8) \quad V[e^{-\mu_K \Delta t}] = \left(1 + \frac{2\Delta t \sigma_K^2}{\mu_K}\right)^{-\frac{\mu_K^2}{\sigma_K^2}} - \left(1 + \frac{\Delta t \sigma_K^2}{\mu_K}\right)^{-\frac{2\mu_K^2}{\sigma_K^2}}$$

$$(9) \quad \eta = 1 - 2 \left(1 + \frac{\Delta t \sigma_K^2}{\mu_K}\right)^{-\frac{\mu_K^2}{\sigma_K^2}} + \left(1 + \frac{2\Delta t \sigma_K^2}{\mu_K}\right)^{-\frac{\mu_K^2}{\sigma_K^2}}$$

and σ_{M,I_j}^2 represents the variance of error in measuring an increment I_j . Negative growth in sea urchin test diameters can occur, particularly if urchins are starved (Leviton 1988). Negative growth cannot result from this model, but measurement error can cause negative growth increments.

Maximum likelihood estimation

Maximum likelihood parameter estimates are obtained by minimizing the sum of the negative ln-likelihood of each datum. For our model, two likelihood functions are required, one for the size distribution data and another for the growth increments. The likelihood function for a simultaneous analysis of these data is the product of the likelihood function (or the sum of the negative ln-likelihood) for each data type if the growth increment and size frequency data are independent. This independence occurs when no individual (sea urchin) that provides growth increments also occurs as a member of the size distribution data.

Growth increments

We assumed a Gaussian distribution of observed growth increments (I_j) with mean μ_{I_j} and variance $\sigma_{I_j}^2$. Strictly speaking, the distribution of increments would be a combination of the Gaussian and gamma distributions of L and K , respectively, with the distribution tending to be truncated as l approaches L . However, the choice of a gamma distribution is arbitrary, having been made only to constrain $K > 0$ (Sainsbury 1980). If growth rates are always positive, then the distribution of increments must be truncated for values of l within the domain of the distribution of L (see fig. 5 of Sainsbury 1980 and fig. 6 of Smith and Botsford 1998). We deal with truncation by reshaping the Gaussian distribution of increments conditional on l and Δt to incorporate this truncation. If there is no measurement error, then our choice of a negative ln-likelihood function for growth increments is

$$(10) \quad \Theta_1(\mu_L, \sigma_L, \mu_K, \sigma_K | l, \Delta t) = \sum_{j=1}^v \ln \left(\sqrt{2\pi} \sigma_{I_j} \right) + \frac{(I_j - \mu_{I_j})^2}{2\sigma_{I_j}^2} + \ln(1 - \zeta_l)$$

which is modified from the strictly Gaussian function of Smith and McFarlane (1990) to incorporate truncation. The

term $1 - \zeta_l$ is the cumulative probability density of the Gaussian distribution of positive growth increments at size l . Equation 10 assures that the expected value of an increment remains greater than zero while the variance of the distribution of increments decreases as l approaches and exceeds μ_L .

We found that our urchins grown in the laboratory often yielded negative growth increments. Since these well-fed urchins were unlikely to have undergone negative growth, we attributed the negative increments to measurement error. Incorporation of measurement error in the likelihood function involves convolving the truncated Gaussian distribution (eq. 10) of true increments (I_j) with a Gaussian distribution representing measurement error for each increment. Measurement error variance for a growth increment I_j is

$$(11) \quad \sigma_{M,I_j}^2 = \sigma_{M,I_j}^2 + \sigma_{M,I_j+I_j}^2.$$

For the red sea urchin, measurement error appeared to be proportional to test diameter; hence:

$$(12) \quad \sigma_{M,I_j} = \sqrt{(0.01I_j\sigma_{M,l=100})^2 + (0.01(I_j + I_j)\sigma_{M,l=100})^2}$$

where we have introduced the parameter $\sigma_{M,l=100}$ as the SE of measurement at 100 mm, or percent measurement error. True test diameters can never be known exactly; therefore, we show by simulation that the model error introduced by (i) assuming that the initial measurement of I_j is error free and (ii) using μ_{I_j} as a surrogate for I_j in eq. 12 tends to be small and unimportant for measurement error less than 5% of l .

The revised negative ln-likelihood function is thus

$$(13) \quad \Theta_2(\mu_L, \sigma_L, \mu_K, \sigma_K, \sigma_{M,l=100} | l, \Delta t) = \sum_{j=1}^v \ln(2\pi\sigma_{M,I_j}\sigma_{I_j}) \\ \times \int_{I_j=0}^{I_j=\infty} \frac{(\tilde{I}_j - I_j)^2}{2\sigma_{M,I_j}^2} + \frac{(I_j - \mu_{I_j})^2}{2\sigma_{I_j}^2} + \ln(1 - \zeta_l).$$

In eq. 13, we distinguish a true growth increment (I_j) from a growth increment measured with error (\tilde{I}_j). Although measurement error ($\sigma_{M,l=100}$) is an estimable parameter, in practice, it would be preferable to provide a value for measurement error ($\sigma_{M,l=100}$) obtained from measurement experiments performed independently of the measurement of growth increments.

Size distributions

We used the separation statistic of Schnute and Fournier (1980), without their factor 2,

$$(14) \quad \Theta_3(\mu_L, \sigma_L, \mu_K, \sigma_K, Z, b, F(l), \mu_\psi, \sigma_\psi) \\ = \sum_{i=1}^m O_i \ln \left[\frac{O_i}{P_i} \right] \text{ for all } O_i > 0$$

to evaluate the fit of estimated size frequency distributions to observed distributions. Equation 14 measures the discrepancy between the observed (O_i) and predicted (P_i) numbers of individuals within each size frequency cell i and is the negative ln-likelihood function for a multinomial distribution (i.e., the

probability distribution corresponding to a size distribution) without the additive constant (Schnute and Fournier 1980).

Minimization

We used the software of Mittertreiner and Schnute (1985) to minimize Θ_2 when using only growth increments, Θ_3 when using only size distribution data, and $\Theta_2 + \Theta_3$ when using both types of data. The SEs of the maximum likelihood parameter estimates were calculated using their approximate numerical method. Model parsimony was achieved by fixing nonsignificant parameters at zero. Diagnostics of model fit for the distribution of growth increment residuals and the distribution of size frequency data were based on chi-square probabilities (p) calculated using the Monte Carlo method of Roff and Bentzen (1989). Their diagnostic evaluates the probability of the observed data given the model and parameter estimates. A satisfactory diagnostic would be a probability value that suggests that the data are reasonably likely given the model. This diagnosis is the antithesis to null hypothesis testing where one generally tests to reject the null model. Thus, higher values of p will be associated with more likely models.

Evaluation of model performance

Approach

We evaluated performance of the method by calculating the bias and precision of estimates obtained for data simulated using known parameter values. These known parameter values were chosen based on the results of preliminary analyses of red sea urchin size frequencies and growth increments ($\mu_L = 120$ mm, $\sigma_L = 11$ mm, $\mu_K = 0.3$ year⁻¹, $\sigma_K = 0$ year⁻¹, $Z = 0.1$ year⁻¹). A growth-dominated size structure is typical of the northern California red sea urchin distributions to which we plan to apply this method, so we choose that distributional form for rigorous statistical evaluation. We subjected the model to a variety of imperfect data and conditions that could be encountered by practitioners (Table 1). Specifically, we tested the robustness of our assumption of constant recruitment by evaluating the way in which random variability in recruitment affects parameter estimates. The influences of practical values for sample size, measurement error, bin size, and size selectivity on parameter estimates were also evaluated. We also estimated parameters using only growth increments under various conditions.

Additionally, to address the concern that the expeditious use of laboratory data (or any other data that could misrepresent true growth rates) would give misleading results for wild urchins, we tested the consequence of analyzing simulated growth data that overrepresented true growth rates by 1.5, 2, and 3 times. We analyzed these growth data in combination with a typical steady-state growth-dominated distribution experiencing a fishing mortality rate of $F(l) = 0.3$ year⁻¹ for $l \geq 76$ mm, the minimum legal size. It should be noted that this is not a test of the efficacy of the model's estimation ability; it is an assessment of the effect of misrepresentative growth data on the estimates of other parameters, particular the mortality parameters.

We focused all of our evaluations on the key parameters describing growth (μ_L, σ_L, μ_K), natural mortality (Z), fishing mortality ($F(l)$), and measurement error ($\sigma_{M,l=100}$). We did not evaluate estimation of variability in K (σ_K) because our

Table 1. Percent bias and precision (in parentheses) expressed as percent SE. These are calculated using the results of 30 replicates of each of the simulation cases considered.

Consideration	μ_L	σ_L	μ_K	Z	ME ($\sigma_{M,l=100}$)
Baseline distribution					
400 frequencies, 60 increments	0.7 (1.2)	1.5 (5.8)	-1.8 (3.7)	-12.5 (13.8)	—
Frequency data only ^a					
400 frequencies	0.8 (1.3)	-1.0 (8.6)	-0.4 (17.5)	—	—
Increment data only					
60 increments	0.3 (3.0)	-2.0 (8.8)	-0.8 (6.6)	—	—
60 increments, $\sigma_K = 0.1$ (not estimated)	-14.0 (5.4)	49.0 (<i>15.1</i>)	36.7 (20.0)	—	—
60 increments, 2% ME (estimated)	1.5 (4.9)	0.2 (<i>20.1</i>)	-2.9 (9.0)	—	1.3 (17.4)
60 increments, 2% ME (estimated)	2.9 (10.0)	19.9 (45.8)	-2.1 (15.6)	—	-3.8 (13.1)
Frequency and increment data					
100 frequencies, 30 increments	0.6 (2.1)	0.1 (9.9)	-2.7 (5.7)	-18.3 (26.7)	—
200 frequencies, 30 increments	1.0 (1.6)	-2.8 (8.5)	-1.4 (5.1)	-4.6 (19.6)	—
400 frequencies, 30 increments	1.0 (1.2)	-2.8 (6.7)	-0.9 (4.7)	-7.9 (14.2)	—
200 frequencies, 60 increments	0.6 (<i>1.5</i>)	4.6 (7.4)	-0.5 (4.3)	-10.9 (19.1)	—
800 frequencies, 120 increments	0.7 (0.8)	-0.6 (4.2)	-1.0 (2.6)	-5.1 (9.8)	—
Nonzero σ_K					
$\sigma_K = 0.1$ (not estimated)	-3.2 (1.3)	36.8 (6.9)	10.8 (5.7)	-11.2 (16.0)	—
Measurement error					
2%	0.4 (1.4)	7.0 (7.8)	-1.2 (4.3)	-5.8 (14.8)	-7.4 (14.3)
5% (not estimated)	-7.4 (1.6)	71.2 (9.6)	31.3 (8.7)	-44.0 (21.0)	—
5% (estimated)	-0.2 (2.1)	50.5 (13.2)	-0.9 (9.1)	-9.3 (18.4)	0.1 (10.2)
Monthly recruitment variability					
RV = 2	-0.4 (<i>1.2</i>)	4.4 (6.1)	0.5 (3.9)	-15.8 (<i>14.4</i>)	—
RV = 4	-0.7 (<i>1.3</i>)	-6.4 (6.4)	0.1 (4.0)	-17.8 (<i>14.9</i>)	—
Combination cases					
RV = 4, 5% ME (not estimated)	-8.1 (<i>1.7</i>)	83.9 (<i>10.7</i>)	34.4 (9.6)	-45.2 (<i>18.4</i>)	—
RV = 4, 5% ME (estimated)	-0.9 (<i>1.0</i>)	23.4 (5.6)	1.2 (5.8)	-10.2 (<i>13.8</i>)	-3.1 (11.3)
Size selectivity					
$\mu_\psi = 10$ mm; $\sigma_\psi = 5$ mm	0.2 (1.2)	-0.2 (6.7)	-0.8 (3.8)	-4.9 (15.7)	—
$\mu_\psi = 20$ mm; $\sigma_\psi = 10$ mm	-0.0 (1.3)	-0.9 (6.7)	0.5 (3.9)	-1.3 (19.6)	—
$\mu_\psi = 40$ mm; $\sigma_\psi = 20$ mm	0.5 (1.6)	-0.5 (6.9)	-0.5 (4.1)	14.2 (48.7)	—
Bin size					
2 mm	-0.0 (1.2)	2.4 (6.0)	0.4 (3.8)	-8.7 (14.4)	—
10 mm	0.3 (1.2)	2.4 (6.1)	-1.2 (3.8)	-8.3 (14.2)	—

Note: These cases address concerns that the bin size, large measurement error, poor size selectivity, or failure of the constant recruitment assumption might result in seriously biased estimates of the tabled parameters. We use bold type to indicate that the bias is significant (t -test, $\alpha = 0.05$, $df = 29$), although possibly small. Similarly, we use italic bold type to indicate if the SD of the 30 estimates is significantly different from the mean of the 30 SEs of those estimates provided by Mittertreiner and Schnute's (1985) numerical method. The baseline case has $\mu_L = 120$ mm, $\sigma_L = 11$ mm, $\mu_K = 0.3$ year⁻¹, $\sigma_K = 0$ year⁻¹, $Z = 0.1$ year⁻¹, ME = 0, RV = 0, 400 size frequencies, 60 growth increments, a bin size of 5 mm, and no size selectivity. All other cases are modifications, as indicated, of this growth-dominated case. RV, coefficient of monthly recruitment variability; ME, percent measurement error.

^aFor this case with just size frequency data, μ_K refers to the ratio μ_K/Z .

previous work (Botsford et al. 1994) indicated that variability in K is not likely to be at detectable levels in constant-recruitment size frequency distributions of the red sea urchin. However, we did test whether the presence of variability in the growth parameter K (i.e., $\sigma_K > 0$) affected the estimates of other parameters.

The bias and precision associated with each parameter were measured by conducting 30 replications of each simulation. To measure bias, we compared the simulated true value with the mean of the 30 replicates. To measure precision, we calculated the SD of those 30 replicates (i.e., the SE from simulation) and

compared it with the SE of the estimate provided by Mittertreiner and Schnute's (1985) numerical method.

Simulations

Growth increments were simulated by choosing an initial test diameter l_j and then drawing a random value for L_j from a Gaussian distribution with mean μ_L and variance σ_L^2 . If the value for l_j exceeded L_j , then it was rejected and the draw repeated until $L_j > l_j$. A random value of K_j was then drawn from a gamma distribution with mean μ_K and variance σ_K^2 . A simulated increment was calculated using

$$(15) \quad I_j = (L_j - l_j)(1 - e^{-K_j \Delta t}).$$

Measurement error was added to I_j as

$$(16) \quad \tilde{I}_j = I_j + \sigma_{M,I_j} \epsilon_j,$$

where ϵ_j is an independent standard Gaussian deviate. For each replicate, growth increments were drawn until there were equal numbers of individuals for each of 30 initial sizes spaced 5-mm apart and ranging from 17.5 to 162.5 mm.

Size distributions were simulated by sampling the continuous distributions generated by integrating solutions to eq. 2 over the range of values of L and K and then summing the results in proportion to the probability densities of L and K . Measurement error was added to the sampled distributions according to eq. 12. Recruitment variation was imposed by assuming monthly lognormal recruitment variability having a specified coefficient of variation (RV). Distributions were randomly sampled as many times as required to produce the sampled distributions of 1-mm bins. These bins were then summed to create bins of 2, 5, or 10 mm as required.

Results

The estimation method yielded acceptable estimates, even when challenged with small sample sizes, imperfect data (i.e., measurement error), and compromised model assumptions (Table 1). In some cases, bias was shown to be significant, but it was typically less than 10%. The SEs were generally on the order of 1–20% and were almost always not significantly different from the SE estimated numerically (Mittertreiner and Schnute 1985). For the baseline case, bias and precision of the parameters other than mortality are very low when compared with estimates of vital rates in general, and even though a bit higher, the bias and precision in the estimate of mortality are in the low range of many estimates. The method appears to be useful in estimating parameters from size frequency data only, except that μ_K and Z cannot be independently estimated (Barry and Tegner 1990; Botsford et al. 1994). The model can also be used to analyze just growth increment data, as long as measurement error is also estimated or known.

The method is robust to a variety of sampling conditions. The one case with a larger sample size than the baseline provided better estimates than the baseline, while the cases with fewer samples provided generally poorer estimates. However, even the smallest sample sizes provided adequate estimates. Using different bin sizes in the size frequency had almost no effect on the estimates. Size selectivity at lower sizes had an effect mainly on the estimate of natural mortality, with Z tending to be less well estimated as mean selectivity increased. This result is intuitively reasonable. Mortality is estimated by formally comparing the abundance of older (larger) and younger (smaller) individuals in the distribution. If smaller individuals are not well represented in the distribution, then natural mortality cannot be as confidently estimated. The method tolerated incomplete sampling of the smallest individuals in a size distribution for sizes up to about one third of μ_L .

The method also yielded reasonable estimates when there was variability in the data due to either measurement error or variable recruitment. The method was robust to practical

variability in measurement error, so long as it was estimated. The primary effect of measurement error was to increase the bias in σ_L . Levels of recruitment variability typical of what we have observed for the red sea urchin increased the negative bias in the estimate of mortality, but did not substantially degrade the estimates. The presence of both measurement error and recruitment variability, when measurement error is estimated, led to a better estimate of mortality. This occurs because some of the recruitment variability was absorbed in the estimate of measurement error, although the bias in σ_L increased. Measurement error was well estimated by this method.

The method appears to depend critically on accurate growth increment data to reliably estimate Z and F . Measured growth rates higher than true growth rates led to seriously biased estimates of K , Z , and F (Fig. 1). This result makes sense in the context of eq. 2 in that to maintain the form of the steady-state size distribution when individuals grow faster, both natural and fishing mortality would have to increase proportionately. Despite this obvious concern for practitioners, it is important to recognize that this bias originates with the data and not with the model.

Red sea urchin example

Growth increments only

To demonstrate the use of our method, we estimated growth rate using 215 growth increment records obtained from well-fed red sea urchins held in tanks of flowing seawater at the Bodega Bay Marine Laboratory from 18 July 1991 until 23 July 1992. During this period, nine series of sequential measurements of test diameter provided growth data for eight time periods ranging in length from 23 to 83 days (Fig. 2). We chose smaller rather than larger urchins for this experiment, since smaller urchins provide better information on the value of μ_K than do larger, slow-growing urchins. In contrast, size distribution data provide no data on μ_K , but very good information on μ_L (cf. Smith and McFarlane 1990).

The growth rates that we estimated from our laboratory-grown urchins (Table 2) seem fast when compared with results others have obtained for wild urchins (Ebert and Russell 1992; 1993). We note that our estimate for μ_K is 1.14 year⁻¹. The estimate for μ_L of 72.1 mm seems low, possibly because selecting smaller, faster-growing individuals for the growth increment experiment resulted in the increment data containing less information about the value of μ_L (Smith and McFarlane 1990). Our estimate of measurement error of 2.4% (SE 0.2%) is close to the estimate of 1.8% (SE 0.3%) that we obtained independently by blindly measuring three times the test diameters of 39 urchins ranging in test diameter from 26 to 78 mm. The p -value of 0.02 for this model indicates that the model is an imperfect fit to the data. This imperfect fit occurs because we chose not to omit a few outlier data points.

Growth increments with size frequency data: estimating F

We followed the analysis of growth increments alone with an analysis of size frequency data alone collected from an unharvested site, the Point Cabrillo Marine Reserve, in 1989 (Kalvass et al. 1991). Then, we simultaneously analyzed the growth increments and these size frequency data. The results

Table 2. Parameter estimates (with SEs in parentheses) for those analyses illustrating the use of (i) growth increments alone, (ii) size frequencies alone and size frequencies with growth increments for the unharvested site (Point Cabrillo Marine Reserve), and (iii) size frequencies with growth increments for the harvested site (near Fort Bragg, Mendocino County).

Analysis	<i>p</i>	μ_L (mm)	σ_L (mm)	μ_K (year ⁻¹)	σ_K (year ⁻¹)	<i>Z</i> (year ⁻¹)	<i>F</i> (year ⁻¹)	$\sigma_{M,l=100}$ (%)	μ_{ψ} (mm)	σ_{ψ} (mm)
Growth increments (Fig. 2)	0.02	72.1 (6.0)	18.3 (2.3)	1.14 (0.19)	0 (—)	—	—	2.4 (0.2)	—	—
Unharvested site (Fig. 3)										
Size frequencies only ^a	>0.1	113.1 (1.5)	14.4 (0.9)	4.9 (1.2)	—	—	—	—	13.2 (2.4)	7.4 (2.4)
Size frequencies and increments	>0.1	110.4 (1.7)	16.5 (1.2)	0.61 (0.2)	—	0.064 (0.03)	—	3.4 (0.3)	11.4 (2.3)	6.6 (2.1)
Harvested site (Fig. 3)										
Size frequencies and increments (unconditional)	>0.1	78.3 (3.8)	19.7 (0.9)	0.98 (0.08)	—	0.80 (0.61)	0 (—)	2.4 (0.2)	1576 (1058)	164 (83)
Size frequencies and increments (conditional)	>0.1	110.4 (—)	16.5 (—)	0.61 (—)	—	0.064 (—)	0.36 (0.04)	3.4 (—)	43 (6)	26 (5)

Note: For the harvested site, one analysis attempts to estimate all parameters (unconditional) and the other is conditional upon the growth and natural mortality estimates. Note that *F* refers to *F*(*l*) where *l* ≥ 76 mm, the minimum legal size.

^aFor this case with just size frequency data, μ_K refers to the ratio μ_K/Z .

(Table 2; Fig. 3, top panel) illustrate the benefit of analyzing growth increments and size frequency data together. This latter analysis relies mainly on the size frequency data to estimate μ_L and σ_L , while the growth increments are used to estimate μ_K . The simultaneous analysis can also provide an estimate for natural mortality, $Z = 0.064 \text{ year}^{-1}$.

The similarity of the size distributions from the unharvested (Point Cabrillo Marine Reserve) and heavily harvested (near Fort Bragg in Mendocino, Calif.) sites for urchins larger than 76 mm test diameter (Fig. 3) suggests that it would be difficult to estimate fishing mortality using only a harvested distribution, even though our simulations showed that, in principle, this is feasible. Indeed, when we first attempted to estimate all parameters from the harvested distribution (Fig. 3), we found that *F* need not exceed zero to explain the form of the size distribution ($p = 0.18$, Table 2). We also obtained an unrealistically high and uncertain estimate for natural mortality ($Z = 0.8 \text{ year}^{-1}$) and dissatisfying estimates for the selectivity parameters.

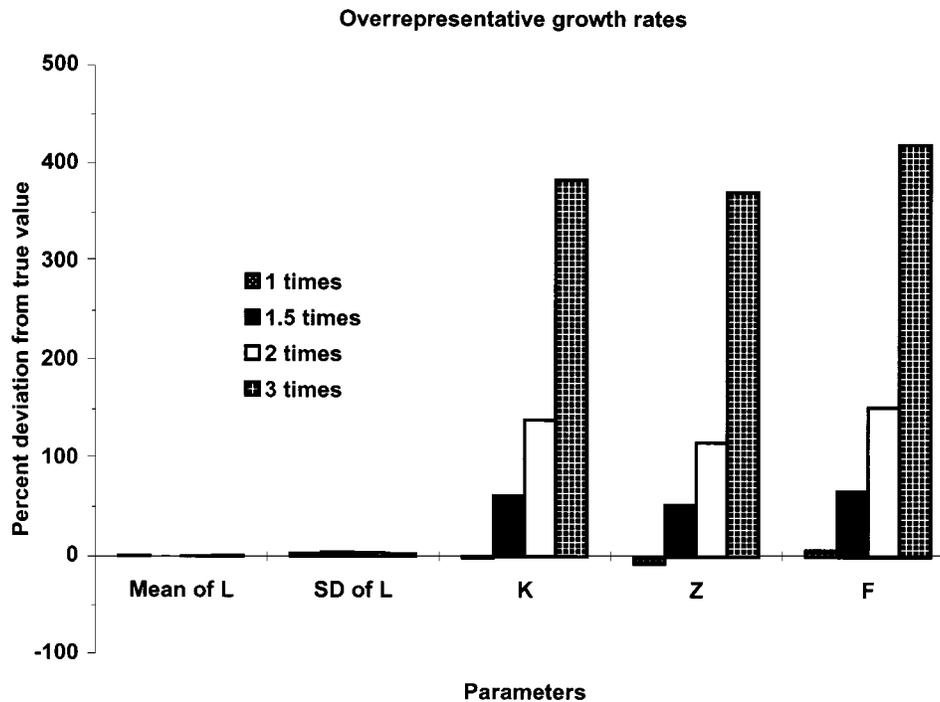
We therefore suggest a two-step procedure in which parameters are first estimated for the unharvested distribution (i.e., $F(l) = 0$) and then fishing mortality is estimated for the harvested distribution conditional on estimates for the unharvested distribution. With this procedure, only fishing mortality above the minimum legal size limit of 76 mm plus the two size selectivity parameters are estimated. This two-step analysis yielded satisfactory estimates of all parameters. Despite the method providing reliable estimates of growth and mortality for those data analyzed, we caution that our estimate of μ_K (0.61 year^{-1}) for urchins grown under ideal laboratory conditions might be 2–3 times higher than would be obtained for wild urchins. Estimates of *Z* and *F* may therefore be similarly inflated (Fig. 3).

Discussion

Size distributions lacking age structure are quantitatively less informative about growth and mortality than are size distributions with age patterns (Macdonald and Pitcher 1979; Schnute and Fournier 1980; Fournier and Breen 1983). Here, we have demonstrated using simulation and an example that estimation of growth, natural mortality, and fishing mortality from size frequency distributions lacking age patterns is feasible and practical when information on growth rate is also available. Reliable estimates can be obtained even when the fundamental assumption of constant recruitment cannot be strictly met. Bias is typically less than 10% for all parameters except mortality, while SEs are on the order of 1–20%. Mortality estimates are the most uncertain resulting in higher biases and SEs for them. Additionally, the SEs of the parameter estimates provided by Mittertreiner and Schnute's (1985) numerical method were generally in good agreement with the SDs of the parameter estimates obtained from the 30 replicates for each simulation.

In principle, fishing mortality should be estimable using only growth increments and the harvested distribution, as we did using simulated data (Fig. 1). The growth increments are necessary to resolve the ambiguity between the mortality rates and von Bertalanffy's *K* parameter, both of which affect the slope of the size distribution in the same way (our eq. 2; Barry and Tegner 1990; Botsford et al. 1994). However, in

Fig. 1. Effect of misrepresentative growth increments on the mean percent bias (histograms, mean of 30 replicates) and the percent SE from simulation (error bars, mean of 30 replicates) for estimates of the mean of L (μ_L), the SD of L (σ_L), the mean of K (μ_K), the natural mortality rate (Z), and fishing mortality rate (F). Estimates were obtained for simulated growth-dominated size distributions with 400 individuals and 60 simulated growth increments ($\mu_L = 120$ mm, $\sigma_L = 11$ mm, $\mu_K = 0.3$ year⁻¹, $\sigma_K = 0$ year⁻¹, $Z = 0.1$ year⁻¹, $F(l) = 0$ year⁻¹ for $l < 76$ mm, $F(l) = 0.3$ year⁻¹ for $l \geq 76$ mm).



practice the available size distribution data are not likely to be as ideal as simulated data. Thus, as in our example (Fig. 3), we suggest that to obtain estimates of growth and natural and fishing mortality from a harvested size distribution, a third source of information should be used, a comparable unharvested size distribution. This distribution would first be analyzed to estimate growth and natural mortality parameters and then the harvested distribution would be analyzed to estimate fishing mortality conditional on those growth and natural mortality parameter estimates.

Even if the cost of these two additional data requirements is considered, use of the method presented here to estimate fishing mortality would be justified in many cases. For example, since invertebrates typically cannot be reliably aged, invertebrate populations that do not display age modes in their size distributions would require such a method. For populations that can be aged, but only at considerable expense, this method may still be the most feasible. We foresee this analytical approach having utility for many invertebrate species that are difficult to age but for which high-quality growth-at-size and size distribution data can be collected rather easily and inexpensively. Although our example was for the growth-dominated distributional form, the method and its evaluation are equally valid for the mortality-dominated and bimodal distributional forms (Botsford et al. 1994; Smith and Botsford 1998).

We assumed constant recruitment, but the relative robustness of the method to failure of this assumption would make it suitable for many populations with undramatic monthly or

annual recruitment variability. We note that our simulation with a monthly RV of 4 corresponds to an annual RV slightly greater than 1. For populations that only occasionally present an age mode, we are considering development of a method that uses growth increments in combination with size distributions obtained sequentially in time and that estimates annual recruitment. Another approach would filter recruitment that occurs as uncorrelated periodic, say monthly, events.

One consideration when using this method to estimate fishing mortality is the comparability of vital rates for harvested and unharvested distributions. Harvested and unharvested sites should be chosen with habitat comparability in mind. Practitioners must also consider if density-dependent processes could cause marked differences in growth and mortality rates between the unharvested and harvested sites. For our example of the red sea urchin, the protection of small urchins from mortality by a spine canopy of adult urchins has received much study as a population regulation mechanism involving predation and recruitment of small sea urchins to the adult population (Tegner and Dayton 1981, 1991; Tegner and Levin 1983; Tegner 1989). If adults are harvested, then the relationship between size and mortality for smaller urchins (eq. 4) might change.

There are few size-based estimation methods with which we can compare our method. Ebert (1980) and Ebert and Russell (1992, 1993) have collected red sea urchin growth increments and have estimated growth and mortality rates in a variety of ways. However, they have presented no statistical

Fig. 2. Laboratory-obtained growth increments (points) for well-fed red sea urchins held in tanks at the Bodega Bay Marine Laboratory from 18 July 1991 until 23 July 1992. Estimated von Bertalanffy growth models (lines) are also presented for eight time periods between measurements (Table 2). Note that the different slopes are due to the variable number of days between successive measurements of test diameters.

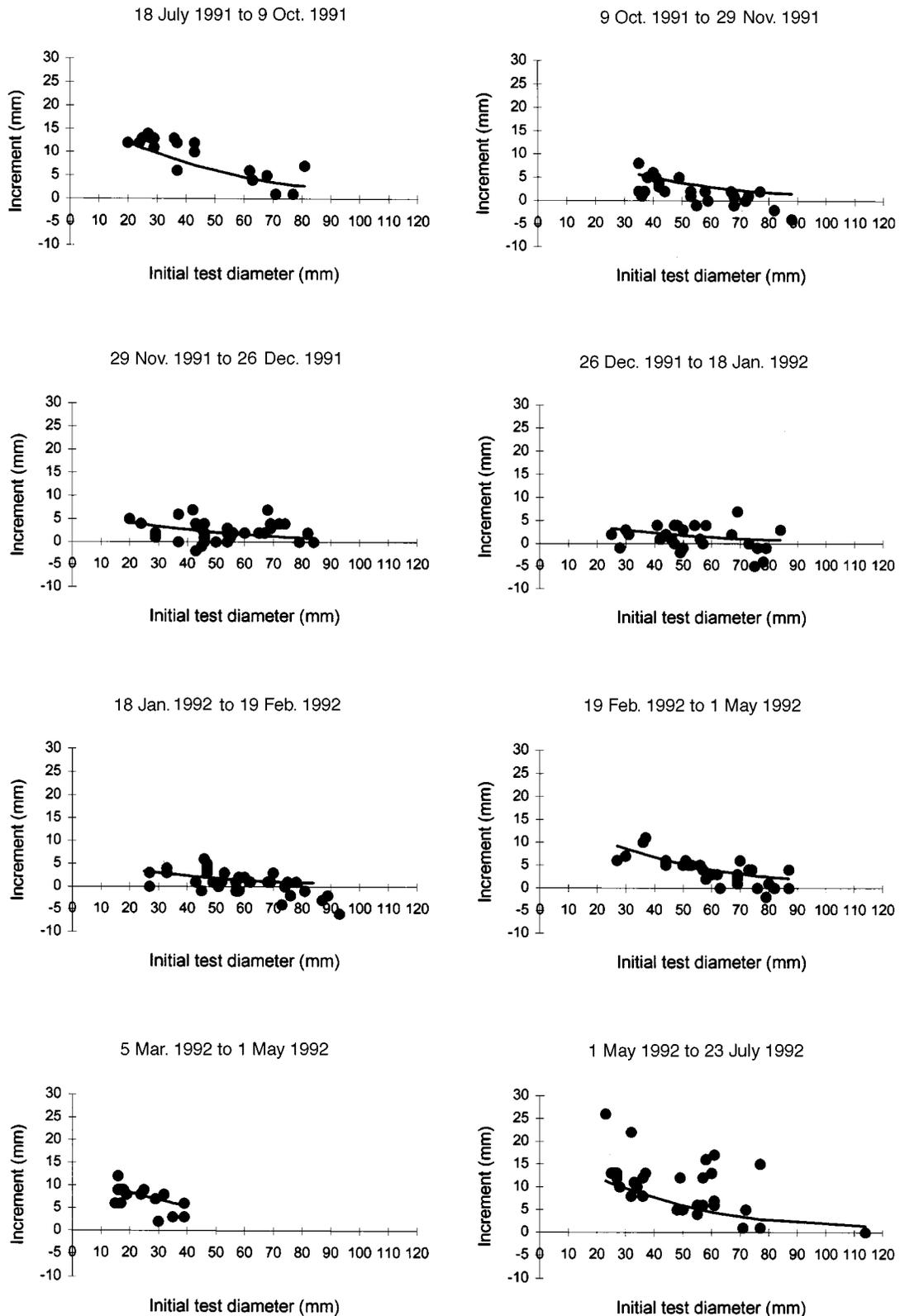
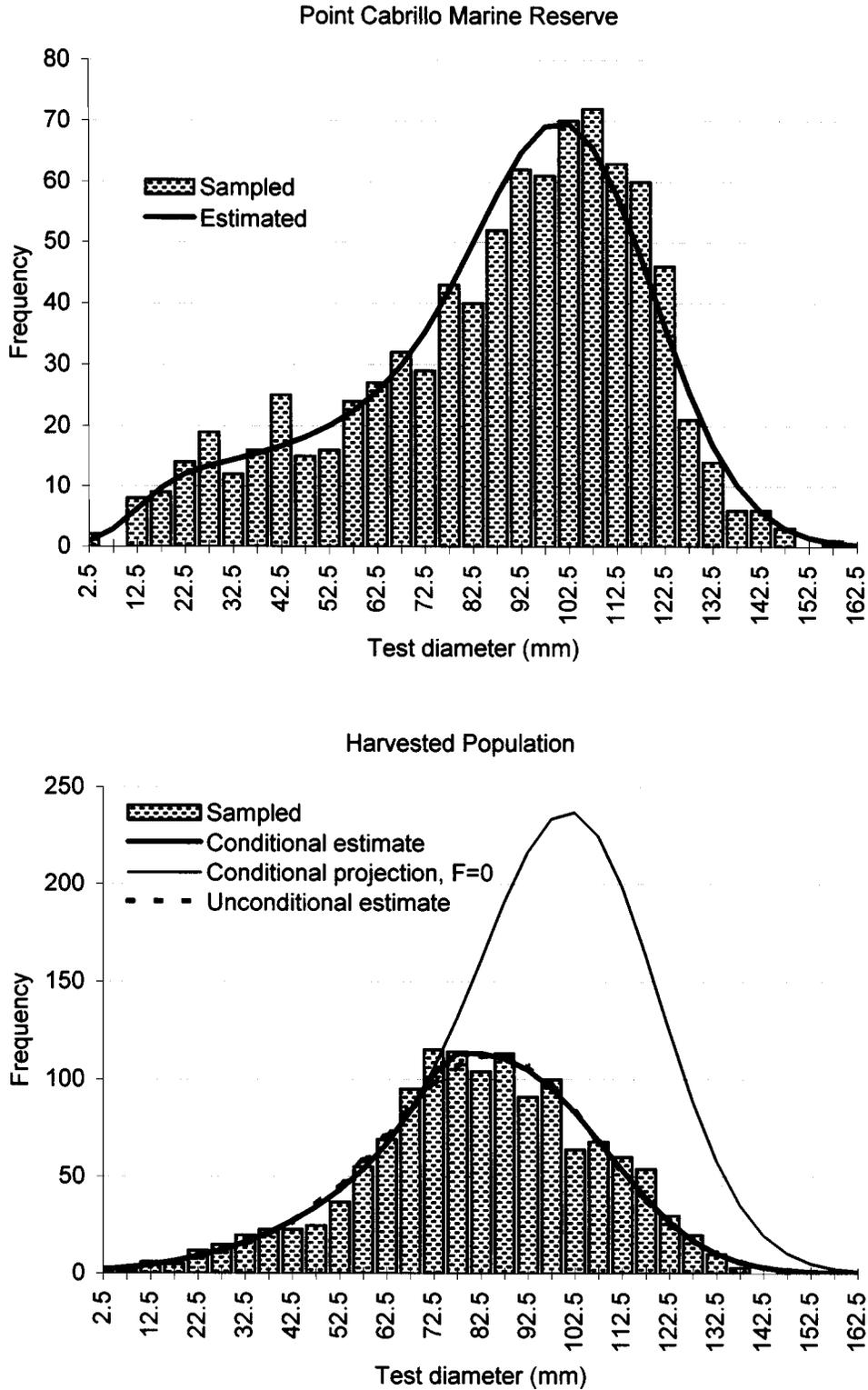


Fig. 3. Histograms of red sea urchins collected from harvested (near Fort Bragg, Mendocino County) and unharvested (Point Cabrillo Marine Reserve) sites in northern California in 1989. Top panel: unharvested site ($n = 868$). The line indicates the estimated unharvested size distribution (Table 2). Bottom panel: harvested site ($n = 1337$). The heavy line draws the estimated harvested size distribution (conditional estimate) conditional on the growth and natural mortality estimates obtained for Point Cabrillo Marine Reserve (Table 2). Only fishing mortality (F), the mean of size selectivity (μ_ψ), and the SD of size selectivity (σ_ψ) were estimated. The light line projects the form of the corresponding unharvested distribution (conditional projection, $F = 0$). The broken line draws the harvested distribution obtained by estimating all parameters (unconditional estimate).



evaluation of their methods similar to the evaluation conducted here. They interpreted the asymptotic approach of the growth increment prediction to the abscissa of initial test diameter for a given time period at large as indicating a Richards growth curve. We find that Sainsbury's (1980) assumptions regarding statistical variability provide a more satisfactory explanation of variability in positive growth increments than does a Richards curve. One limitation of our implementation of Sainsbury's (1980) assumptions is that negative growth cannot be accommodated. Negative growth of urchins has been reported by Levitan (1988), and we have observed negative growth in starved red sea urchins.

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