# Comparing Dynamic Versions of the Schaefer and Fox Production Models and Their Application to Lobster Fisheries

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Dynamic approaches (integrated and finite difference) to the Schaefer and Fox production models are applied to four commercial lobster fisheries. The integrated versions provided better predictions than their finite difference counterparts. Only the integrated version of the Fox model provides realistic (positive) biological parameter estimates for all four fisheries, and bootstrapping reveals those estimates to be generally stable. Additionally, this model periorms well when applied to data where certain assumptions of surplus production modeling are fulfilled. The results suggest further investigation of the integration procedure.

Des méthodes dynamiques (méthode intégrée et méthode des différences finies) sont appliquées aux modèles de production de Schaeler et de Fox dans le cas de quatre pèches commerciales au homard. Les versions utilisant la méthode intégrée permettent d'obtenir de meilleures prévisions par rapport aux versions fondées sur la méthode des différences finies. Seule la version intégrée du modèle de Fox fournit des estimations réalistes (valables) des paramètres biologiques pour les quatre pèches, et l'application de la technique du bootstrapping démontre que ces estimations sont généralement stables. En outre, on obtient de bons résultats lorsque l'on applique ce modèle aux données qui confirment certaines hypothèses relativement aux modèles de production excédentaire. Ces résultats incitent donc à pousser les recherches du côté de la méthode intégrée.

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ne of the simplest approaches to modeling a fishery is applying a surplus production model to a time series of catch and effort data. Schaefer (1957) and Fox (1970) helped pioneer this approach and used the concept of equilibrium to model a fishery over the long run. They first applied a dynamic model to estimate various biological parameters of a fishery. The parameters were then used in an equilibrium model to estimate fishery management parameters (e.g. maximum sustainable yield). The dynamic models therefore had a dual purpose: to account for the nonequilibrium portions of a fishery and to accurately estimate the biological parameters so the resulting management parameters could be trusted. Many authors (Walter 1973; Schnute 1977; Uhler 1980; Lleonart and Salat 1989) have since developed their own dynamic versions of the Schaefer (1957) and Fox (1970) models to better assess unstabilized fisheries. The two dynamic approaches examined in this paper are the original (finite difference) versions and the integrated versions (Schnute 1977: Clarke et al. 1992).

The Schaefer (1957) and Fox (1970) models have the continuous forms

(1) 
$$dX/dt = rX - rX^2/K - C$$

and

(2) 
$$dX/dt = rX \ln(K/X) - C,$$

respectively, where X represents the population, dX/dt the growth rate of the population. C the catch rate, r the intrinsic growth rate, and K the maximum stock level or virgin biomass.

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Equation (1) assumes that the growth rate to biomass relationship is logistic (parabolic), while Equation (2) assumes a Gompertz distribution (Richards 1959).

Fishing effort is taken into consideration by substituting C = qEX, with q defined as the catchability coefficient and E as the rate of fishing effort (e.g. the effort expended in 1 yr). Equations (1) and (2) are then converted to

(3) 
$$(1/U)dU/dt = r - r/(qK)U - qE$$

and

(4) 
$$(1/U)dU/dt = r \ln(qK) - r \ln(U) - qE$$
.

respectively, where U = C/E is the instantaneous catch per unit effort (CPUE). Schaefer (1957) and Fox (1970) estimated parameters r, q, and K by converting Equations (3)and (4) into their finite difference forms:

Schaefer:

(5) 
$$\Delta U_n / U_n = r - r / (qK) U_n - qE_n$$

Fox:

(6) 
$$\Delta U_n/U_n = r \ln(qK) - r \ln(U_n) - qE_n$$

where  $U_n$  is the average CPUE and  $E_n$  is the total effort expended for year *n* and  $\Delta U_n = (U_{n+1} - U_{n-1})/2$ . Both Equations (5) and (6) are considered dynamic given that  $U_{n+1}$ can be expressed in terms of past variables  $U_n, E_n$ , and  $U_{n-1}$ . Originally, Equations (5) and (6) were used only to estimate parameters *r*. *q*, and *K*. However, we test the applicability of the dynamic models for predictions and parameter estimation in nonequilibrium conditions. Hereafter, Equations (5) and (6)

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will be called the FD (finite difference) - Schaefer and FD-Fox models, respectively.

Upon scrutiny, the FD-Schaefer and FD-Fox models possess some questionable properties. One problem is the approximation  $dU/dt = \Delta U_n$ , which assumes that CPUE is linearly distributed over the course of 2 yr. Another problem is that the CPUE of year n + 1.  $U_{n+1}$ , can be predicted without the anticipated effort being specified for that year. Such a condition is questionable, given the definition of CPUE: U = C/E.

Rather than using a finite difference approximation. Schnute (1977) integrated Equation (3) and approximated the average annual CPUE as the geometric mean of the instantaneous CPUEs at the beginning and end of the year. Schnute's dynamic version of the Schaefer model, henceforth referred to as the Schnute model, is

(7) 
$$\ln (U_{n+1}/U_n) = r - (r/(qK)) (U_n + U_{n+1})/2 - q(E_n + E_{n+1})/2.$$

As noted by Uhler (1980), the Schnute model, unlike the FD-Schaeter and FD-Fox models, has the desirable property that  $U_{n+1}$  tends to zero as  $E_{n+1}$  becomes large. Another advantage of this model is that the predicted CPUE,  $U_{n+1}$ , can be estimated for a range of anticipated effort,  $E_{n+1}$ , to allow fishery managers to approximate the effort level needed for a targeted yield. In Uhler (1980), the Schnute model was shown to have less bias than an FD-Schaefer model (with a 1-yr time lag) when applied to a computer-simulated fishery.

An integrated version of the Fox model has been applied to the lobster fishery in the Northwestern Hawaiian Islands (NWHI) (Clarke et al. 1992). This model uses the same assumptions as the Schute model and incorporates a Taylor series approximation (Appendix A):

(8) 
$$\ln(U_{n+1}) = [2r \ln(qK) + (2 - r) \ln(U_n) - q(E_n + E_{n+1})]/(2 + r).$$

Unlike the other models presented, this model is a simple, lagged logarithmic equation of CPUE. This gives the model an advantage over the Schnute and finite difference models when regression analysis is performed. This model has been applied to a limited time series of eatch and effort data (8 yr of the NWHI lobster tishery: Clarke et al. 1992), but its applicability to fisheries with longer time series is unknown. Hereafter, this model will be called the 1 (integrated) - Fox model.

Our paper examines the assumption that the integrated models will yield better predictions and biological parameter estimates than the finite difference models. The models are applied to four commercial lobster fisheries with substantial time series of catch and effort data, and each model's ability to predict annual CPUE is investigated. Biological parameter estimates for each fishery also are presented. However, since little is known of these parameters, only general conclusions are made about them. Each model's ability for parameter estimation is tested using data sets in which the biological parameter q is known.

### Methods

A frequently used approach to estimate a model's predictive power of catch is applying an ordinary least squares (OLS) regression on all years of data for a fishery. The points on the resulting regression curve are then interpreted as catch (or CPUE) predictions for the original data. Wittink (1988) pointed out that this approach depends heavily on the *R*-squared ( $R^2$ ) value and does not test for predictive power, since the regression curve is created using the original data (i.e. the curve has prior knowledge of what it is supposed to predict).

The approach used in this paper is to make annual predictions only using data prior to that year. Mathematically, OLS is performed on the first m - 1 years of data, and a prediction is made for year m using the results of that regression. A regression is then performed on the first m years for the prediction of year m + 1, and this procedure is continued until a prediction is made for the last year of available data. The predicted and actual values are then compared to determine predictive power. This approach better approximates what fishery managers actually face because having data for future years is unrealistic.

Each model's estimates of the biological parameters r, q, and K, using all years of data for a fishery, are also examined. From definitions presented in Schnute (1977), each biological parameter should be positive. The parameter estimates presented in our paper are unconstrained estimates. Other papers (e.g. Schaefer 1957) take absolute values to ensure the analyses have realistic (positive) results. We use the unconstrained approach to look at the mathematical relations of the models rather than to thoroughly analyze a specific fisherv.

The four dynamic models are applied to catch and effort data from tour lobster fisheries: Western Australian rock lobster. Panulirus cygnus (years 1944-64 from table 1 in Morgan 1979a: years 1965-78 from tables 6 and 8 in Morgan et al. 1982): American lobster. Homarus americanus (years 1950-79 from table 1 in Townsend 1986); Tasmanian rock lobster. Jasus novaehollandiae (years 1947-84 from table 1 in Campbell and Hall 1988); and New Zealand lobster, Jasus edwardsii (years 1945-90 from the totals in table 1 in Breen 1991). The Western Australian data take into account seasonal variability and area distribution (Morgan 1979b). The New England data are only inshore data, and a modified Schaefer model was applied to them in Townsend (1986). An FD-Fox model and an FD-Schaefer model with 1-vr time lags have been applied to the Tasmanian data (Campbell and Hall 1988). Finally, the New Zealand data are composed of the total of commercial and estimated unreported, amateur, and illegal catch data. To our knowledge, each data set has not been proven to satisfy all assumptions of surplus production modeling. However, the applicability of these models to commercial data can be gauged by each model's ability to forecast catch (or CPUE).

A prediction for the CPUE of year m + 1 is made in the following manner. An OLS regression is applied to the models by using catch and effort data for the first m years of a fishery. The resulting regression on data for years n = 1 to n = m estimates the parameters r, q, and K:

FD-Schaefer:

(9) 
$$\Delta U_{n-1}/U_{n-1} = c1 + c2U_{n-1} + c3E_{n-1}$$
  
with  $r = c1$ ,  $q = -c3$ , and  $K = -r/(ac2)$ ;

FD-Fox:

(10) 
$$\Delta U_{n-1}/U_{n-1} = c1 + c2 \ln(U_{n-1}) + c3E_{n-1}$$
  
with  $r = -c2$ ,  $q = -c3$ , and  $K = e^{c1/r}/q$ ;

Schnute:

(11) 
$$\ln(U_n/U_{n-1}) = c1 + c2(U_{n-1} + U_n)/2 + c3(E_{n-1} + E_n)/2$$

with 
$$r = c1$$
,  $q = -c3$ , and  $K = -r/(qc2)$ ; and

I-Fox:

(12) 
$$\ln(U_n) = c1 + c2 \ln(U_{n-1}) + c3(E_{n-1} + E_n)$$

with r = 2(1 - c2)/(1 + c2), q = -c3(2 + r), and  $K = e^{c1(2 + r)/(2r)}/q$ . The FD-Schaefer and FD-Fox models predict the following year's CPUE with

FD-Schaefer:

(13) 
$$U_{m+1} = U_{m-1} + 2U_m[r - r/(qK) U_m - qE_m]$$

and

FD-Fox:

(14) 
$$U_{m+1} = U_{m-1} + 2U_m[r \ln(qK) - r \ln(U_m) - qE_m].$$

For the I-Fox model, after the anticipated effort  $E_{m+1}$  is specified, the predicted CPUE is

(15) 
$$U_{m+1} = e^{\frac{(2r\ln(qK) + (2-r)\ln(U_m) - q(E_m + E_{m+1}))}{(2+r)}}.$$

For the Schnute model,  $U_{m+1}$  was estimated from Equation (31) in Schnute (1977). Confidence intervals for the Schnute model's prediction are in Schnute (1977); those for the I-Fox are in Appendix B.

The predictive ability of the models is tested by using Theil's U-statistic (Wittink 1988):

(16) 
$$U_T = \sqrt{\sum_{\substack{n=k \ N} \\ N = k}^{N} (U_n - U_{p,n})^2} \sum_{\substack{n=k \ N} \\ N = k}^{N} (U_n - U_{n-1})^2}$$

where  $U_{p,n}$  is the predicted CPUE for year *n*. and *k* and *N* are equal to the first and last year, respectively, that a CPUE prediction was made. The numerator of  $U_T$  is the sum of the squared differences of the actual and predicted CPUEs, and the denominator is the sum of the squared differences between the actual CPUEs of adjacent years. Thus, this statistic adjusts a model's predictive error by considering the year-to-year variation of the actual CPUE. If  $U_T > 1$ , the model is not considered useful for forecasting purposes.

For the overall estimation of biological parameters (r, q, andK), the following procedure is used. First, regressions of the four models are performed on all years of data. The presence of autocorrelation is then investigated. Since the I-Fox model has a lagged dependent variable, the Durbin-Watson statistic is inappropriate to detect autocorrelation, and the test statistic used is the Durbin h-statistic (Pindyck and Rubinfeld 1981). When the Durbin h-statistic is undefined, the Durbin t-statistic test is applied (King 1987). If the FD-Schaefer, FD-Fox, or Schnute model passes either the Durbin h-test or the regular Durbin-Watson test, then the results of that model's regression are used. When evidence of autocorrelation is detected, the Cochrane-Orcutt procedure for autocorrelation correction (Wittink 1988) is applied until the model's test statistic is not significant in showing autocorrelation. The model loses a degree of freedom for each Cochrane-Orcutt iteration performed.

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TABLE 1. Average percent prediction errors from the I-Fox, Schnute, FD-Fox, and FD-Schaefer models for four lobster fisheries.

| Location          | I-Fox | Schnute | FD-Fox | FD-Schaefer |
|-------------------|-------|---------|--------|-------------|
| New England       | 11.58 | 10.35   | 18.56  | 18.56       |
| New Zealand       | 18.86 | 16.58   | 20.92  | 20.62       |
| Tasmania          | 12.20 | 12.26   | 21.54  | 21.01       |
| Western Australia | 12.49 | 12.75   | 25.69  | 24.26       |

TABLE 2. Theil's U-statistic test applied to the I-Fox, Schnute, FD-Fox, and FD-Schaefer models for four lobster fisheries.

| Location          | I-Fox  | Schnute            | FD-Fox | FD-Schaefer |
|-------------------|--------|--------------------|--------|-------------|
| New England       | 0.780ª | 0.750ª             | 1.44   | 1.43        |
| New Zealand       | 1.86   | 3.20               | 2.46   | 2.43        |
| Tasmania          | 0.827° | 0.910 <sup>*</sup> | 1.60   | 1.55        |
| Western Australia | 1.01   | 1.21               | 2.70   | 2.45        |

\*Model is considered an adequate predictor.

## **Results and Discussion**

The lack of degrees of freedom for regression analysis with the FD-Fox and FD-Schaefer models. which have a 2-yr time lag, prevented predictions from being made for the first 6 yr of each fishery. Therefore, CPUE predictions for years 1956–79, 1951–90, 1953–84, and 1950–78 were obtained for the New England. New Zealand, Tasmanian, and Western Australian lobster fisheries, respectively. A model's CPUE prediction for the seventh year used the regression results from the first 6 yr of data, the prediction for the eighth year used those from the first 7 yr of data, and so on.

The percent prediction error

(17) 100 
$$|U_n - U_{p,n}|/U_n$$

was calculated for each model's prediction of CPUE, with  $U_{p,n}$ being the predicted CPUE for year *n*. The means of the percent prediction errors from each model (Table 1) show that the I-Fox model is the most accurate predictor for two of the four fisheries, and the Schnute model is the more accurate predictor for the other two. In all four fisheries, the I-Fox and Schnute models have lower average percent prediction errors than the finite difference models. According to Theil's U-statistic test (Table 2), the I-Fox and Schnute models are adequate predictors for the Tasmanian and New England fisheries, while the FD-Fox and FD-Schaefer models failed the test for all four fisheries.

From the regressions on all data of a fishery, only the I-Fox model provides positive biological parameters for all four fisheries (Tables 3-6). The I-Fox model also had high  $R^2$  values (>0.8), but this goodness of fit was expected. The low  $R^2$ values from the other three models reveal problems in explaining the variation in their more complex dependent variables ( $\Delta U_n/U_n$  for the FD-Fox and FD-Schaefer models and  $\ln(U_{n+1}/U_n)$  for the Schnute model) over substantially long time series. This was probably a major reason for their unrealistic (negative) estimates of the biological parameters. Another possible explanation is that the data sets examined do not satisfy the assumptions of surplus production modeling. The higher  $R^2$  values of the I-Fox model compared with those of the Schnute model reveal that a better regression fit does not necessarily imply better predictive power (Ferber 1956).

Bootstrapping (Efron and Tibshirani 1986) was applied to the I-Fox model to test the stability of the biological parameters. Sampling with replacement was applied to the residuals of each

TABLE 3. Final regression coefficients and parameter estimates for the New England inshore lobster fishery (NA = not applicable). \*P < 0.05.

|                               | I-Fox                  | Schnute                | FD-Fox*                | FD-Schaefer*           |
|-------------------------------|------------------------|------------------------|------------------------|------------------------|
| cl                            | -1.62                  | -0.444                 | 0.399                  | -0.308                 |
| t-ratio for cl                | - 2.57*                | -1.40                  | 0.742                  | ~1.11                  |
| c2                            | 0.416                  | 7.94                   | 0.176                  | 4.68                   |
| t-ratio                       | 1.79                   | 1.28                   | 0.911                  | 0.830                  |
| c3                            | $-2.41 \times 10^{-4}$ | $1.61 \times 10^{-4}$  | $1.75 \times 10^{-4}$  | $1.15 \times 10^{-4}$  |
| t-ratio for c3                | - 2.42*                | 1.26                   | 1.07                   | 1.04                   |
| df                            | 26                     | 26                     | 24                     | 24                     |
| R <sup>2</sup>                | 0.943                  | 0.0606                 | 0.0493                 | 0.0439                 |
| R <sup>2</sup> adj            | 0.939                  | -0.0117                | -0.0299                | -0.0358                |
| Durbin h                      | Undefined              | Undefined              | Undefined              | Undefined              |
| Durbin t                      | 1.32*                  | NA                     | NA                     | NA                     |
| Durbin-Watson                 | 1.19                   | 1.95*                  | 1.69*                  | 1.70*                  |
| r (yr <sup>-1</sup> )         | 0.826                  | -0.444                 | -0.176                 | -0.308                 |
| $q (1000 \text{ traps}^{-1})$ | $6.80 \times 10^{-4}$  | $-1.61 \times 10^{-4}$ | $-1.75 \times 10^{-4}$ | $-1.15 \times 10^{-4}$ |
| K (millions of pounds)        | 92.6                   | - 347                  | - 591                  | - 571                  |

\*One iteration of the Cochrane-Orcutt procedure was applied.

TABLE 4. Final regression coefficients and parameter estimates for the New Zealand inshore lobster fishery (NA = not applicable). \* $P \le 0.05$ .

|                                   | I-Fox*                 | Schnute <sup>b</sup>   | FD-Fox                 | FD-Schaefer            |
|-----------------------------------|------------------------|------------------------|------------------------|------------------------|
| cl                                | 0.369                  | -0.0773                | -0.0446                | -0.0523                |
| t-ratio for cl                    | 2.18*                  | -0.539                 | -0.366                 | -0.464                 |
| c2                                | 0.718                  | 0.0158                 | 0.0165                 | 0.00875                |
| t-ratio for c2                    | 6.06*                  | 0.391                  | 0.192                  | 0.281                  |
| c3                                | $-4.24 \times 10^{-5}$ | $2.01 \times 10^{-6}$  | $-1.30 \times 10^{-6}$ | $-1.58 \times 10^{-6}$ |
| t-ratio for c3                    | -2.41*                 | 0.0902                 | -0.0502                | -0.0870                |
| df                                | 40                     | 41                     | 41                     | 41                     |
| <b>R</b> <sup>2</sup>             | 0.934                  | 0.0108                 | 0.00974                | 0.0108                 |
| R <sup>2</sup> adj                | 0.930                  | -0.0374                | -0.0386                | -0.0375                |
| Durbin h                          | - 1.05*                | -0.163*                | 1.31*                  | 1.09*                  |
| Durbin-Watson                     | NA                     | 2.05*                  | 1.68*                  | 1.68*                  |
| r (yr <sup>-1</sup> )             | 0.329                  | -0.0773                | -0.0165                | -0.0523                |
| q (1000 pot-lifts <sup>-1</sup> ) | $9.88 \times 10^{-5}$  | $-2.01 \times 10^{-6}$ | $1.30 \times 10^{-6}$  | $1.58 \times 10^{-6}$  |
| K (tonnes)                        | 37 469                 | -2 440 845             | 11 527 340             | 3 788 069              |

"Two iterations of the Cochrane-Orcutt procedure were applied.

"One iteration of the Cochrane-Orcutt procedure was applied.

| TABLE 5. Final regression coefficients and param | eter estimates for the | e Tasmanian lobster | fishery (NA |
|--|------------------------|---------------------|-------------|
| = not applicable). $*P < 0.05$ .                 |                        |                     |             |

|                                     | I-Fox  | Schnute                | FD-Fox  | FD-Schaefer            |
|-------------------------------------|--------|------------------------|---------|------------------------|
| cl                                  | 6.40   | 0.494                  | 1.34    | 0.272                  |
| <i>i</i> -ratio for <i>c</i> 1      | 5.41*  | 1.36                   | 0.978   | 1.03                   |
| c2                                  | 0.256  | $-1.14 \times 10^{-4}$ | -0.162  | $-6.64 \times 10^{-5}$ |
| t-ratio for c2                      | 1.89   | -1.66                  | -1.02   | -1.29                  |
| c3                                  | -0.416 | -0.311                 | -0.135  | -0.174                 |
| t-ratio for c3                      | -4.30* | -1.11                  | -0.660  | -0.889                 |
| df                                  | 34     | 34                     | 33      | 33                     |
| R <sup>2</sup>                      | 0.833  | 0.0953                 | 0.0452  | 0.0624                 |
| R² adj                              | 0.823  | 0.0421                 | -0.0126 | 0.00556                |
| Durbin h                            | 0.976* | -1.35*                 | 5.46    | 1.52*                  |
| Durbin-Watson                       | NA     | 2.44                   | 1.44    | 1.49                   |
| $r(yr^{-1})$                        | 1.19   | 0.494                  | 0.162   | 0.272                  |
| q (million pot-days <sup>-1</sup> ) | 1.33   | 0.311                  | 0.135   | 0.174                  |
| K (tonnes)                          | 4079   | 13 997                 | 29 056  | 23 467                 |

of the four I-Fox data sets (a Cochrane–Orcutt-transformed data set was used for the New Zealand fishery), and a regression was performed on each new data set. This procedure was replicated 1000 times with each regression yielding new estimates of r, q, and K. The mean, standard deviation, and coefficient of variation of the r, q, and K bootstrap estimates for each fishery are shown in Table 7. The coefficients of variation suggest that the parameters derived from the I-Fox model are relatively stable for all parameters except K (high variability was shown in the New England and New Zealand lobster fisheries).

The integrated models predict CPUE reasonably (<20% error) for all four lobster fisheries but fail to pass Theil's U-

|                           | I-Fox   | Schnute | FD-Fox*  | FD-Schaefer |
|---------------------------|---------|---------|----------|-------------|
| <i>c</i> 1                | 0.617   | 0.106   | -0.284   | -0.411      |
| t-ratio for cl            | 3.73*   | 0.304   | -1.42    | - 1.58      |
| c2                        | 0.429   | -0.0369 | 0.209    | 0.127       |
| t-ratio for c2            | 2.88*   | -0.297  | 1.22     | 1.41        |
| c3                        | -0.0354 | -0.0113 | 0.032    | 0.0332      |
| t-ratio for c3            | - 3.67* | -0.410  | 1.33     | 1.51        |
| df                        | 31      | 31      | 29       | 29          |
| R <sup>2</sup>            | 0.882   | 0.00725 | 0.0572   | 0.0735      |
| $R^2$ adi                 | 0.875   | -0.0568 | -0.00781 | 0.00955     |
| Durbin h                  | 1.58*   | 0.144*  | 2.58     | 0.608*      |
| Durbin-Watson             | NA      | 1.97*   | 1.78*    | 1.81*       |
| $r(vr^{-1})$              | 0.799   | 0.106   | -0.209   | -0.411      |
| q (million pot-lifts )    | 0.0991  | 0.0113  | -0.0317  | -0.0332     |
| K (millions of kilograms) | 29.7    | 253     | - 123.4  | 98.0        |

TABLE 6. Final regression coefficients and parameter estimates for the Western Australian lobster fishery (NA = not applicable). \*P < 0.05.

"One iteration of the Cochrane-Orcutt procedure was applied.

TABLE 7. Bootstrap estimates of the means, standard deviations (SD), and coefficients of variation (CV) of parameter r, q, and K when applying the I-Fox model to four lobster fisheries.

| Parameter   | Mean                        | sD                           | CV                   |
|-------------|-----------------------------|------------------------------|----------------------|
|             | New Eng                     | land                         |                      |
| r<br>4<br>K | 0.912<br>0.000755<br>120.2  | 0.509<br>0.000430<br>399.8   | 0.56<br>0.57<br>3.33 |
|             | New Zea                     | land                         |                      |
| r<br>4<br>K | 0.340<br>0.000102<br>44 061 | 0.170<br>0.0000513<br>96 482 | 0.50<br>0.50<br>2.19 |
|             | Tasma                       | nia                          |                      |
| r<br>4<br>K | 1.23<br>1.38<br>4355        | 0.368<br>0.469<br>1573       | 0.30<br>0.34<br>0.36 |
|             | Western A                   | ustralia                     |                      |
| r<br>4<br>K | 0.838<br>0.103<br>33.7      | 0.316<br>0.0400<br>18.6      | 0.38<br>0.39<br>0.55 |

statistic for the New Zealand and Western Australian fisheries. Also, despite providing positive, unconstrained estimates of the biological parameters, instability with the I-Fox model is shown in parameter K. These findings could indicate a theoretical problem with all of the models investigated: the assumption that C = qEX. Since the estimates of biomass are not known, verification of this assumption is difficult. However, data sets designed to fit this assumption exist. The applicability of the I-Fox model toward these data sets is explored.

#### Application to the Silliman and Gutsell (1958) Data Sets

Guppy populations (*Lebistes reticulatus*) were introduced into four similarly designed tanks, and two (called populations A and B) were "fished" with a certain percent removal during each 3-wk interval (Silliman and Gutsell 1958). Fishing effort data were computed so that U = qX with q = 0.1. Since two

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tanks were unfished, the maximum stock level each tank achieved could be thought of as estimates of the virgin biomass K. The maximum weight attained in tanks C and D equaled 37.1 and 36.0 g, respectively. This suggests that reasonable estimates of K for populations A and B are probably in the range of 30-40 g. Pella and Tomlinson (1969) estimated q = 0.071 and K = 49.3 for population A and q = 0.078 and K = 39.5 for population B.

Tables 8 and 9 present the catch and effort data along with estimates of q. K. and predicted CPUE  $U_p$  from the I-Fox model for each 3-wk interval. The catch data are from Silliman and Gutsell 1958) whereas the effort data are adjusted by scaling the percent weight removals as suggested in Pella and Tomlinson (1969). Each estimate of q. K. and  $U_p$  is obtained from the I-Fox regression on all data prior to that 3-wk interval. Because of a lack of degrees of freedom, the I-Fox regression estimates could not be obtained for the first four observations of each table.

The tables present some revealing points of the I-Fox model. For example, the initial estimates of q and K are unrealistic (negative). This could be due either to the lack of data or to the effort levels for the first 13 observations being in a narrow range. Also, despite obtaining negative values of q and K, the I-Fox model still predicted CPUE accurately. This implies that a model that estimates biological parameters poorly could still prove useful when predicting future catch (e.g. the Schnute model applied to the New England lobster fishery). Finally, the I-Fox model's estimates become unrealistic for the last observations, suggesting that the model encounters problems when applied to fisheries nearing extinction.

The main point of the tables is that the I-Fox model accurately assesses "fisheries" A and B for a large portion of their life spans. In both populations, estimates of q and K become fairly stable by week 100, with the estimates of population B hovering around the "true" values of q (0.1) and K (between 30 and 40). Considering the I-Fox model is an adequate predictor of CPUE (Theil's U-statistic was 0.751 for population B), the model seems to be a valuable management tool for fisheries that satisfy the assumption of C = qEX.

The ability of the other three models to estimate parameter q has also been analyzed. As was done in Tables 8 and 9 with the I-Fox model, values of q were obtained from each model (Fig. 1). The deviation of each q estimate from 0.100,

| Week       | Catch | Effort | CPUE | U <sub>p</sub> | % error | K      | <i>q</i> |
|------------|-------|--------|------|----------------|---------|--------|----------|
| 40         | 6.0   | 2.58   | 2.33 |                |         |        |          |
| 43         | 4.9   | 2.49   | 1.97 |                |         |        |          |
| 46         | 3.7   | 2.06   | 1.80 |                |         |        |          |
| 49         | 4.4   | 2.50   | 1.76 |                |         |        |          |
| 52         | 4.1   | 2.43   | 1.69 | 1.82           | 7.69    | -2.9   | -0.326   |
| 55         | 3.5   | 2.15   | 1.63 | 1.68           | 3.07    | 30.1   | 0.072    |
| 58         | 3.5   | 2.32   | 1.51 | 1.63           | 7.95    | 35.6   | 0.058    |
| 61         | 3.8   | 2.59   | 1.47 | 1.51           | 2.72    | -98.5  | -0.014   |
| 64         | 3.3   | 2.36   | 1.40 | 1.45           | 3.57    | 41.0   | 0.049    |
| 67         | 3.3   | 2.23   | 1.48 | 1.40           | 5.41    | 31.5   | 0.099    |
| 70         | 2.8   | 1.90   | 1.47 | 1.52           | 3.40    | 26.5   | 0.131    |
| 73         | 3.0   | 2.00   | 1.50 | 1.50           | 0.00    | 31.0   | 0.079    |
| 76         | 3.9   | 2.62   | 1.49 | 1.49           | 0.00    | 31.5   | 0.077    |
| 7 <b>9</b> | 1.4   | 1.05   | 1.33 | 1.52           | 14.29   | 31.5   | 0.076    |
| 82         | 2.1   | 1.41   | 1.49 | 1.29           | 13.42   | - 15.5 | -0.064   |
| 85         | 1.9   | 1.23   | 1.54 | 1.53           | 0.65    | 39.4   | 0.050    |
| 88         | 2.0   | 1.33   | 1.50 | 1.58           | 5.33    | 37.7   | 0.054    |
| 91         | 1.7   | 1.06   | 1.60 | 1.53           | 4.38    | 51.1   | 0.035    |
| 94         | 1.5   | 0.90   | 1.67 | 1.64           | 1.80    | 40.0   | 0.049    |
| 97         | 1.9   | 1.06   | 1.79 | 1.69           | 5.59    | 37.6   | 0.054    |
| 100        | 1.7   | 0.97   | 1.75 | 1.81           | 3.43    | 34.2   | 0.067    |
| 103        | 1.2   | 0.62   | 1.94 | 1.79           | 7.73    | 35.0   | 0.062    |
| 106        | 2.0   | 0.94   | 2.13 | 1.96           | 7.98    | 33.2   | 0.075    |
| 109        | 2.0   | 0.87   | 2.30 | 2.14           | 6.96    | 35.5   | 0.084    |
| 112        | 2.6   | 1.12   | 2.32 | 2.31           | 0.43    | 42.3   | 0.089    |
| 115        | 2.9   | 1.23   | 2.36 | 2.29           | 2.97    | 43.2   | 0.089    |
| 118        | 3.0   | 1.31   | 2.29 | 2.32           | 1.31    | 47.0   | 0.089    |
| 121        | 11.2  | 4.77   | 2.35 | 1.95           | 17.02   | 45.3   | 0.089    |
| 124        | 7.0   | 4.58   | 1.53 | 1.91           | 24.84   | 88.7   | 0.063    |
| 127        | 5.2   | 4.37   | 1.19 | 1.21           | 1.68    | 51.6   | 0.097    |
| 130        | 5.7   | 5.09   | 1.12 | 0.95           | 15.18   | 52.8   | 0.098    |
| 133        | 5.6   | 5.05   | 1.11 | 0.93           | 16.22   | 40.3   | 0.088    |
| 136        | 4.2   | 4.38   | 0.96 | 1.00           | 4.17    | 36.7   | 0.079    |
| 139        | 4.3   | 4.78   | 0.90 | 0.89           | 1.11    | 37.2   | 0.080    |
| 142        | 3.5   | 4.32   | 0.81 | 0.85           | 4.94    | 37.0   | 0.080    |
| 145        | 3.9   | 5.42   | 0.72 | 0.76           | 5.56    | 38.2   | 0.080    |
| 148        | 3.5   | 5.00   | 0.70 | 0.67           | 4.29    | 39.7   | 0.080    |
| 151        | 3.4   | 6.54   | 0.52 | 0.63           | 21.15   | 38.3   | 0.080    |
| 154        | 2.1   | 7.00   | 0.30 | 0.44           | 46.67   | 42.8   | 0.082    |
| 157        | 2.4   | 7.27   | 0.33 | 0.24           | 27.27   | 71.3   | 0.084    |
| 160        | 1.2   | 6.32   | 0.19 | 0.30           | 57.89   | 39.3   | 0.092    |
| 163        | 1.2   | 6.67   | 0.18 | 0.17           | 5.56    | 71.8   | 0.083    |
| 166        | 0.9   | 6.92   | 0.13 | 0.16           | 23.08   | 60.5   | 0.087    |
| 169        | 1.0   | 7.14   | 0.14 | 0.11           | 21.43   | 91.9   | 0.080    |
| 172        | 0.2   | 3.33   | 0.06 | 0.15           | 150.00  | 59.7   | 0.088    |

TABLE 8. Predicted CPUE  $U_p$ , prediction error, and parameters K and q from the I-Fox model for each 3-wk interval in the population A data set of Silliman and Gutsell (1958).

|q - 0.1|, was then computed for each 3-wk interval after week 82 (the last week that the models estimated a negative value of q). The average deviations for each model reveal that the integrated models are superior to the finite difference models in estimating q. For population A, the average deviations for the 1-Fox and Schnute models are 0.024 and 0.029, respectively. The FD-Fox and FD-Schaefer models estimate q more poorly; the average deviation is 0.043 for each model. For population B, the I-Fox and Schnute models estimate q more accurately, with average deviations of 0.012 and 0.013, respectively. Although the FD-Schaefer and FD-Fox models are also more accurate in population B than in population A (0.030 and 0.033 average deviations, respectively), their q estimates are still not as accurate as the integrated models.

# Conclusion

Ideally, fishery managers require a model that accurately predicts catch (or CPUE) while also estimating reasonable biological parameters. None of the models performed exceptionally well when applied to the four commercial lobster data sets, although a case could be made for the applicability of the I-Fox model to the Tasmanian lobster fishery. The model passed Theil's U-statistic when predicting CPUE and had positive (and stable) biological parameters. Yet specific instances of inaccurate CPUE predictions by the I-Fox model were still found. This supports the consensus that surplus production models are too simple to accurately reflect fish and fishery interactions. Temperature, spawning stock information, and operational

| TABLE 9. Predicted   | CPUE $U_{p}$ , prediction | error, and paramet   | ers K and q fi | rom the I-Fox | model for each |
|----------------------|---------------------------|----------------------|----------------|---------------|----------------|
| 3-wk interval in the | population B data se      | et of Silliman and G | utsell (1958)  | ۱.            |                |

| Week | Catch | Effort | CPUE | U <sub>p</sub> | % error | K                      | q      |
|------|-------|--------|------|----------------|---------|------------------------|--------|
| 40   | 8.0   | 2.60   | 3.08 |                | <u></u> |                        |        |
| 43   | 5.0   | 2.13   | 2.35 |                |         |                        |        |
| 46   | 5.6   | 2.55   | 2.20 |                |         |                        |        |
| 49   | 5.6   | 2.86   | 1.96 |                |         |                        |        |
| 52   | 4.5   | 2.57   | 1.75 | 1.89           | 8.00    | 12.0                   | 0.417  |
| 55   | 4.0   | 2.50   | 1.60 | 1.84           | 15.00   | 14.4                   | 0.453  |
| 58   | 3.1   | 2.18   | 1.42 | 1.61           | 13.38   | 24.8                   | 0.142  |
| 61   | 3.5   | 2.57   | 1.36 | 1.35           | 0.74    | -12.0                  | -0.053 |
| 64   | 3.5   | 2.63   | 1.33 | 1.32           | 0.75    | -15.7                  | -0.046 |
| 67   | 3.7   | 2.50   | 1.48 | 1.30           | 12.16   | -14.4                  | -0.049 |
| 70   | 3.6   | 2.45   | 1.47 | 1.44           | 2.04    | -9.6                   | -0.078 |
| 73   | 3.4   | 2.30   | 1.48 | 1.43           | 3.38    | - 10.7                 | -0.074 |
| 76   | 3.8   | 2.70   | 1.41 | 1.46           | 3.55    | -18.6                  | -0.052 |
| 79   | 1.5   | 1.13   | 1.33 | 1.36           | 2.26    | - 18.5                 | -0.051 |
| 82   | 1.9   | 1.22   | 1.56 | 1.22           | 21.79   | -8.7                   | -0.084 |
| 85   | 1.9   | 1.17   | 1.62 | 1.65           | 1.85    | 30.4                   | 0.083  |
| 88   | 2.1   | 1.30   | 1.62 | 1.68           | 3.70    | 31.2                   | 0.078  |
| 91   | 2.3   | 1.42   | 1.62 | 1.64           | 1.23    | 33.3                   | 0.067  |
| 94   | 2.2   | 1.26   | 1.75 | 1.64           | 6.29    | 34.0                   | 0.064  |
| 97   | 1.9   | 1.02   | 1.86 | 1.77           | 4.84    | 31.8                   | 0.074  |
| 100  | 2.3   | 1.10   | 2.09 | 1.89           | 9.57    | 30.7                   | 0.083  |
| 103  | 2.4   | 1.09   | 2.20 | 2.09           | 5.00    | 30.3                   | 0.098  |
| 106  | 2.8   | 1.24   | 2.26 | 2.18           | 3.54    | 31.1                   | 0.104  |
| 109  | 2.7   | 1.14   | 2.37 | 2.23           | 5.91    | 31.9                   | 0.107  |
| 112  | 3.3   | 1.39   | 2.37 | 2.32           | 2.11    | 33.7                   | 0.111  |
| 115  | 1.9   | 0.89   | 2.13 | 2.36           | 10.80   | 34.5                   | 0.112  |
| 118  | 2.2   | 1.02   | 2.16 | 2.19           | 1.39    | 31.9                   | 0.107  |
| 121  | 10.2  | 4.66   | 2.19 | 1.85           | 15.53   | 31.8                   | 0.106  |
| 124  | 7.0   | 4.70   | 1.49 | 1.67           | 12.08   | 38.2                   | 0.086  |
| 127  | 6.8   | 5.62   | 1.21 | 1.13           | 6.61    | 33.8                   | 0.105  |
| 130  | 5.3   | 5.64   | 0.94 | 0.95           | 1.06    | 34.1                   | 0.097  |
| 133  | 4.3   | 4.67   | 0.92 | 0.81           | 11.96   | 34.1                   | 0.098  |
| 136  | 4.8   | 4.80   | 1.00 | 0.86           | 14.00   | 32.1                   | 0.094  |
| 139  | 4.2   | 4.94   | 0.85 | 0.93           | 9.41    | 30.5                   | 0.092  |
| 142  | 3.5   | 5.07   | 0.69 | 0.81           | 17.39   | 30.9                   | 0.094  |
| 145  | 2.6   | 4.81   | 0.54 | 0.68           | 25.93   | 32.5                   | 0.095  |
| 148  | 2.8   | 4.52   | 0.62 | 0.54           | 12.90   | 38.0                   | 0.092  |
| 151  | 3.7   | 6.98   | 0.53 | 0.57           | 7.55    | 33.7                   | 0.096  |
| 154  | 2.9   | 6.44   | 0.45 | 0.46           | 2.22    | 34.6                   | 0.097  |
| 157  | 1.2   | 6.00   | 0.20 | 0.42           | 110.00  | 34.8                   | 0.097  |
| 160  | 1.7   | 1.15   | 0.22 | 0.17           | 22.73   | 64.6                   | 0.092  |
| 163  | 1.1   | 8.46   | 0.13 | 0.18           | 38.46   | 42.7                   | 0.101  |
| 166  | 0.3   | 6.00   | 0.05 | 0.12           | 140.00  | 54.9                   | 0.101  |
| 169  | 0.2   | 10.00  | 0.02 | 0.03           | 50.0    | 4.6 × 10 <sup>-4</sup> | 0.071  |

changes should be incorporated to better approximate the dynamics of a fishery. Both integrated models, however, show adequate predictive power for the four lobster fisheries and estimate q accurately for the Silliman and Gutsell (1958) data sets. We believe that as mentioned in Silliman (1971), surplus production models can be valuable as first approximations and should be considered in time- or data-limiting conditions.

More sophisticated nonlinear approaches to the FD-Schaefer, FD-Fox, and Schnute models are found in Pella and Tomlinson (1969), Fox (1975), and Schnute (1977), respectively. These observation error fitting procedures (Hilborn and Walters 1992) use an iterative procedure with a least squares criterion to obtain estimates of r, q, and K which minimize predictive error. The parameters obtained from the linear models examined here are first approximations to that criterion. Using simulated populations, Hilborn (1979) showed that the nonlinear FD-Schaefer and Schnute models produced positive parameters, while their linear counterparts gave negative results; however, the nonlinear methods were not shown to assess those fisheries any better than the linear methods. A nonlinear approach applied to the I-Fox model could possibly produce better results, but this is beyond the scope of the current study. A more complete discussion on the inclusion of a model's observed error structure is found in Schute (1989).

The present paper has compared two linear dynamic approaches with the Schaefer and Fox production models. The results suggest that the integration approach of Schnute (1977) should be explored more extensively. For example, the integration procedure could incorporate a longer time lag (Walter 1973) to account for the recruitment patterns of lobster. A 4-yr period was shown to work for the Western Australian lobster fishery in Phillips (1986). Additionally, the integration approach could be applied to a more general class of curves, such as the Bernoulli curves used in Pella and Tomlinson (1969), with the chosen curve satisfying some statistical criterion. Research in these areas could lead to a better under-



FIG. 1. Estimates of q obtained from the I-Fox. Schnute. FD-Fox, and FD-Schaefer models for the population (A and B) data sets of Silliman and Gutsell (1958)

standing of the relative usefulness of surplus production modeling in specific fishery applications.

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# Appendix A. Derivation of the I-Fox Model

Integrating Equation (4) from t = year n to t = year n + 1 yields

(A1) 
$$\ln(U < n + 1 > /U < n >)$$
  
=  $r \ln(qK) - r \int_{t=0}^{n+1} \ln(U) dt - qE_n$ 

where  $U \le n >$  is the instantaneous CPUE at the start of year n and  $E_n$  is the total effort for year n.

The first-degree Taylor polynomial for  $\ln(U)$  centered at  $U_n$ , the average CPUE for year *n*, is

$$n(U) \approx \ln(U_n) + (1/U_n) (U - U_n)$$
  
=  $\ln(U_n) - 1 + (U/U_n).$ 

1

This approximation assumes that U will not fluctuate far from  $U_n$  over the course of year n. Thus, high variability of instantaneous CPUE due to seasonal effects may render this assumption (and the 1-Fox model) invalid for a specific fishery.

Integration of the Taylor approximation yields

(A2) 
$$\int_{n}^{n+1} \ln(U) dt = \ln(U_n) - 1 + (1/U_n) \int_{n}^{n+1} U dt.$$
  
By definition.  $U_n = \int_{n}^{n+1} U dt$ , so Equation (A2) becomes

$$\int_{n}^{n+1} \ln(U) \, dt = \ln(U_n) - 1 + 1 = \ln(U_n).$$

Putting this result into Equation (A1) gives

$$\ln(U < n + 1 > / U < n >) = r \ln(qK)$$

 $-r \ln(U_n) - qE_n$ 

Adding this equation to its corresponding (n + 1)th equation gives

(A3) 
$$\ln((U < n+2 > U < n+1 >)/(U < n+1 > U < n>))$$

$$= 2r \ln(qK) - r(\ln(U_{n+1}) + \ln(U_n)) - q(E_n + E_{n+1})$$

Schnute's (1977) assumption is used to estimate instantaneous CPUE:

$$U_n = \sqrt{U < n + 1} > U < n > ,$$

that is, the CPUE of a given year is the geometric mean of the CPUEs at the beginning and ending of that year. Using this CPUE estimate in Equation (A3) and solving algebraically for  $\ln(U_{n+1})$  gives

$$\ln(U_{n+1}) = (2r/(2+r)) \ln(qK) + ((2-r)/(2+r))$$
$$\ln(U_n) - (q/(2+r)) (E_n + E_{n+1}).$$

# Appendix B. Confidence Intervals for the I-Fox Model's Prediction of Catch per Unit Effort

The standard error of forecast  $S_f$  for the I-Fox model's prediction of CPUE for year m + 1 is found by applying the procedure in Ezekiel and Fox (1959):

$$S_{f} = \sqrt{S_{1}^{2} \left(1 + \frac{1}{m-1} + c_{XX} \left(X_{m} - M_{X}\right)^{2} + 2c_{XY} \left(X_{m} - M_{Y}\right) \left(Y_{m} - M_{Y}\right) + c_{YY} \left(Y_{m} - M_{Y}\right)^{2}\right)}$$

where  $X_n = \ln(U_n)$ ,  $Y_n = E_n + E_{n+1}$ ,  $Z_n = \ln(U_{n+1})$ ,  $M_X = \sum X_n/(m-1)$ ,  $M_Y = \sum Y_n/(m-1)$ ,  $S_X = \sum (X_n - M_X)^2$ ,  $S_Y = \sum (Y_n - M_Y)^2$ ,  $S_{XY} = \sum (X_n - M_X)(Y_n - M_Y)$ ,  $c_{XX} = S_Y/(S_X S_Y - S_{XY}^2)$ ,  $c_{XY} = -S_{XY}/(S_X S_Y - S_{XY}^2)$ ,  $c_{YY} = S_X/(S_X S_Y - S_{XY}^2)$ ,  $S_1^2 = \sum (Z_n - c_1 - c_2X_n - c_3Y_n)^2/(m-4)$ , and m is the number of years of data used. All sums ( $\Sigma$ ) are from n = 1 to n = m - 1, and  $c_1$ ,  $c_2$ , and  $c_3$  are the regression coefficients of the I-Fox regression. Also, the number of degrees of freedom is m - 4 because of the 1-yr time lag.

Using the formula for  $S_f$ , a confidence interval for  $\ln(U_{m+1})$  can be calculated:

Lower limit: 
$$l = \ln(U_{m+1}) - S_f t_{p/2}$$

and

Upper limit:  $u = \ln(U_{m-1}) + S_r t_{n,2}$ 

where  $t_{p/2}$  is the critical value of the Student's *t*-distribution statistic of p/2 probability.

Since the natural log function  $\ln(U)$  is an increasing function and is well defined for U > 0, confidence limits for the prediction  $U_{m+1}$  can be estimated by taking the inverse (exponent) of the confidence limits for  $\ln(U_{m+1})$ :

Lower limit: e<sup>t</sup>

and