Abstract—The green sea urchin (*Strongylocentrotus droebachiensis*) is important to the economy of Maine. It is the state's fourth largest fishery by value. The fishery has experienced a continuous decline in landings since 1992 because of decreasing stock abundance. Because determining the age of sea urchins is often difficult, a formal stock assessment demands the development of a size-structured population dynamic model. One of the most important components in a size-structured model is a growth-transition matrix. We developed an approach for estimating the growth-transition matrix using von Bertalanffy growth parameters estimated in previous studies of the green sea urchin off Maine. This approach explicitly considers size-specific variations associated with yearly growth increments for these urchins. The proposed growth-transition matrix can be updated readily with new information on growth, which is important because changes in stock abundance and the ecosystem will likely result in changes in sea urchin key life history parameters including growth. This growth-transition matrix can be readily incorporated into the size-structured stock assessment model that has been developed for assessing the green sea urchin stock off Maine.

Developing a growth-transition matrix for the stock assessment of the green sea urchin (*Strongylocentrotus droebachiensis*) off Maine

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The green sea urchin (*Strongylocentrotus droebachiensis*) fishery is the state's fourth largest fishery by value, worth $20.3 million to harvesters in 1999. The fishery is managed by limited entry, a limited number of opportunity dates that are established each year by recommendation of the sea urchin zone council (SUZC), and minimum and maximum size limits. The fishery is further regulated seasonally by two zones that correspond to variation in spawning time along the coast (Vadas et al., 1997).

The Maine sea urchin fishery began in the late 1980s and reached its peak in landings in 1992. It has since experienced a continuous decline in landings, mainly resulting from large decreases in sea urchin stock abundance (Fig. 1). Although the large decrease in abundance is evident in many studies (Steneck and Vadas[1]; Harris[2]) and apparent to the sea urchin fishing industry, the catch-per-unit-of-effort (CPUE) data derived from the fishery have shown no significant decreases over the last 10 years (Fig. 1). We need to perform a formal stock assessment to better understand the population dynamics of the sea urchin stock and to develop an optimal management strategy.

A population dynamics model for the sea urchin stock should provide reliable estimates of model parameters with suitable statistical methods (Hilborn and Walters, 1992; Chen and Paloheimo, 1998; Walters, 1998). A size-structured population dynamics model is needed for the sea urchin fishery because sea urchins are difficult to age and growth varies widely among individuals (Quinn and Deriso, 1999).

One of the key components of a size-structured population dynamics model is a growth-transition matrix, which describes the probability of an organ-

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ism growing from one size class to another size class in a given unit of time (Sullivan et al., 1990; Sullivan, 1992). In practice, two approaches can be used to incorporate a growth-transition matrix into a stock assessment: one is to incorporate the growth-transition matrix and simultaneously estimate matrix parameters with parameters that describe other biological processes in the fishery (Sullivan et al., 1990), and the other approach is to estimate the growth-transition matrix independent of other stock assessment models (Chen et al., 2000). The former considers covariance among different processes by estimating all parameters simultaneously, but makes the analysis more complicated. The latter approach reduces the complexity of modeling but does not consider the covariance of growth and other biological processes. Because size-structured models are often complicated and have many parameters to be estimated, the estimation of a growth-transition matrix outside the main modeling process may be preferable (Chen et al., 2000). In either case, the quality of the growth-transition matrix can greatly influence the quality of the stock assessment. It is thus essential to develop a growth-transition matrix for the Maine sea urchin stock that can capture the variations in growth increments among individuals.

The information required in estimating a growth-transition matrix includes the mean growth increment in a given unit of time and its associated variation for sea urchins of different sizes. Because growth rates of sea urchins vary with size, growth increments also vary with size, and this variation in growth with size is rarely constant. This has been implicit in the statements of model assumptions in many papers (e.g. Sullivan et al., 1990; Sullivan, 1992, Quinn and Deriso, 1999). However, because the variance for growth increments is difficult to estimate, it is often assumed to be constant for organisms of different sizes (Quinn and Deriso, 1999). Such an assumption of constant variation in growth increment is rather unrealistic and may introduce biases in estimating a growth-transition matrix. Thus, for the Maine sea urchin we need to develop an approach that can explicitly consider nonconstant variances for growth increments of sea urchins of different sizes.

Growth of the sea urchin along the Maine coast has not been studied extensively and the data are limited. The data we used for this study were from Vadas et al. (2002) who collected size-at-age data on sea urchins in two habitats (barren and kelp) from three areas along the coast of Maine.

Methods and materials

Previous studies have indicated that many environmental variables might influence the growth of the sea urchin (Meidel and Scheibling, 1998; Russell, 1998). Sea urchins in favorable habitats, feeding on preferred seaweeds, grow faster than those feeding on less favorable algae and mussels, and sea urchins on barren grounds grow slower. Even in the same habitat, different rates of growth were identified (Vadas, 1977). Previous studies divided the
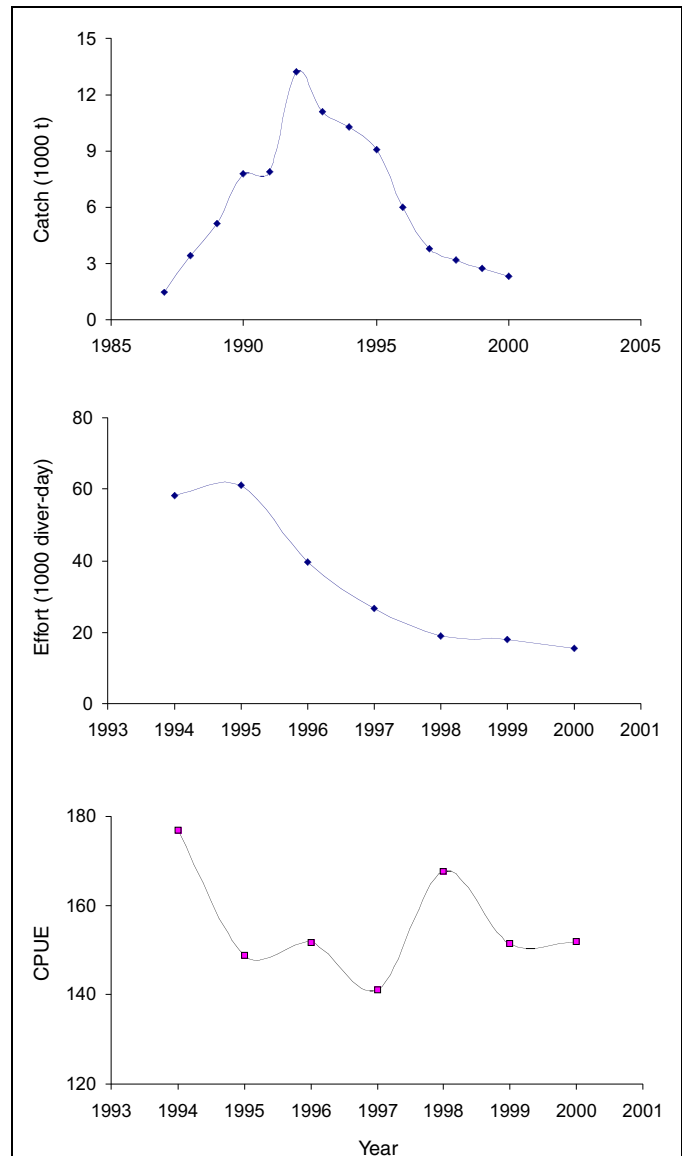

Figure 1

Observed catch measured in metric tons, effort measured in diver-hours, and catch per unit of effort measured in pounds per diver-hour for the sea urchin fishery in management zone 2 in Maine. Zone 1 has a similar temporal pattern.

coast of Maine into three regions, northeast, center, and southwest (Vadas et al., 1997). For each region, sea urchin samples were randomly taken from two habitats, barren and kelp. Size-at-age data were collected in 1997–98 for sea urchins in each habitat and area (Vadas and Beal[3]). Detailed descriptions about the derivation of size and age

[3] Vadas, R. L., and B. F. Beal. 1999. Temporal and special variability in the relationships between adult size, maturity and fecundity in green sea urchins: the potential use of a roe-yield standard as a conservation tool. Report to the Maine Department of Marine Resources, Augusta, Maine 04333.

information, justification for dividing the Maine coast, and selection of the habitats can be found in Vadas et al. (1997) and Vadas et al. (2002).

Vadas et al. (1997) modeled the size-at-age data using the von Bertalanffy growth function (VBGF) described as

$$L_t = L_\infty(1 - e^{-K(t-t_0)}), \qquad (1)$$

where L_t = size at age t;

L_∞ = defined as the mean asymptotic length that the sea urchin may attain;

K = the Brody growth parameter; and

t_0 = the hypothetical age of size 0 (Ricker, 1975).

For each area and habitat, a VBGF was used to fit the size-at-age data. Three parameters in the VBGF (i.e. L_∞, K, and t_0) and their standard errors were estimated by using the nonlinear least squares method. These estimates were presented in Vadas and Beal[3] and Vadas et al. (2002), and were made available to the authors of the present study (Table 1). Clearly there were large differences in the estimates of L_∞ and K and their associated variations among different areas and habitats (Table 1).

The L_∞'s estimated for different areas and habitats ranged from 63.1 (northeast region with barren habitat) to 95.2 mm (southeast region with kelp habitat) (Table 1) and tended to be smaller than some large individuals observed in the fishery (about 100 mm, Vadas, 1977; Hunter, unpubl. data). This likely resulted from relatively small sample sizes that covered relatively small areas, in a relatively short period, compared with the fishery catch, which targeted larger-size individuals. The exclusion of individuals in the fishery catch that were larger than the L_∞'s estimated in Vadas and Beal[3] and Vadas et al. (2002) from the calculation of the growth-transition matrix may underestimate the variability in sea urchin growth, thus introducing errors in stock assessment. Based on the data collected in the Maine sea urchin fishery (Hunter, unpubl. data) and previous studies (Vadas, 1977), 100 mm was considered a reasonable value for the average asymptotic size (L_∞) for sea urchins on the coast of Maine. However, more extensive sampling needs to be done in the future to verify this estimate.

We might be able to derive an estimate of L_∞ for the Maine sea urchin stock based on the examination of the data collected from the fishery and other studies (Ricker, 1975; Moreau, 1987; Chen et al., 1992). An estimate of K for the whole Maine urchin stock is, however, more difficult because K is an abstract rate describing how fast organisms approach the L_∞ and there are no observations or background information with which to compare estimates (Ricker, 1975; Moreau, 1987). We thus need to develop an approach to estimate K for the Maine sea urchin stock which corresponds to the value we assumed for the L_∞. Many studies have indicated that estimates of K and L_∞ tend to be highly and negatively correlated (e.g. Moreau, 1987; Chen and Harvey, 1994). Thus, a fish population or species with a large L_∞ tends to have a low K value, and *vice versa* (Gallucci and Quinn, 1979; Chen et al., 1992). This suggests a strong relationship between L_∞ and K estimates

Table 1

The average asymptotic size (L_∞) and Broady growth coefficient (K) estimated for different areas and habitats along the coast of Maine in the study done by Vadas et al. (1997, 2002). Coefficient of variation (CV) was calculated by using Equation 2.

		Parameter		Coefficient of variation (CV)	
Area	Habitat	L_∞	K	CV(L_∞)	CV(K)
Northeast	Barren	63.1	0.1404	0.242	1.209
Northeast	Kelp	88.5	0.1263	0.224	0.543
Center	Barren	67.0	0.2315	0.084	0.354
Center	Kelp	63.4	0.3268	0.065	0.248
Southeast	Barren	80.1	0.1776	0.099	0.397
Southeast	Kelp	95.2	0.1181	0.128	0.338

(Pauly, 1980; Stergiou, 1993). Such a relationship may be used to estimate K for a given L_∞ or to estimate L_∞ for a given K. In this study we developed and used the following empirical approach to derive K for a given value of L_∞ and its associated uncertainties in the development of a growth-transition matrix: 1) conduct a regression analysis for K and L_∞ estimated for different areas and habitats along the coast of Maine (Table 1); 2) calculate coefficients of variation (CV) for each K and L_∞ (Table 1) as

$$CV(K) = \frac{\text{standard error for } K}{K}, \text{ and}$$
$$CV(L_\infty) = \frac{\text{standard error for } L_\infty}{L_\infty}, \qquad (2)$$

and conduct a regression analysis of CV(K) and CV(L_∞) estimates of different areas and habitats (data in Table 1); 3) use 100 mm to approximate L_∞ and use this L_∞ to estimate K from the regression analysis between K and L_∞; and 4) calculate the average CV for L_∞'s of different areas and habitats and then use the average CV(L_∞) to estimate CV(K) from the CV(K)–CV(L_∞) regression equation.

Because K and L_∞ were estimated for different areas and habitats and had different precisions, outliers might arise in the regression analyses. To avoid possible bias introduced by outliers, we used a reweighted least squares (RLS) method for the regression analyses (Chen et al., 1994). This method involves conducting a robust least median of squares (LMS) analysis to identify outliers (Rousseeuw and Leroy, 1987) and justifying the identified outliers by using background information, followed by a weighted LS analysis where justified outliers are weighted by 0 and other data have a weight of 1 (Chen et al., 1994). In the two regression analyses (i.e. steps 1 and 2), L_∞ and CV(L_∞) were used as the independent variables and K and CV(K) were used as the dependent variables. The reason for this choice (instead of the other way around) is that L_∞ is often estimated more reliably and with much smaller

variations (Chen et al., 1992; also see Table 1), whereas K is often less reliably estimated (Moreau, 1987). One of the basic assumptions for a regression analysis is that the independent variable is error free. In practice, this assumption is often relaxed when the independent variable has a much smaller error than the dependent variable (McArdle, 1988). The violation of the normal distribution assumption for the errors in the regression analyses may bias the test for the significance of the regression model and its parameters using common parametric tests (F- or t-tests), but does not necessarily result in biases in the regression analysis (Sen and Srivastava, 1990)."

Given K and L_∞, the growth increment during a unit of time (i.e. year) can be calculated as

$$\Delta L_n = (L_\infty - L_n)(1 - e^{-K}), \tag{3}$$

where K and L_∞ are the true values without errors; n indexes size class; and L_n is the middle point of the nth size class. With Equation 3, we can develop two approaches to estimate the growth-transition matrix. One approach is a Monte Carlo simulation. We can randomly sample H sets of K and L_∞ values from their joint distributions (thus consider their covariance) and then use them in Equation 3 to calculate H sets of ΔL for each size group. We can then derive the probability distribution for ΔL from these H sets of ΔL values for each size group. The Monte Carlo simulation approach is straightforward but requires extensive calculations, in particular when there are a large number of size groups. It is also inconvenient to update the growth-transition matrix when there are new growth data or large changes in growth due to changes in the environment. The second approach is analytic and not so straightforward, but it is easy to update with new information and is less computationally intensive. It is likely that the growth-transition matrix for the Maine sea urchin fishery will need to be updated because of possible changes in growth caused by changes in the sea urchin population size and its ecosystem. Thus we used the second approach, which is described as follows.

Assuming the uncertainties associated with the VBGF parameters L_∞ and K are ΔL_∞ and ΔK respectively, where, $\Delta L_\infty \in N(0, \sigma^2_{L_\infty})$ and $\Delta K \in N(0, \sigma^2_K)$, we have

$$L_\infty = \overline{L}_\infty + \Delta L_\infty \text{ and } K = \overline{K} + \Delta K, \tag{4}$$

where $\overline{L}_\infty$ and $\overline{K}_\infty$ are the estimated parameters. Replacing the true values of L_∞ and K in Equation 3 with Equation 4 and using the approximation $e^{\Delta X} \approx 1 + \Delta X$ for small ΔX, we have

$$\Delta L_n \approx (\overline{L}_\infty - L_n)(1 - e^{-\overline{K}}) +$$
$$\left[\Delta L_\infty (1 - e^{-\overline{K}}) - (\overline{L}_\infty - L_n)\Delta K e^{-\overline{K}} - \Delta L_\infty \Delta K e^{-\overline{K}} \right] = \overline{\Delta L}_n + \varepsilon_n, \tag{5}$$

where

$$\overline{\Delta L}_n = (\overline{L}_\infty - L_n)(1 - e^{-\overline{K}}) \tag{6}$$

$$\varepsilon_n = \Delta L_\infty (1 - e^{-\overline{K}}) - (\overline{L}_\infty - L_n)\Delta K e^{-\overline{K}} - \Delta L_\infty \Delta K e^{-\overline{K}}. \tag{7}$$

Thus, the expected (mean) value of ΔL_n is $\overline{\Delta L}_n$ and variance of ΔL_n can be estimated from Equation 7 as

$$\text{Var}(\overline{\Delta L}_n) \approx \sigma^2_{L_\infty}(1 - e^{-\overline{K}})^2 + (\overline{L}_\infty - L_n)^2 \sigma^2_K e^{-2\overline{K}} -$$
$$2\text{Cov}(L_\infty, K)(1 - e^{-\overline{K}})(\overline{L}_\infty - L_n)e^{-\overline{K}}. \tag{8}$$

Items with the order of three and above for ΔL_n and ΔK are omitted in deriving Equation 8 from Equation 7. From Equation 8, it is clear that the variance of the growth increment varies among different size classes.

From $\overline{\Delta L}_n$ estimated in Equation 6, an expected average yearly growth increment was calculated for each size class. The variability for the average yearly growth increment was assumed to follow a normal distribution with a mean of $\overline{\Delta L}_n$ and variance of $\text{Var}(\overline{\Delta L}_n)$ estimated from Equation 8. This distribution was used to determine the vector of probabilities of growing from size class k to other size classes. If d_{low} and d_{up} are the lower and upper ends of size class d, the probability of a sea urchin growing from size class n to size class d can be computed as
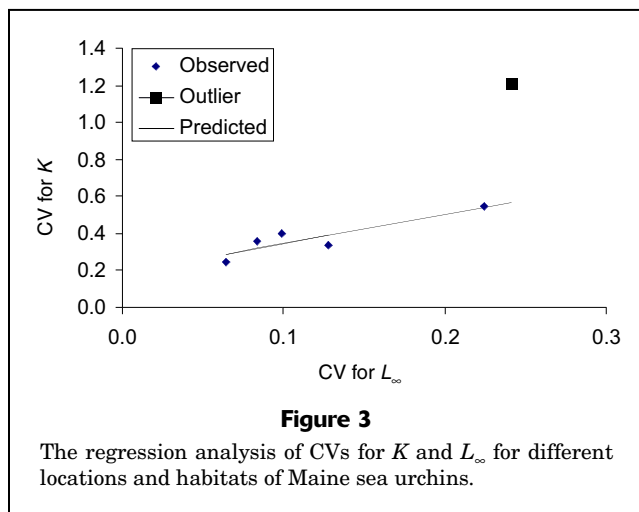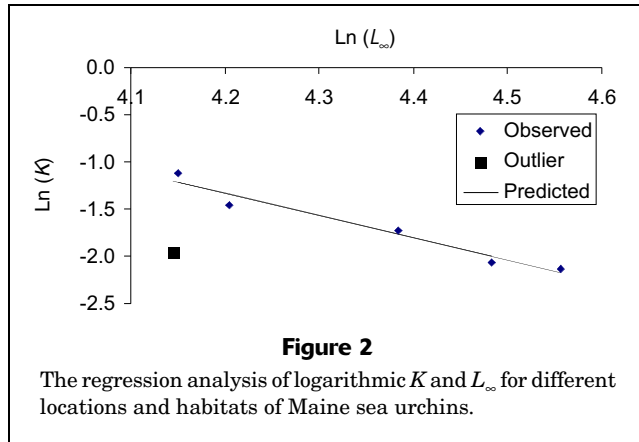
$$P_{n \to d} = \int_{d_{low}}^{d_{up}} f(x | \overline{\Delta L}_n, \text{Var}(\Delta L_n)) dx, \tag{9}$$

where x is a random variable having a density probability distribution defined by $f(x | \overline{\Delta L}_n, \text{Var}(\Delta L_n))$ with its expected value of $\overline{\Delta L}_k$ and variance of $\text{Var}(\overline{\Delta L}_k)$ (Quinn and Deriso, 1999). In the present study we assumed that the x variable was a normal density distribution function with a mean of $\overline{\Delta L}_k$ defined by Equation 6 and with a variance of $\text{Var}(\overline{\Delta L}_k)$ defined by Equation 8. The probability of a sea urchin growing from one size to another was estimated for all size classes to form the matrix. Negative growth increments were not permitted. The largest size class acts as a plus group; therefore sea urchins in this group have a probability of 1 of remaining in the group. The model contains 61 size classes, each with 1-mm interval width, ranging from 40 mm in size (midpoint value for size class from 39.5–40.5 mm) to 100 mm.

Because no negative growth was allowed, the summation of the probabilities of a sea urchin of size class k growing into all other size classes was smaller than 1 (because the normal distribution is symmetric). This problem was avoided by standardization which involved dividing the probability of an urchin in a given size class n growing into each size class by the summation of the probabilities of growing from a given size n to all the size classes. All calculations were done in MS-Excel© (Microsoft Office 2000, Microsoft Corporation, Redmond, WA). A worksheet for estimating a growth-transition matrix as described above is available upon request.

Results

The LMS analysis suggested that the logarithmic K and L_∞ data for the barren habitat in the Southwest area was an outlier in the K and L_∞ regression analysis (Fig. 2). The estimated K and L_∞ values for the barren habitat in the Southwest had CVs over 120% and 24%, respectively, much

Figure 2

The regression analysis of logarithmic K and L_∞ for different locations and habitats of Maine sea urchins.

Figure 3

The regression analysis of CVs for K and L_∞ for different locations and habitats of Maine sea urchins.
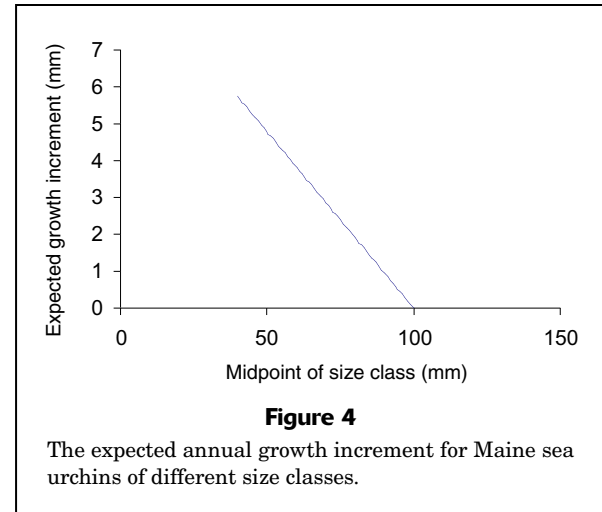
larger than the estimates for other locations and habitats (Table 1). This was the only site where the K estimate was not significantly different from 0 (thus the VBGF was not significant). We thus concluded that this data point was an outlier because of the poor fit of the VBGF, and subsequently it was given a zero weight in the RLS analysis. The RLS regression equation for K and L_∞ was estimated by

$$Ln(K) = 8.653 - 2.3777\ Ln(L_\infty),$$
$$P=0.0038, \text{adj. } r^2=0.94. \quad (10)$$

The standard deviations for the intercept and slope were 1.2605 and 0.28923, respectively. The P value for Equation 10 indicates that the regression model is significant. The adj. r^2 is the coefficient of determination adjusted for the sample size, suggesting 94% of the variance in ln(K) could be explain by the model.

The LMS analysis of the CVs of parameters K and L_∞ also suggested that the barren habitat in the southwest area was an outlier because it had an exceptionally large CV for K (Fig. 3). We thus concluded that this data point was an outlier and should be given a weight of zero in the RLS analysis. The RLS regression equation for the CVs of parameters K and L_∞ was estimated by

Figure 4

The expected annual growth increment for Maine sea urchins of different size classes.

$$CV(K) = 0.189 + 1.5602\ CV\ (L_\infty),$$
$$P=0.034, \text{adj. } r^2 = 0.76. \quad (11)$$

The standard deviations for the intercept and slope were 0.0561 and 0.42319, respectively. The P value suggested the regression model was significant ($P<0.05$). The value of r^2 suggests 76% of the variance in CV(K) could be explained by the model.

The average CV for L_∞'s of different areas and habitats was 15%. The L_∞ was assumed to have a value of 100 mm in this study as discussed previously. This gave the L_∞ a standard error estimate of 15.0 mm, making its 95% confidence intervals 70 mm to 130 mm. The K value was estimated to be 0.1006 using Equation 10 and L_∞ of 100 mm. Using Equation 11 and the CV for L_∞, the CV for K was estimated to be 42.3%, which yielded the value of 0.0426 for the standard error for K.

The annual expected growth increment decreased quickly with sea urchin size (Fig. 4). The largest expected annual increment was 6 mm for the smallest size class (39.5–40.5 mm) included in the study. The variance for annual growth increments calculated by using Equation 8 was large for small sea urchins. It decreased initially with size, reaching the smallest value at the 59 mm size class (58.5–59.5 mm), followed by a progressive increase with size (Fig. 5). The expected annual growth increment for the largest size class included in this study had the highest variance, which was over eight times as high as the smallest variance (Fig. 5).

The probability distribution of annual growth increment varied among size classes (Fig. 6), reflecting the differences in variances associated with different size classes. The last size class was a plus class, with the probability of staying in the same size class being 1. Figure 6 clearly indicated that no negative growth was allowed.

Discussion

Great variation in growth was observed in the Maine sea urchin stock (Vadas et al., 2002). Such a pattern of variation was reflected in estimating the VBGF parameters for dif-
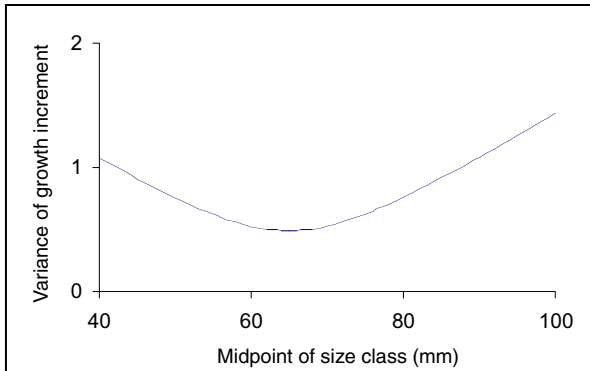
Figure 5

The variances of growth increment estimated for different sea urchin size classes by using Equation 8.

ferent areas and habitats (Table 1). Large standard errors were estimated for the VBGF parameters for sea urchins of the same area and habitat, and large differences occurred in the estimated VBGF parameters between different areas and habitats (Table 1). The approach developed in the present study considered observations made in both the fishery and scientific studies and provided a systematic way to incorporate the large variation in growth into the estimation of a growth-transition matrix, and subsequently into the sea urchin stock assessment.

It should be noted that the algorithm developed for estimating the variance of growth increments is approximate, and violations of the assumptions used in deriving the algorithm may introduce errors in estimating a growth-transition matrix. For example, large errors in estimating K and L_∞ will introduce errors in Equation 5, which was derived by assuming small errors for the two growth parameters. Nonnormal distribution of ΔL with its mean defined by Equation 6 and variance defined by Equation 8 will also result in errors in developing a growth-transition matrix. Other factors that may influence the quality of the estimated growth transition matrix include errors in estimating CVs for K, L_∞ estimated from Equations 10 and 11, and omitting high order items in deriving Equation 8.

Unlike most studies in which the variance for the annual growth increment was assumed to be the same for all size classes (Quinn and Deriso, 1999), our study explicitly suggested that the variance for the annual growth increment changed with size (Fig. 4). The differences in the variance were large between size classes, and changed nonlinearly with size. If a constant variance were used for all size classes, the variance in growth increment would be severely underestimated for large and small fish. This could introduce large biases in a stock assessment.

Size-dependent variation might better describe the variation in annual growth increment. Fish in small size classes tend to grow fast, but their growth tends to be more susceptible to environmental variation than adult growth, often resulting in large variation among individuals (Summerfelt and Hall, 1987). Fish in large size classes (older fish) have to divert some energy to reproduction but tend

to have considerable variation in energy allocation strategies among individuals. Differences among adults in the ability to grow can also be considerable because of genetics, specific growth patterns during juvenile stages, and differences in energy allocation between growth and maturation during younger ages (Nikolskii, 1969). This difference may cause large variations in growth for large and old fish (Summerfelt and Hall, 1987; Chen et al., 1988). Compared with old and young ages, growth rates for medium-size and medium-age fish may be less varied (Nikolskii, 1969). This pattern can be reflected realistically in the estimated variation by using the approach derived in our study.

Although the choice of L_∞ was a bit arbitrary in our study, it reflects observations from both the fishery and scientific studies. The largest sea urchins observed in the different scientific studies tend to be smaller than 100 mm, as indicated by the estimated L_∞ values for different areas and habitats (Fig. 1). The inability to observe larger sea urchins in scientific studies may result from relatively small sample sizes, the focus of research (small areas), and the large growth variations even in small spatial scales. The data collected from the fishery were more extensive and covered more areas. This, together with the tendency for taking large individuals in the fishery, may suggest that large individuals are more likely to appear in the fishery, rather than in scientific studies. Thus, it may be reasonable to set the expected value of L_∞ at 100 mm. Also, this higher value corresponds more closely to the upper growth estimates for green sea urchins from the northeast Pacific (Vadas, 1977). The CV was assumed to be 15% for L_∞, resulting in the 95% confidence interval of L_∞ ranging from 70 mm to 130 mm. This range was believed to be a reasonable estimate for the maximum attainable length for green sea urchins on the coast of Maine (Vadas, 1977).

The approach developed in our study can be readily used to incorporate the VBGF parameters estimated from different studies. This can be accomplished by rerunning the regression analyses between K and L_∞ and between CVs for K and L_∞. As more information about the growth of sea urchins on the coast of Maine becomes available, the growth transition matrix can be easily updated to reflect the variation identified in newer studies. The flexibility and ability to easily update and incorporate new information makes this approach desirable to the Maine sea urchin fishery, which is currently undergoing large changes in its population size and has only limited growth data.

The value of 100 mm chosen for L_∞ was rather arbitrary. However, because we considered the negative correlation between K and L_∞ in deriving the growth transition matrix, a small error in the L_∞ estimate would not change the growth-transition matrix greatly. In the future, however, we can conduct a systematic sampling of the stock across its geographical range and derive some forms of weighted average size with a composite variance that captures the range of sizes exhibited by the species. Such an approach would provide us with a better estimate of L_∞.

The growth-transition matrix developed in our study summarizes the growth patterns of sea urchins along the coast of Maine. It can be updated whenever new growth data become available. It can be readily incorporated into
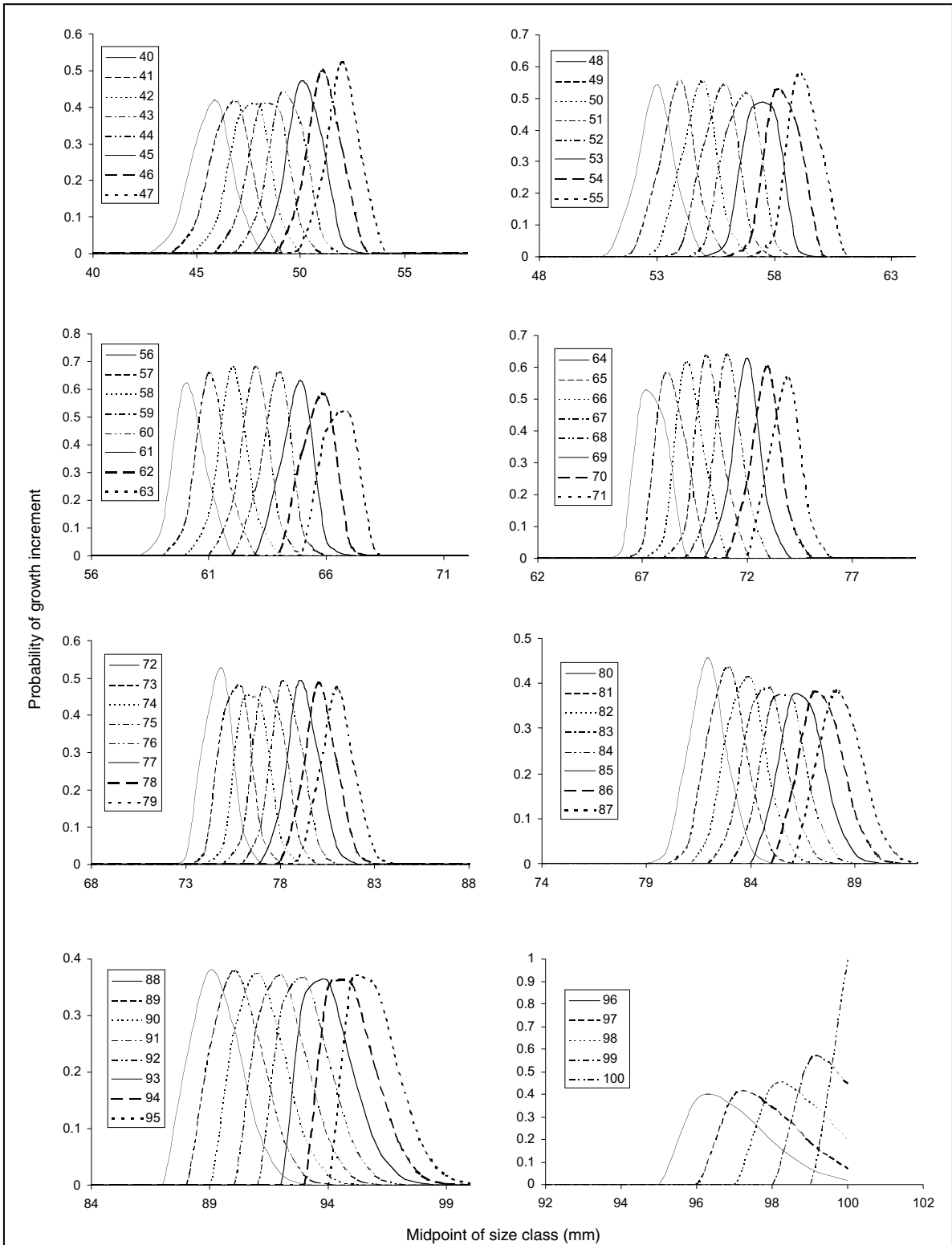
Figure 6

Probabilities of sea urchins growing from one size class to others. Each probability distribution was labeled with the midpoint value of the current size class of the sea urchin.

a size-structured stock assessment model to evaluate the status of sea urchin stock and to evaluate alternative management strategies for the Maine sea urchin fishery (Chen and Hunter, 2003).

Acknowledgments

We would like to thank the Maine Department of Marine Resources, the Northeast Consortium, and the Maine Sea Urchin Zone Council for supporting this study. Constructive and detailed comments from two anonymous reviewers and the scientific editor greatly improved an early version of the manuscript, for which we are grateful.

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