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Growth and mortality of subtidal red sea urchins (*Strongylocentrotus franciscanus*) at San Nicolas Island, California, USA: problems with models

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Abstract. Red sea urchins, *Strongylocentrotus franciscanus*, were tagged with tetracycline in 1990 at subtidal sites off San Nicolas Island, California, USA. After one year in the field, the sea urchins were collected and growth increments were measured based on tetracycline marks, which indicated initial slow growth, a maximum rate, and finally a prolonged period of very slow growth. Small red sea urchins (4 cm diam) were estimated to be 3 to 4 yr old, which is much older than has previously been reported. It is estimated that about 12 yr would be required to attain 10 cm diam. Survival has previously been modeled assuming a constant rate. If the population of red sea urchins is assumed to be stable and stationary, annual survival rate was between 71 and 77% yr^{-1}. Census data for the two years of study have permitted annual survival to be estimated without assuming stable and stationary population structure. Under these conditions, annual survival rate was between 79 and 86% yr^{-1}. Analysis of transitions in the size distributions from 1990 to 1991 suggested that annual survival may have been size-specific: 91% yr^{-1} for individuals 1.1 to 4.0 cm diam, 82% yr^{-1} for individuals 4.1 to 7.0 cm diam, and 63% yr^{-1} for those of 7.1 to 10.0 cm diam. An alternative explanation to size-specific survival in our study is size-specific immigration.

Introduction

Modeling growth and using parameters to estimate survival rates or to analyze attributes of life-history evolution requires the selection of appropriate growth and survival functions. A simple three-parameter growth model in wide use is the Brody–Bertalanffy equation (von Bertalanffy 1938, Brody 1945, Ricker 1975) which has been used for a variety of sea urchin species (Ebert 1975, Walker 1981, Duineveld and Jenness 1984, Karlson and

Levitan 1990, Gage 1991, Freire et al. 1982). A generalization of this model has four parameters and has become known as the Richards function (Richards 1959); it has proved to be a useful way of describing growth for a wide variety of organisms (Lundgren and Dolid 1970, Morrison et al. 1977, Causton et al. 1978, Muhlia-Melo et al. 1980, Innes et al. 1981, Zach et al. 1984, Brisbin and Kennamer 1987, Waters and Shay 1991), including sea urchins (Ebert 1980, Russell 1987, Ebert and Russell 1992, Kenner 1992). The Richards function is:

$$S_t = S_\infty (1 - b e^{-Kt})^{-n}, \tag{1}$$

and is the same as the Brody–Bertalanffy model, as presented by Fabens (1965), except for the addition of an exponent, n. S_t is size at time t, S_∞ is asymptotic size, K is the growth rate constant, and b is a scaling parameter that adjusts the curve on the time axis to account for the fact that size is not 0 at $t = 0$. The exponent n is a "shape parameter": When $n = -1$ the equation is the Brody–Bertalanffy function, when $n = +1$ it is the logistic function, and as $|n| \to \infty$, Eq. (1) approaches the Gompertz equation (Fletcher 1975).

Reported growth curves for sea urchins have included S-shaped curves, i.e., with an initial exponential phase, as well as curves with no exponential phase. Of 11 tropical and warm-temperate sea urchin species examined by Ebert (1982), 8 had estimated shape parameters (n) from -0.14 to -0.37, two more extended the range to -0.60, and one had $n = -1.13$. Small negative values for n imply rapid initial growth followed by along period of very slow and nearly constant growth. One sample of *Heliocidaris erythrogramma* from Australia ($N = 65$) had a negative n (-0.37), whereas a second sample ($N = 15$) had $n = +0.15$, implying an initial exponential growth phase. Because of small sample size and the fact that all other species showed negative values for n, the positive n was viewed as unrepresentative (Ebert 1982). However, there are a number of reports that indicate other sea urchin species may have an initial exponential phase of growth. Studies using natural growth lines have found an exponential growth phase (Gage and Tyler 1985, Nichols et al.

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1985, Gage et al. 1986, Gage 1987, Comely and Ansell 1988), but natural growth lines may or may not be annual (Ebert 1988). Formation of more that one line per year in young individuals would lead to an erronous conclusion of an early exponential phase. More compelling has been analysis of size-frequency distributions for the green sea urchin *Strongylocentrotus droebachiensis* (Raymond and Scheibling 1987), which showed an exponential phase at least during the first year following metamorphosis. Rowley (1990) used tetracycline tagging with purple sea urchins (*S. purpuratus*), and concluded that growth of newly settled individuals was slower than predicted from studies of larger individuals extrapolated to small sizes (Ebert 1967, 1977, Pearse et al. 1970, Tegner and Dayton 1981).

Here we present data for subtidal red sea urchins (*Strongylocentrotus franciscanus*) that suggest that the Richards function may be inadequate, at least for this species, as an appropriate growth model, and we explore two other growth functions (Tanaka 1982, 1988, Jolicoeur 1985). We show the consequences of using mean sizes in populations together with the Richards vs Tanaka functions to estimate mortality (cf. Ebert 1987) and compare mortality estimates with estimates obtained from growth-transition matrices that link size-frequency distributions (Sainsbury 1982).

Materials and methods

Red sea urchins, *Strongylocentrotus franciscanus*, were collected from two large concrete blocks at a depth of 8 to 9 m, $\simeq 100$ m offshore of Coast Guard Beach on San Nicolas Island, California, USA (33°15'N; 119°30'W: Fig. 1). The blocks were $\simeq 1$ to 1.5 m on each side, and surrounded by sand. Sea urchins were measured with knife-edged vernier calipers and then tagged with tetracycline using from 0.2 to $\simeq 1$ ml of a solution of 1 g of tetracycline in 100 ml of sea water (cf. Ebert 1982, Russell 1987). Individuals were collected and tagged on 10 February ($N = 276$) on one block and on 25 March 1990 ($N = 232$) on the other block. Sea urchins were again collected one year later on 10 February ($N = 281$) and 20 March 1991 ($N = 249$), so that both samples remained in the field for one year. Both in 1990 and in 1991, special effort was made to collect all individuals on the blocks, making it possible to use growth transitions and size structure to estimate survival without having to assume that the populations were stable and stationary (Sainsbury 1982).

All sea urchins were frozen and taken to San Diego State University, where they were cleaned with 10% sodium hypochlorite, washed, and dried. Diameter and height of the test and length of one of the ten jaws (demi-pyramids) were measured using digital calipers. Tetracycline fluoresces when exposed to ultraviolet illumination and all individuals were checked for the presence of a tetracycline tag by examining a jaw with a Wild dissecting microscope equipped with an ultraviolet epi-illuminator. Growth increments of tagged jaws were measured with an ocular micrometer (10 × ocular and 12 × objective) from the glowing tetracycline mark to the outer edge of the jaw. The measured jaw ($J_{t+\Delta t}$) minus the growth increments at the esophageal and labial ends is an estimate of the length of the jaw at the time of tagging (J_t).

Marks in demi-pyramids ("jaws") were used in preference to marks in the test ossicles because of the ease with which the former measurements can be made. Other than cleaning to remove tissue, no additional preparation is required to determine growth increments in jaws, whereas plates of the test often require grinding to reveal tetracycline lines. Furthermore, the widest plate ossicle is at the ambitus where diameter measurements are made. However, as
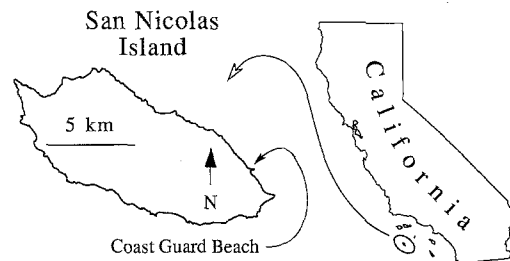

Fig. 1. Location of study site off Coast Guard Beach on San Nicolas Island, California (33°15'N; 119°30'W)

the sea urchins grow, new plates are added at the aboral ends of rows of plates and so a plate at the ambitus may become part of the oral surface (Deutler 1926). In order to obtain size-pairs for estimating growth parameters, the widest glowing image inside a plate which was the ambital plate at the time of tagging, must be matched with the widest plate at the time of final collection. Such matching requires grinding and measuring a series of plates from the ambitus toward the oral surface. A size-series showing these relative changes is illustrated with natural pigment lines (Deutler 1926) and tetracycline tagging (Gage 1991).

Analysis of growth was done using three models (Richards 1959, Tanaka 1982, 1988, Jolicoeur 1985). No Model II regression model exists for the Tanaka and Jolicoeur functions, so a Model I or predictive regression was employed. Estimating parameters for the Richards function (Eq. 1) used a Model II reduced major-axis regression of $J_{t+\Delta t}^{-1/n}$ vs $J_t^{-1/n}$ (Ebert 1980):

$$J_{t+\Delta t}^{-1/n} = J_\infty (1 - e^{-K\Delta t}) + J_t^{-1/n} e^{-K\Delta t}. \qquad (2)$$

A reduced major axis regression is appropriate because both J_t and $J_{t+\Delta t}$ are subject to the same degree of measurement error (Ricker 1973). If $|n| \to \infty$, indicating that the Gompertz equation would be appropriate, the difference-equation (Eq. 2) becomes

$$\ln(J_{t+\Delta t}) = \ln(J_\infty)(1 - e^{-K\Delta t}) + \ln(J_t)e^{-K\Delta t}. \qquad (3)$$

The scaling parameter b (Eq. 1) is:

$$b = \frac{J_\infty^{-1/n} - J_0^{-1/n}}{J_\infty^{-1/n}} \qquad (4)$$

and, for the Gompertz function,

$$b = \frac{\ln(J_\infty) - \ln(J_0)}{\ln(J_\infty)}, \qquad (5)$$

where J_0 is jaw length at $t = 0$.

The Tanaka function (Tanaka 1982, 1988), is a four-parameter equation that accommodates an early lag and exponential phase followed by a declining growth rate. The function lacks an asymptotic size and animals may continue to grow for as long as they live:

$$J_t = \frac{1}{\sqrt{f}}\ln|2f(t - c) + 2\sqrt{f^2(t - c)^2 + f a}| + d, \qquad (6)$$

Eq. (6) is the integrated form of the instantaneous growth rate, $\dfrac{dJ}{dt}$, with respect to time:

$$\frac{dJ}{dt} = \frac{1}{\sqrt{f(t - c)^2 + a}}. \qquad (7)$$

Parameters are:

$$c = a/E, \qquad (8)$$

where c is the age where growth rate is maximum, $\dfrac{1}{\sqrt{a}}$ is the maximum growth rate, and

$$E = \exp(\sqrt{f}(J_0 - d)), \qquad (9)$$

where J_0 is the jaw length at $t = 0$ and f is related to the rate of change of the growth rate (Eq. 7): the larger f is, the faster the

growth rate changes with time. The parameter d is sensitive to the initial and final slope of the growth curve. Small values of d indicate slow initial and final growth, whereas larger values of d reflect more rapid initial and final growth.

The difference equation for the Tanaka function is

$$J_{t+1} = \frac{1}{\sqrt{f}} \ln |2\,G + 2\sqrt{G^2 + f\,a}| + d, \qquad (10)$$

where

$$G = E/4 - f\,a/E + f, \qquad (11)$$

and

$$E = \exp(\sqrt{f}\,(J_t - d)). \qquad (12)$$

Eq. (10) is a symmetrical bell-shaped curve that is rotated so that it is asymptotic to a $45°$ line in a plot of J_{t+1} vs J_t. The peak of the curve is at the point of maximum growth and the parameter d is sensitive to the magnitude of the difference between J_{t+1} and J_t for the largest individuals. A shortcoming of the model is that a *symmetrical* curve always will be fit, even though the data may hint at asymmetry.

Parameters a, d, and f (Eqs. 10-12) were estimated by nonlinear regression (SYSTAT, Wilkinson 1987) with a model:

MODEL $Y = 1/SQR(F)*LOG(2*ABS((EXP(SQR(F)*(X - D)))/4 -$,
$F*A/(EXP(SQR(F)*(X - D)))$
$\qquad\qquad + F + SQR(((EXP(SQR(F)*(X - D)))/4 - F*,$
$A/(EXP(SQR(F)*(X - D))) + F)^2 + F*A)) + D$

with $X =$ jaw length at time t and $Y =$ jaw length at $t + 1$ yr.

The third growth model we examined (Jolicoeur 1985) was derived from the logistic and has three parameters:

$$J_t = J_\infty (1 - b\,t^{-K})^{-1}. \qquad (13)$$

It resembles the Richards function (Eq. 1) with $n = +1$, and differs in that time (t) in the Richards function is replaced by its natural logarithm. A difference-equation version of Eq. (13) is:

$$J_{t+\Delta t} = \frac{J_\infty}{1 - b\left(\left(\dfrac{J_t - J_\infty}{b\,J_t}\right)^{-1/K} + \Delta t\right)^{-K}}. \qquad (14)$$

The parameter b is the same as Eq. (4), with $n = +1$, which is the appropriate shape parameter for the logistic equation and so,

$$b = \frac{J_0 - J_\infty}{J_0}. \qquad (15)$$

Survival was modeled using a simple decaying exponential equation of number, N, as a function of time:

$$N_t = N_0\,e^{-Zt}. \qquad (16)$$

The mortality coefficient, Z (Eq. 16), was estimated from size-frequency data plus either parameters from a growth function or a transition matrix for growth. Our approach using growth functions makes use of the relationship between mean size, growth and survival (Ebert 1987) and has the restrictive assumption that the population being studied has seasonally stable and stationary structure; that is, the population is neither growing nor decreasing across years (seasonally stationary), although there will be changes within each year. Density will be highest following recruitment and lowest just before recruitment. "Seasonally stable" means that annual recruitment has been sufficiently constant for the proportions among size classes to have become fixed across years, although there will be changes within each year due to individual growth.

Mean test diameter, $\overline{D_T}$, for a size distribution at some time T following annual recruitment, is the sum of all individuals of a particular size, D_{T+t}, multiplied by the number in that age class and divided by the sum of individuals of all ages:

$$\overline{D_T} = \frac{\sum D_{t+T} N_t}{\sum N_t}, \qquad (17)$$

where T is time within a year since annual recruitment; for example, if recruitment were in March and sampling in July, 4 mo later, T would be 4/12 or 0.333. Actual sizes for each age class are important in determining means size, which is why T must be added to their ages, but only the relative contributions of each age class are important and so T does not have to be added to age for numbers, N_t.

It is necessary to establish the relationship between test diameter and jaw length in order to obtain a growth curve for test diameter, which is accomplished using the allometric relationship between test diameter (D) and jaw length (J):

$$D = \alpha J^\beta. \qquad (18)$$

A reduced major-axis regression of ln-transformed data (Ricker 1973) was used to estimate parameters α and β. The shape parameter for growth in test diameter was changed to:

$$n = \beta\,n_{\text{jaw}}. \qquad (19)$$

Because the Jolicoeur model is based on the logistic (Eq. 13), n is $+1$ and so β takes the place of the exponent -1 in Eq. (13).

Time since annual recruitment (T), size at recruitment (D_0), and the scaling parameter (b), are interrelated, and frequently neither T nor D_0 can be estimated from existing data or extrapolated with confidence from growth parameters based on tagged juveniles and adults. A solution to this problem is to use the mean of the first mode of a size-frequency distribution as an estimate of D_0, which as a consequence, makes $T = 0$; individuals recruit to the population at Size D_0 on the day of collection.

To estimate Z using the Richards, Tanaka and Jolicoeur functions, D_t is replaced in Eq. (17) by Eqs. (1), (6), or (13), following suitable changes of parameters from jaw growth to diameter growth (Eqs. 18 and 19). Also, N_t is replaced by Eq. (16), which makes mean size, $\overline{D_T}$, a function of diameter growth and survival parameters. One convenient substitution is based on the limit of a sequence of partial sums of $\sum N_t$, that is, $\sum e^{-Zt}$:

$$\sum e^{-Zt} = \frac{1}{1 - e^{-Z}}. \qquad (20)$$

With substitutions for the Richards, Tanaka and Jolicoeur functions, Eq. (17) becomes a suitable nonlinear regression model for estimating Z:
for the Richards function,

$$\overline{D_T} = D_\infty (1 - e^{-Z}) \sum_{t=0}^{\omega} e^{-Zt}(1 - b \cdot e^{-K(t+T)})^{-n}; \qquad (21)$$

for the Tanaka function,

$$\overline{D_T} = (1 - e^{-Z}) \sum_{t=0}^{\omega} e^{-Zt}\alpha\left[\frac{1}{\sqrt{f}}\ln|2f((t+T) - c)\right.$$
$$\left. + 2\sqrt{f^2((t+T) - c)^2 + fa}| + d\right]^\beta; \qquad (22)$$

and for the Jolicoeur function,

$$\overline{D_T} = D_\infty (1 - e^{-Z}) \sum_{t=0}^{\omega} e^{-Zt}[1 - b\,t^{-K(t+T)}]^{-\beta}. \qquad (23)$$

Using the Richards function parameters (Eq. 21), estimates of Z were obtained using a program written in BASIC (Ebert 1987) for an APPLE II+ but now in double-precision Microsoft Quick BASIC for a Macintosh. It also is possible to use commercially available software to estimate Z with Eqs. (21) to (23). The requirement is a nonlinear regression module and the ability to link an external subroutine (Table 1). For example, BMDP (Dixon 1985) has this capability but SYSTAT (Wilkinson 1987) does not.

Data used to estimate Z (Eqs. 21-23) are mean sizes, $\overline{D_T}$, and so there are two data points for each concrete block in our study: mean diameters for the size distributions in 1990 and 1991. Growth parameters were determined from tagging and allometry parameters were estimated from measured individuals; the only unknown parameter in Eqs. (21) to (23) is Z.

Table 1. *Strongylocentrotus franciscanus.* External subroutine for use with BMDPAR (Ralston 1985) for estimating mortality rate constant, Z, from mean size and Tanaka function parameters (Eq. 22); f, d, and a are defined by Eqs. (10) to (12), and allometry parameters relating diameter to jaw size are defined by Eq. (18)

The following FORTRAN code must be compiled and linked with BMDPAR:

```
C       P(1)=f, Tanaka function parameter
C       P(2)=d, Tanaka function parameter
C       P(3)=mortality rate constant, Z
C       P(4)=a, Tanaka function parameter
C       P(5)=size at recruitment, SR
C       P(6)=alpha for diameter vs jaw allometry
C       P(7)=beta for diameter vs jaw allometry
        S0=(P(5)/P(6))**(1/P(7))
        E=DEXP(DSQRT(P(1))*(S0-P(2)))
        C=P(4)/E
        G=DLOG(.000001)
        G=-G
        F=0
        DN=0
        DO 10 TI=0, (G/P(3)+.5)
        V=X(1)+TI
        W=2*DSQRT(P(1)*P(1)*(V-C)**2+P(1)*P(4))
        W=W+2*P(1)*(V-C)
        W=1/DSQRT(P(1))*DLOG(DABS(W))+P2(2)
        W=P(6)*W**(P(7))
        D=DEXP (-P(3)*TI)
        DN=DN+D
        F=F+D*W
10      CONTINUE
        F=F/DN
```

Associated command file for BMDPAR:

```
/PROBLEM TITLE IS 'Z analysis with Tanaka function'.
/INPUT VARIABLES ARE 2.
    FILE IS 'snmar.dat'.
/VARIABLE NAMES ARE TIME, SIZE.
/REGRESS DEPENDENT IS SIZE.
    PARAMETERS ARE 7.
/PARAMETER INITIAL ARE
    9.095,.1164,.3,7.415,1.0,4.896,1.2143.
    MAX ARE 10,0,1,8,3,7,2.
    MIN ARE 7,-.3,.08,7,1,3,1.
    FIXED ARE 1,2,4,5,6,7.
/END
```

March data file, called "snmar.dat", is:
```
 0  4.9309
 0  4.03
```

With Richards function, command file is:
```
/PROBLEM TITLE='ZKAN ANALYSIS'.
/INPUT VARIABlES=2.
    FORMAT=FREE.
    FILE='snmar.dat'.
/VARIABLE NAMES=TIME,SIZE.
/REGRESS DEPENDENT=SIZE.
    PARAMETERS=5.
/PARAMETER INITIAL=9.393,.511,.3,-6.756,1.8.
    MAX=12,.2,1,-.1,3.
    MIN=5,.07,.05,-25,1.
    FIXED=1,2,4,5.
/END
```

Table 1 (continued)

External function that must be linked with BMDPAR for Richards function is:

```
C       P(1)=maximum size
C       P(2)=the growth rate constant, K
C       P(3)=the mortality rate constant, Z
C       P(4)=the Richards function shape parameter, n
C       P(5)=size at recruitment, SR
        D=-1/P(4)
        G=DLOG(.000001)
        G=-G
        B=(P(1)**D-P(5)**D)/P(1)**D
        F=0.
        DO 10 TI=0, (G/P(3)+.5)
        V=X(1)+TI
        V=DEXP(-P(2)*V)
        F=F+DEXP(-P(3)*TI)*(1.0-B*V)**(-P(4))
10      CONTINUE
        F=P(1)*(1.0-DEXP(-P(3)))*F
```

A second method for estimating survival was to use growth transitions and size-frequency data without a specific growth model and without the restrictions of stable and stationary size structure. In matrix notation,

$$N(T+1) = A N(T), \qquad (24)$$

where A is the transition matrix, $N(T)$ is the size-frequency distribution in 1990, and $N(T+1)$ is the size distribution in 1991. Elements of $N(T)$ are actual counts, not relative frequencies. If relative frequencies were used so that the size distribution would sum to 100%, it would be necessary to assume that the population was stable and stationary.

In order to analyze size transitions based on test diameter, it is necessary to recast original and final sizes as test diameters rather than jaw lengths using the allometric relationship between test diameter and jaw length:

$$D_t = D_{t+1} - \alpha(J_{t+1}^\beta - J_t^\beta). \qquad (25)$$

After values of D_t were estimated (Eq. 25), the original (1990) sizes of the tagged sea urchins were grouped into size classes with a width of 1.5 cm and their growth (g) from 1990 to 1991 was tallied and then expressed as a probability, g_{ij}. The subscript j is the original size category in 1990, and i is the size category in 1991; i and j are rows and columns of the transition matrix. For example, g_{41} is the growth transition in the 4th row and 1st column of the matrix and would be the probability that an individual in the 1st size class in 1990 grew into the 4th size class in one year. All transitions are from a column to a row.

The transition matrix A is composed of two sets of probabilities, growth, g_{ij}, and survival, s_j. In order to make analysis possible with the data we have, we assumed that annual survival was determined by initial size regardless of how much or little growth took place during a year. This assumption results in all survival probabilities in a column of A being the same. Also, tetracycline tagging does not permit detection of negative growth so all matrix elements above the diagonal are impossible and so are not shown in the matrix. A tagged individual that shrank would not be recognized as tagged and hence would not be included in the estimates of transitions (Eq. 26).

$$
\begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ \vdots \\ n_i \end{pmatrix}(T+1) =
\begin{pmatrix}
s_1 g_{11} & \cdots & \cdots & \cdots & \cdots \\
s_1 g_{21} & s_2 g_{22} & \cdots & \cdots & \cdots \\
s_1 g_{31} & s_2 g_{32} & s_3 g_{33} & \cdots & \cdots \\
\vdots & \vdots & \vdots & \vdots & \vdots \\
s_1 g_{i1} & s_2 g_{i2} & s_3 g_{i3} & \cdots & s_j g_{ij}
\end{pmatrix}
\begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ \vdots \\ n_i \end{pmatrix}(T). \qquad (26)
$$

Data are the 1990 and 1991 size-frequency distributions $N(T)$ and $N(T + 1)$. The growth transitions, g_{ij}, were determined from tagged individuals and so the problem in analysis is to solve for annual survival rates, s_j, which was done by multiple regression (Eqs. 27–30).

$$n_1(T + 1) = s_1 g_{11} n_1(T), \tag{27}$$

$$n_2(T + 1) = s_1 g_{21} n_1(T) + s_2 g_{22} n_2(T), \tag{28}$$

$$n_3(T + 1) = s_1 g_{31} n_1(T) + s_2 g_{32} n_2(T) + s_3 g_{33} n_3(T), \tag{29}$$

$$n_i(T + 1) = s_1 g_{i1} n_1(T) + s_2 g_{i2} n_2(T) + s_3 g_{i3} n_3(T) + \dots s_j g_{ij} n_i(T). \tag{30}$$

Results

Growth

Of the 281 individuals of *Strongylocentrotus franciscanus* collected in February and the 249 collected in March of 1991, 114 and 99, respectively, displayed clear tetracycline tags, which is 41 and 43% of the original numbers tagged in 1990. A plot of initial and final jaw sizes (Fig. 2) shows that growth on the two concrete blocks was similar; consequently, the data were combined to estimate growth parameters (Table 2). Sums of squares error (SSE) are similar for the three growth models, although largest for the Richards function, which was expected because a Model II regression was used. Although the SSE are similar for the Richards, Tanaka and Jolicoeur functions, the Richards and Jolicoeur function do not appear to behave appropriately for either the largest or smallest individuals. The line (Fig. 2B) is slightly too high for small sea urchins, which means that they are predicted to grow faster than they actually did. For large individuals, the regression line is too low, which means that large individuals are expected to grow more slowly than than they did or not to grow at all.

Over the range of data values, the fitted lines from the Richards and Jolicoeur functions can not be distinguished, and so a single line for both functions was plotted (Fig. 2B). Like the Richards function, the smallest individuals are estimated to be growing too fast and the largest too slowly. The only comparable parameter for the Richards and Jolicoeur functions in Table 2 is J_∞: the difference is quite small (< 2%). All three functions show a rise to a maximum followed by a decline towards the 45° line, which implies that there is an accelerating growth phase for small individuals. The estimates for the Tanaka function indicate that the maximum annual jaw increment is about 0.37 cm $\left(\dfrac{1}{\sqrt{a}}\right)$, which occurs at an age of 5 yr (c in Eq. 8).

The significant point is that regardless of how the analysis is conducted, there is a definite bending down of the regression line (Fig. 2) for small individuals, so that there must have been a lag or an exponential phase early in growth followed by a maximum growth rate and then a decline with very slow growth for large individuals.

To establish the relationship between test diameter and jaw length, and so estimate growth parameters for test diameter from parameters for jaw growth, we first determined whether the February and March measurements of diameter and jaw length could be combined. An
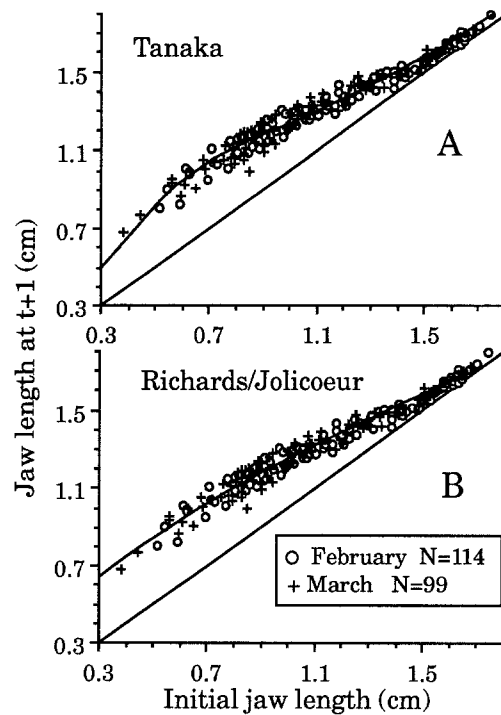
Fig. 2. *Strongylocentrotus franciscanus.* Change in sizes of jaws (j) during one year for subtidal individuals off San Nicolas Island, California, based on tetracycline tagging; data combined for February 1990/1991 and March 1990/1991; (A) Line fitted using Tanaka function parameters; (B) line fitted using Richards or Jolicoeur function parameters; 45° line is line of zero growth

Table 2. *Strongylocentrotus franciscanus.* Parameter estimates for jaw growth using Richards, Tanaka, and Jolicoeur functions; Richards function parameters were estimated using Ebert (1980); Tanaka function parameters ($\pm$SE) were estimated using SYSTAT (Quasi-Newton method); Jolicoeur function parameters were estimated using SYSTAT (SIMPLEX method); $N = 213$ size pairs of jaws for combined February and March samples; parameters were describe following Eqs. (1), (6) and (13); SSE: residual sum of squares

Richards		Tanaka		Jolicoeur	
n	-5.5636	f	9.192 ± 0.424	b	-126.6396
K yr^{-1}	0.5108	d	-0.112 ± 0.022	K yr^{-1}	3.2997
J_∞ cm	1.7100	a	7.396 ± 0.219	J_∞ cm	1.7414
SSE	0.3514	SSE	0.3450	SSE	0.3363

ANCOVA (Table 3) showed that slopes were homogeneous ($p = 0.36$), and so were adjusted means ($p = 0.66$). Consequently, a common allometric equation for estimating diameter from jaw length is appropriate. Using a reduced major-axis regression of ln-transformed data, the allometry equation for diameter (D) vs jaw (J) length (Fig. 3) is:

$$D = 4.8962 J^{1.21428}. \tag{31}$$

A comparison of growth curves for test diameter (Fig. 4) shows the same patterns as evident in Fig. 2. The Richards function indicates faster growth than does the Tanaka function for small individuals, but slower growth for large individuals. The Jolicoeur function shows the

Table 3. *Strongylocentrotus franciscanus.* Test for homogeneity of slopes for ln(diameter) vs ln(jaw) for February and March subtidal samples of red sea urchins off San Nicolas Island, California; SS: sum of squares; MS: mean square

	SS	df	MS	F-ratio	p
Homogeneity of slopes					
Sample	0.000	1	0.000	0.223	0.637
ln(jaw)	74.358	1	74.358	36909.182	0.000
Sample × ln(jaw)	0.002	1	0.002	0.857	0.356
Error	0.447	222	0.002		
Significance of difference of adjusted means					
Sample	0.000	1	0.000	0.199	0.656
ln(jaw)	83.404	1	83.404	41425.793	0.000
Error	0.449	223	0.002		

Fig. 3. *Strongylocentrotus franciscanus.* Relationship between test diameter and jaw length; fitted line is for combined samples from February and March 1991 (Eq. 31)

Table 4. *Strongylocentrotus franciscanus.* Estimates of mortality rate-constant, Z ($\pm$SE), using a growth function and means for size-frequency distributions; size at recruitment is $\simeq 1.8$ cm for both February and March (Fig. 5) and so each date is assigned $T = 0$; for Richards function, Z was estimated using Eq. (21) (Ebert 1987); for Tanaka function, Eq. (22) (Table 1) and the BMDP nonlinear regression package (BMDPAR) were used

Month	Richards function (Z yr^{-1})	Tanaka function (Z yr^{-1})
February	0.284 ± 0.016	0.261 ± 0.014
March	0.337 ± 0.007	0.303 ± 0.006

Fig. 4. *Strongylocentrotus franciscanus.* Growth curve for data combined for both February and March blocks using Richards, Tanaka, and Jolicoeur functions

longest period of slow initial growth, is closest to the Tanaka function from 3 to about 10 yr and then is indistinguishable from estimates based on the Richards function.

Survival

The first step in estimating Z from Eqs. (21)–(23) was to calculate mean sizes for each size distribution (Fig. 5). The estimates of Z (Table 4) were then based on assigning a time of 0 to both February and March samples, and size at recruitment (D_0) a value of 1.8 cm, based on the positions of the first modes in Fig. 5. Because the Richards and Jolicoeur functions were indistinguishable over the range of tagged individuals (Fig. 2), Z was calculated for just the Richards and Tanaka functions. Estimates of Z using nonlinear regression with either the Richards or Tanaka functions were very similar (Table 4), with a range of Z-values from 0.26 to 0.34 yr^{-1} which represent annual survival rates from 71 to 77%.
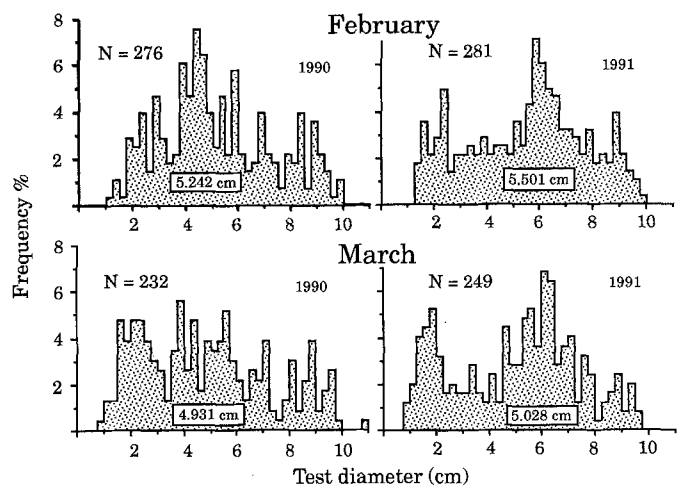
A required assumption to produce Table 4 is a seasonally stable and stationary population, and although the means from 1990 to 1991 changed little, the shapes of the distributions did not remain the same, as shown by a Kolmogorov–Smirnov two-sample test (Tate and Clelland 1957). The greatest percent difference between cumulative size distributions for the February samples was

Fig. 5. *Strongylocentrotus franciscanus.* Size-frequency distributions at time of tagging on 10 February and 25 March 1990 and at collection on 10 February and 20 March 1991; means are shown for each frequency distribution

16.7% for the size interval 5.26 to 5.50 cm, which is a significant difference at $\alpha < 0.01$. Similarly, comparison of the March samples from 1990 and 1991 revealed the greatest difference, 12.0%, at the 4.26 to 4.50 cm size interval. The critical difference at $\alpha = 0.05$ is 12.41%. It is

Table 5. *Strongylocentrotus franciscanus* at San Nicolas Island subtidal Transitions in February and March are numbers of individuals from an initial size class (columns) in 1990 that were collected one year later in initial or larger size class (rows); "Combined" data show fraction of individuals in each transition for combined February and March samples

Diam (cm) 1991	Initial diameter (cm) in 1990					
	1.1–2.5	2.6–4.0	4.1–5.5	5.6–7.0	7.1–8.5	8.6–10.0
February						
1.1–2.5						
2.2–4.0	1	1				
4.1–5.5	1	11	1			
5.6–7.0		5	32	6		
7.1–8.5				18	17	
8.6–10.0					8	13
Total	2	17	33	24	25	13
March						
1.1–2.5						
2.2–4.0	2					
4.1–5.5	3	13	1			
5.6–7.0		9	33	3		
7.1–8.5			2	15	5	
8.6–10.0					6	5
Total	5	22	36	18	11	5
Combined						
1.1–2.5						
2.6–4.0	0.429	0.026				
4.1–5.5	0.571	0.615	0.029			
5.6–7.0		0.359	0.942	0.214		
7.1–8.5			0.029	0.786	0.611	
8.6–10.0					0.389	1.000

Table 6. *Strongylocentrotus franciscanus.* Size structure for February and March samples on concrete blocks at San Nicolas Island

Size (cm)	Feb. 1990	Feb. 1991	March 1990	March 1991
≤1.0			1	3
1.1–2.5	31	43	49	51
2.2–4.0	53	37	46	27
4.1–5.5	83	43	49	46
5.6–7.0	48	85	37	71
7.1–8.5	35	43	23	31
8.6–10.0	26	30	26	19
10.1–11.5			1	
Total	276	281	232	248
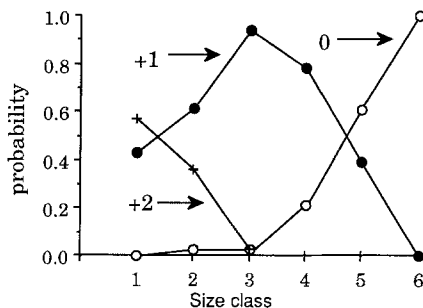
Fig. 6. *Strongylocentrotus franciscanus.* Transition probabilities for individuals in a size class in 1990 remaining in same size class (0), growing to next size class (+1), or skipping a class (+2). Smaller size classes have higher probabilities of moving to larger size classes, larger individuals tend to stay in same size classes from year to year

reasonable to conclude that the populations were not seasonally stable and stationary, so the two years represent samples that may or may not bracket any long-term mean size structure.

In order to analyze size transitions based on test diameter, the allometry parameters (Eq. 31) were inserted into Eq. (25), so that the original test diameters could be estimated from test diameters in 1991 and growth increments of the jaws (Eq. 32):

$$D_t = D_{t+1} - 4.8962(J_{t+1}^{1.21428} - J_t^{1.21428}). \qquad (32)$$

The original sizes of the tagged sea urchins were grouped into size classes with width increments of 1.5 cm, and their growth from 1990 to 1991 was tallied ("Feb." and "March' in Table 5) and then expressed as a probability ("Combined" in Table 5).

The changing transfer probabilities from Table 5 possibly are more readily apparent in Fig. 6. No small individuals remained in the same size class from 1990 to 1991 but grew either to the next size class or moved two classes. Larger individuals had larger fractions remaining within the starting size class, until the largest individuals all stayed in Size Class 6, which represents individuals between 8.6 and 10.0 cm.

Starting with Eq. (26), the regression model relating growth transitions ("Combined" data in Table 5), size distributions (Table 6), and s_j, is:

$$n_i(T + 1) = s_1 g_{i1} n_1(T) + s_2 g_{i2} n_2(T)$$
$$+ s_3 g_{i3} n_3(T) + \dots s_j g_{ij} n_i(T). \qquad (33)$$

Survival coefficients, s_j, could not be estimated for the individual samples (February and March) because there are more coefficients (s_j) than dependent variables $[n_i(T + 1)]$. As a consequence, we combined the February and March samples so that there were 10 dependent variables and 6 survival coefficients (Table 7). The results of the multiple-regression analysis (Table 8) are unsatisfactory because survival rates cannot be greater than 1.0, and 3 of the 6 estimates of s_j were 1.0 or greater.

The regression was recast so that a single survival rate, s_1, was estimated:

$$n_i(T + 1) = s_1 g_{i1} n_1(T) + s_1 g_{i2} n_2(T)$$
$$+ s_1 g_{i3} n_3(T) + \dots s_1 g_{ij} n_i(T). \qquad (34)$$

Because just one coefficient was estimated, it was possible to treat the February and March samples separately as well as estimating an overall survival rate (Table 9).

The final way in which we analyzed the data was to use a common survival rate for every two size classes:

$$n_i(T + 1) = s_1 g_{i1} n_1(T) + s_1 g_{i2} n_2(T) + s_2 g_{i3} n_3(T)$$
$$+ s_2 g_{i4} n_4(T) + \dots s_{j/2} g_{ij} n_i(T). \qquad (35)$$

The results of this analysis are biologically possible because all survival estimates were between 0 and 1 (Table 10).

The survival estimates using size-frequency distributions, and growth transitions are higher than the estimates obtained from using the Richards or Tanaka functions and means of size distributions. Also, there is an

Table 7. *Strongylocentrotus franciscanus*. Growth transitions (g_{ij}) from 1990 to 1991 (Table 5) applied to size-distributions of 1990 (Table 6) to produce size structures observed in 1991 (Table 6); survival rates, s_i, are solutions to $(n_i$ in 1991$)=g_{ij}\times(n_i$ in 1990$)\times s_i$

Size class (cm)	(n_i) 1991	Size classes (cm) in 1990					
		1.1–2.5	2.6–4.0	4.1–5.5	5.6–7.0	7.1–8.5	8.6–10.0
February							
1.1–2.5	43						
2.6–4.0	37=	$0.429\times31s_1$	$0.026\times53s_2$				
4.1–5.5	43=	$0.571\times31s_1$	$0.615\times53s_2$	$0.029\times83s_3$			
5.6–7.0	85=		$0.359\times53s_2$	$0.942\times83s_3$	$0.214\times48s_4$		
7.1–8.5	43=			$0.029\times83s_3$	$0.786\times48s_4$	$0.611\times35s_5$	
8.6–10.0	30=					$0.389\times35s_5$	$1\times26s_6$
March							
1.1–2.5	51						
2.6–4.0	27=	$0.429\times49s_1$	$0.026\times46s_2$				
4.1–5.5	46=	$0.571\times49s_1$	$0.615\times46s_2$	$0.029\times49s_3$			
5.6–7.0	71=		$0.359\times46s_2$	$0.942\times49s_3$	$0.214\times37s_4$		
7.1–8.5	31=			$0.029\times49s_3$	$0.786\times37s_4$	$0.611\times23s_5$	
8.6–10.0	19=					$0.389\times23s_5$	$1\times26s_6$

Table 8. *Strongylocentrotus franciscanus*. Estimates ($\pm$SE) of survival rates, s_i, for each of six size classes from 1990 to 1991; February and March samples combined

Size class (cm)	Coefficient	Survival yr^{-1}
1.1–2.5	s_1	1.474 ± 0.469
2.6–4.0	s_2	0.350 ± 0.457
4.1–5.5	s_3	1.033 ± 0.312
5.6–7.0	s_4	0.523 ± 1.429
7.1–8.5	s_5	1.008 ± 2.627
8.6–10.0	s_6	0.505 ± 1.155

Table 9. *Strongylocentrotus franciscanus*. Estimates ($\pm$SE) of overall survival rate, s_1, (Eq. 34); annual survival rate is e^{-Z} so $Z=-\ln(s_1)$

Sample	Survival (s_1)	Z yr^{-1}
February	0.793 ± 0.092	0.232
March	0.858 ± 0.086	0.153
Combined	0.818 ± 0.061	0.201

Table 10. *Strongylocentrotus franciscanus*. Annual size-class specific survival rates, s_i ($\pm$SE), at San Nicolas Island; size classes as in Table 6 and survival rates determined using Eq. (35)

Size classes (cm)	Survival (s_i) $\pm$SE		
	February	March	Combined
1.1–2.5 ⎫ 2.6–4.0 ⎭	s_1 0.961 ± 0.336 yr^{-1}	0.865 ± 0.122 yr^{-1}	0.911 ± 0.139 yr^{-1}
4.1–5.5 ⎫ 5.6–7.0 ⎭	s_2 0.740 ± 0.137	0.986 ± 0.124	0.817 ± 0.078
7.1–8.5 ⎫ 8.6–10.0 ⎭	s_3 0.727 ± 0.383	0.477 ± 0.229	0.626 ± 0.173

indication that survival was not independent of size; large individuals may have had lower survival rates than smaller individuals.

Discussion

There are a variety of problems associated with the estimates of both growth and survival parameters. At present, the ideal growth model for *Strongylocentrotus franciscanus*, and possibly other sea urchins, has yet to be developed. Some generalization of the Tanaka function seems promising. The fact that the difference equation is a symmetrical bell-shaped curve should be changed so that an asymmetrical curve would be possible. Unfortunately, this probably means yet another parameter. A special feature of the Tanaka function is that growth can continue for as long as individuals live, which makes good sense for sea urchins and, we suspect, for a wide variety of species, such as many fish, reptiles, and molluscs, that now are modeled using the Brody–Bertalanffy equation. Asymptotic size may be a mathematical convenience without biological meaning (Knight 1968).

It is unclear what substantial difference various growth models make in the exploration of general patterns of life-history evolution. Shine and Charnov (1992) have used the Brody–Bertalanffy model together with Eq. (16) as approximations to explore general patterns of survival, growth and age at first reproduction in reptiles. Similar approximations have been made for fish (Beverton and Holt 1959) and sea urchins (Ebert 1975); however, the shapes of the growth and survivorship functions certainly influence fitness. The importance of shape of the survivorship curve has been explored with respect to fitness in sea urchin life histories (Ebert 1985), with the expected effect; namely, fitness can be increased by shifting towards a Deevey I survivorship curve. There are no rigorous analyses for the sensitivity of fitness to changes in the shape parameter in the Richards function, and an elasticity
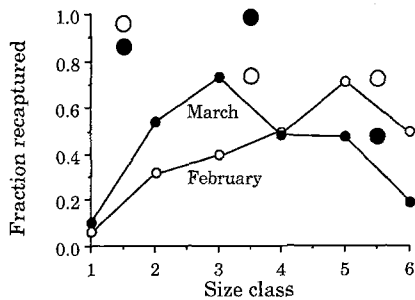
Fig. 7. *Strongylocentrotus franciscanus*. Fraction of tagged individuals in 1990 that were recovered in 1991; o: February sample; ●: March sample; large-sized circles are estimates from Table 10
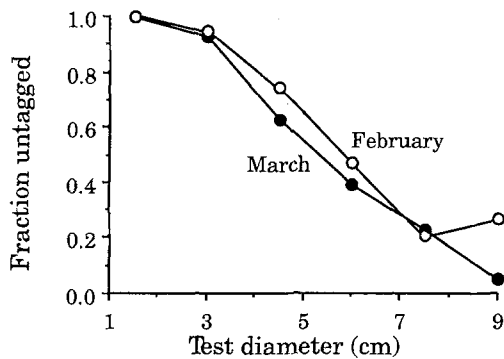

Fig. 8. *Strongylocentrotus franciscanus*. Fractions of untagged sea urchins within size classes in 1991 following tagging of all individuals on two concrete blocks with tetracycline in February and March 1990. Data points for both February and March collections are placed at midpoint of a size class

analysis has not been conducted for fitness and parameters in the Tanaka function or the three-parameter Jolicoeur function. Our point is that the complexity of growth and survivorship functions has not been explored in an evolutionary context and cannot be explored until it is clear what sorts of functions are needed to describe growth. The approximations of Eq. (16) and Brody–Bertalanffy may be good enough. On the other hand, they may be misleading.

From an applied standpoint, selection of appropriate growth and survival models is desperately needed in the development of management programs for sea urchin fisheries. Different growth models provide estimates of how long it takes an individual to reach harvestable size and different survivorship models provide different numbers that can be expected to reach that size. As shown in Fig. 4, all three functions indicate that it would take about 4 yr to grow from 2 to 8 cm. The three functions differ in their extrapolations back to the very smallest sizes, and consequently time to 2 cm differs by about 1.5 yr between the Tanaka/Jolicoeur and Richards functions. All three differ substantially from estimates that employed the Brody–Bertalanffy function (Ebert 1975, 1977), whereby it was estimated that red sea urchins could grow to about 8 cm in 3 yr. Estimates from our tagged red sea urchins also differ from the report that second-year individuals are $\simeq$ 3.6 to 6.0 cm in size (Tegner 1989). At this point, it is not certain how rapidly red sea urchins

grow during their first year after settlement, because there were no tagged individuals in the very smallest sizes. Based on Rowley's (1990) finding of slow growth of newly settled purple sea urchins (*Strongylocentrotus purpuratus*), we would expect similar slow growth for *S. franciscanus*. Tagging studies that start with newly settled sea urchins are needed to remove the problems of extrapolation in the early portions of the growth curve.

There are additional problems with analysis. With the matrix techniques, we assumed that we had a confined population in which all individuals that were tagged in 1990 either died or were still present on the concrete blocks in 1991. The crudest estimate of survival is simply to ask: of individuals in a particular size class in 1990, how many were recovered in 1991? Column totals for February and March in Table 5 are the number recaptured in 1991 from individuals tagged in a size class in 1990. For example, for the March sample, there were 5 sea urchins recaptured that had been in the 1.1 to 2.5 cm size class in 1990. A total of 49 individuals had been tagged in this size class in March 1990 (Table 6), and so the fraction recaptured was 0.10. The match between such crude estimates and the survival estimates in Table 10 is not very good for small individuals, but improves for the larger individuals (Fig. 7). The estimates in Table 10 indicate that survival is very good for small and medium-sized individuals, yet the recovery of tagged sea urchins in these classes was between 10 and 70%. What happened to the missing tagged sea urchins? Furthermore, there were some untagged sea urchins in all size classes in 1991 (Fig. 8). The 100% untagged for the smallest size class is reasonable, because this represents recruitment into the population of new sea urchins during 1991, but we had expected 100% tagged for medium and large individuals also.

There are a number of possibilities to explain both missing tagged sea urchins and the presence of untagged individuals, but none of these hypotheses can be rigorously tested with the existing data. The possibility of poor tagging success seems unlikely, because laboratory studies (Fansler 1983, Russell 1984, Ebert 1988, 1989, Edwards and Ebert 1991) have shown 100% tagging success. There are difficulties with clarity of tetracycline lines in tagged sea urchins that have been stressed by lack of food, and some reworking of the skeleton appears to take place under stress, so tetracycline marks can be lost (Fansler 1983, Edwards and Ebert 1991). Although possible, tag loss seems unlikely for the San Nicolas individuals because growth rates appeared good on the concrete blocks, relative at least to intertidal sites (Ebert and Russell 1992). We now suspect that the concrete blocks might not have been as isolated as they appeared to be, and so sea urchins that were tagged might have left and untagged individuals moved onto the blocks.

A leaky system seems more likely than tagging problems. However, if movement is the explanation, it means that small individuals moved more than large individuals (Fig. 8). We know of no data that have tested this hypothesis for sea urchins; however, agonistic interactions ("spine fencing") between large and small sea urchins favor large individuals (Schroeter 1978), so small sea urchins would be more likely to move. If more small individuals

moved onto the blocks than moved off, estimates of size-specific survival rates would be biased. Estimates of survival rate would be too high for small individuals, and it is possible that this is the explanation for the differences in size-specific survival rates. Clearly, size-specific survival requires further investigation.

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