Abstract—The growth of red sea urchins (*Strongylocentrotus franciscanus*) was modeled by using tag-recapture data from northern California. Red sea urchins (n=211) ranging in test diameter from 7 to 131 mm were examined for changes in size over one year. We used the function $J_{t+1} = J_t + f(J_t)$ to model growth, in which J_t is the jaw size (mm) at tagging, and J_{t+1} is the jaw size one year later. The function $f(J_t)$, represents one of six deterministic models: logistic dose response, Gaussian, Tanaka, Ricker, Richards, and von Bertalanffy with 3, 3, 3, 2, 3, and 2 minimization parameters, respectively. We found that three measures of goodness of fit ranked the models similarly, in the order given. The results from these six models indicate that red sea urchins are slow growing animals (mean of 7.2 ±1.3 years to enter the fishery). We show that poor model selection or data from a limited range of urchin sizes (or both) produces erroneous growth-parameter estimates and years-to-fishery estimates. Individual variation in growth dominated spatial variation at shallow and deep sites (F=0.246, n=199, P=0.62). We summarize the six models using a composite growth curve of jaw size, J, as a function of time, t: $J = A(B - e^{-Ct}) + Dt$, in which each model is distinguished by the constants A, B, C, and D. We suggest that this composite model has the flexibility of the other six models and could be broadly applied. Given the robustness of our results regarding the number of years to enter the fishery, this information could be incorporated into future fishery management plans for red sea urchins in northern California.

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Modeling red sea urchin (*Strongylocentrotus franciscanus*) growth using six growth functions*

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Marine invertebrates are being fished at an increasing pace worldwide (Keesing and Hall, 1998). In California, invertebrates have a greater exvessel (wholesale) value than do fin-fish (Rogers-Bennett, 2001). Invertebrate fisheries are now experiencing serious declines as have fin-fish fisheries (Dugan and Davis, 1993; Safina, 1998; Jackson et al., 2001). The once prosperous commercial abalone fishery in California which landed in excess of 2000 metric tons per year in the 1950s and 1960s was closed in 1997 (CDFG Code 5521) following the serial depletion of stocks over time (Karpov et al., 2000). Commercial divers now target red sea urchins and other invertebrates. Red sea urchin landings in California have also declined dramatically from a high of 24 metric tons (t) in 1988 to 6 t in 2002, despite management efforts (Kalvass and Hendrix, 1997). These declines have generated interest in exploring the use of alternative fishery management policies, such as spatially explicit strategies that would protect large old sea urchins (Rogers-Bennett et al., 1995).

Sea urchin growth models are critical in the development of innovative management strategies to sustain the fishery because, among other things, models can be used to predict the time required for sea urchins to enter the fishery (referred to as "years to fishery") and the age of the broodstock. Despite the interest in examining sea urchin growth, modeling efforts have been hampered by several factors including model selection and a lack of data from a sufficiently wide range of urchin sizes. Perhaps as a consequence, estimates of red sea urchin growth have varied widely, ranging from 3 to 12 years for urchins to grow into the fishery (Kato and Schroeter, 1985; Tegner, 1989; Ebert and Russell, 1992; Smith et al., 1998). Because of the wide variation in growth estimates, the number of models and methods being used, and the difficulties that these present

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for management, there is a need to evaluate a number of growth models with a single data set that encompasses a large range of urchin sizes.

In our study we report the results from six individual growth models applied to data from a one-year tag and recapture study of red sea urchins (*Strongylocentrotus franciscanus*) in northern California. We supplemented the number of juveniles in the field by stocking tagged juveniles. Estimates of the number of years required for urchins to grow to minimum legal size in northern California are generated by the models. We examine the robustness of these results to changes in the parameters and the impact of a limited data set from a small range of urchin sizes on our results. We determine if there are spatial differences in growth between shallow and deep sites. Finally, we rank the models according to quality of fit, present a generic growth curve that combines the six models, and discuss the implications of our results for fishery management.

Materials and methods

Study sites

Growth rates were determined for red sea urchins in the Salt Point (38°33′06″N, 123°19′45″W) and Caspar (39°21′49″N, 123°49′47″W) urchin harvest reserves in northern California. Commercial urchin harvesting is prohibited in these reserves. We examined spatial variation within Salt Point by tagging red sea urchins at one shallow site (5 m) south of the southern border of the Gerstle Cove Reserve and at one deep site (17 m) on the leward side of a large wash-rock. In addition, laboratory-reared juvenile red sea urchins were stocked at the two sites in Salt Point. Both of these sites are relatively isolated, surrounded by sand and seasonally dense kelp (*Nereocystis*). At the Caspar Reserve, sea urchins were tagged outside a small cove with seasonally dense kelp (*Nereocystis*) at a single depth (7 m).

Tagging

Sea urchins at the study sites were tagged internally and recaptured after one year. At Salt Point, wild sea urchins were tagged with tetracycline injections *in situ* by using 0.5–1.2 mL of 1 g tetracycline/100 mL of seawater (cf. Ebert, 1982; Ebert and Russell, 1992). Six hundred and nine red urchins were measured with vernier calipers (±1–2 mm) and tagged at Salt Point on 19 August 1992. Urchins were recaptured from the Salt Point sites on 18 September 1993 (n=374 shallow; n=352 deep). This data set was normalized to one year by using the factor 12/13. Our study was not a longitudinal study examining growth over many years, but rather for one year only.

Juvenile urchins reared in the laboratory for one year (mean test diameter=17.6 mm) were tagged and stocked into the shallow and deep Salt Point sites. Juveniles were tagged by immersion for 24 hours in a calcein solution 125 mg/L seawater, pH adjusted to 8.0 (Wilson et al., 1987). After tagging, juveniles were transported to the Salt Point sites and released. Juveniles were stocked (120 at each of the two depths) on 31 August 1992 and harvested on 18 September 1993 with the adults (see Rogers-Bennett, 2001).

Urchins at the Caspar Reserve were tagged internally with personal individual transponder (PIT) tags on 28 August 1996 and recovered 20 August 1997 (Kalvass[1]). PIT tags are glass coated mini-transponders with unique individual codes that can be read noninvasively by using a Destron® tag reader. Tags were implanted into the body cavity of the sea urchins through the peristomial membrane. PIT tags are too large for tagging small urchins (<40 mm).

Estimates of urchin density were made within a circle (12 m in radius) at each of the two Salt Point sites at the time of harvest. Drift algae collections were made along a 2 × 10 m transect (20 m^2) at each site. Gut contents were collected from a subsample of 20 urchins from each site. Gut contents were fixed in alcohol, sorted on a petri dish, and the most abundant items were recorded from 5 out of 25 10-mm^2 grids (Harrold and Reed, 1985). We used a conservative definition of optimal foods, defining them as fleshy red or brown algae (Harrold and Reed, 1985). Suboptimal foods included green algae, upright and encrusting coralline algae, detritus (animal, plant, and inorganic), plants (*Phyllospadix*), mud, and sand.

Growth measurements

Sea urchins can not be reliably aged by using rings on test ossicles (Pearse and Pearse, 1975; Ebert 1988; Gage, 1992), therefore growth increments after one year must be measured directly. For the urchins tagged with fluorescent dyes (tetracycline and calcein), growth was measured as the change in urchin jaw length ($\Delta J = J_{t+1} - J_t$) after one year (Ebert and Russell, 1993). Urchin jaws were dissected from Aristotle's lantern, excess tissue was removed with 10% sodium hypochlorite, and the jaws were measured to the nearest 0.1 mm. Growth was measured by determining the width of the calcium deposit one year after tagging. Tags on jaws are more accurate than tags on test ossicles because ossicles move toward the oral surface during growth (Duetler, 1926), requiring matching ossicles at the time of tagging with ambitus ossicles at the time of collection (Ebert, 1988).

Fluorescence tagged urchins were identified when exposed to an ultraviolet epi-illuminator (Lite-Mite) on a dissecting scope. Growth increments were determined by using the Confocal Microscope (BioRad MRC-600, BioRad Industries, Hercules, CA) with a BHS fluorescence filter (blue wavelength) and the COMOS software package (BioRad Industries, Hercules, CA). Growth was measured from the fluorescent band (indicating size at tagging) to the esophageal edge of the jaw (final size). Growth was also recorded from a second growth zone at the labial tip of the jaw, represented by a glowing arc when present. Initial jaw size (J_t) equals jaw size after one year (J_{t+1}) minus the

[1] Kalvass, P. 1997. Personal commun. Calif. Dep. Fish and Game, 19160 S. Harbor Dr., Fort Bragg, CA. 95437.

Table 1

Tests for homogeneity of slopes for ln (*diameter*) compared with ln (*jaw*) for shallow and deep samples of red sea urchins from Salt Point, California: SS: sum of squares; df: degrees of freedom; MS: mean square. Treatment (depth) is significant P=0.017 when adjusted for covariate (test diameter).

	SS	df	MS	F-ratio	P
Homogeneity of slopes					
Sample	0.013	1	0.013	3.643	0.058
ln (*jaw*)	21.216	1	21.216	5760.0	0.000
Sample × ln(*jaw*)	0.010	1	0.010	0.723	0.101
Error	0.718	195		0.004	
Adjusted means					
Sample	0.021	1	0.021	5.747	0.017
ln (*jaw*)	29.333	1	29.333	7894.0	0.000
Error	0.728	196			0.004

sum of the esophageal and labial growth. Urchin jaws do not wear or erode as teeth do. Calculating test growth from changes in jaw size may yield a conservative estimate for sublegal red sea urchins (Kalvass et al., 1998).

In the PIT-tagged urchins, growth was measured as the change in test diameter after one year. Juvenile urchins less than 30 mm are too small to survive PIT tag implantation. Large adults (>100 mm) may grow too little in one year to allow growth in test diameter to be measured. Standard errors in measures of test diameter with calipers range from 1–2 mm which may be greater than the growth increment in adults.

Jaw size versus test size

The relationship between jaw length and test diameter was determined from a large sample (n=384) of red sea urchins (sample independent of this study) ranging in size from newly settled individuals to large adults. From this sample we obtained an allometric equation relating jaw and test size. Using this equation we converted all the measures of growth (from fluorescent and PIT tagged urchins) into initial and final jaw size (one year later).

Jaw size is a plastic trait that can vary spatially (Ebert, 1980b; Rogers-Bennett et al., 1995). Food availability has been correlated with the size of Aristotle's lantern (composed of ten jaws and five teeth) such that lanterns are large when food is scarce. Therefore, we examined the relationship between jaw size and test size, segregating the data from the shallow and deep Salt Point sites. To do this we used an ANCOVA (Table 1) with the natural log of test diameter as the covariate. Measurements of the jaw size at tagging from the fluorescent marks allowed for estimates of the test size at tagging using the allometric relationship (Eq. 1). As a control to test for bias in the conversion of jaw size to test diameter with Equation 1, we compared the measured test size at the time of recapture to the predicted test size at the time of recapture using the allometric relationship (Eq. 1). Results indicated that, although there was error in the predicted test size from jaw size, there was no bias.

Results

Red urchin growth

We present growth data from a total of 211 red sea urchins that were tagged internally and recaptured after one year in northern California. Recaptured urchins ranged in test diameter from 7 to 131 mm at the time of tagging. We recovered 161 out of 609 (26.4%) tetracycline-tagged wild urchins from the two sites at Salt Point. In addition, 38 of the 240 (15.8%) stocked juvenile urchins tagged with calcien were also recovered. It is unknown whether untagged urchins included tagged adults which were not growing and therefore not taking up the tetracycline stain. In the Caspar Reserve 12 of 53 (22.6%) PIT-tagged wild urchins were recovered.

We examined spatial variation in growth and found that the change in size (ΔJ) was not significantly different for urchins in the shallow, as compared to the deep Salt Point sites (ANCOVA F=0.246, n=199, P=0.62) with initial jaw size (J_t) as the covariate (independent variable). Similarly, growth rates were not significantly different between juveniles recovered in shallow and deep sites (ANCOVA F=0.387, n=38, P=0.54). Richards function parameter estimates (J_∞, K, n) generated from the shallow site were statistically identical to those for the deep site. Size-frequency distributions of urchins recovered from the shallow site were not significantly different than those at the deep site (K-S mean difference=0.162, P=0.67). Therefore, growth data from the shallow and deep sites were pooled.

Urchin density at the shallow site (4.2 urchins/m^2) was greater than at the deep site (0.75 urchins/m^2). In addition, drift algae abundance was twice as great in the shallow (2.7 g/m^2) as in the deep site (1.4 g/m^2) at the time of urchin harvest (18 September 1993). This resulted in less algae per urchin in the shallow site compared with the deep site (0.63 g/urchin and 1.85 g/urchin respectively) for that sampling date. Guts of urchins from the deep habitats contained more optimal food (fleshy red and brown algae) than guts of urchins in the shallow sites (t=2.79, df=19, P=0.012). Gut fullness was generally uniform, roughly 50 mL/urchin.

Jaw size versus test size

ANCOVA analysis indicated that the slopes of the natural log of test diameter as a function of the natural log of the jaw size are homogenous (P=0.101), but that the adjusted means are significantly different (P=0.017)—urchins in the deeper habitat having larger jaws (Table 1). Therefore, we constructed two allometric equations, one for urchins from the shallow Salt Point site and a second for urchins from the deep Salt Point site. However, the two equations were so similar that they generated identical test diameters for a given jaw size; therefore we pooled our data from the shallow and the deep sites.

We used a larger independent data set of n=384 from wild and cultured urchins to generate the allometric equation relating jaw size to test size. There is a strong relationship (r^2=0.989, df=382) between test diameter (D) and jaw length (J) described by

$$D = 3.31\, J^{1.15}, \quad (1)$$

where D = test diameter (mm); and
J = jaw length (mm).

Equation 1 predicts that urchins of legal size in northern California (test diameters ≥89 mm) have jaw lengths ≥17.5 mm.

A comparison (using the allometric relationship [Eq. 1]) of the measured test size at the time of recapture with the predicted test size revealed no bias in the conversion. Although individual values of measured and predicted test diameters are not identical, the sum of the differences between the two reveals no strong *directional* bias. The sum of the differences between the measured and predicted values equals 41 mm for 139 urchins, resulting in an average discrepancy of 0.30 mm per urchin. This discrepancy is smaller than the initial error in the measurement of test size (see "Materials and methods" section).

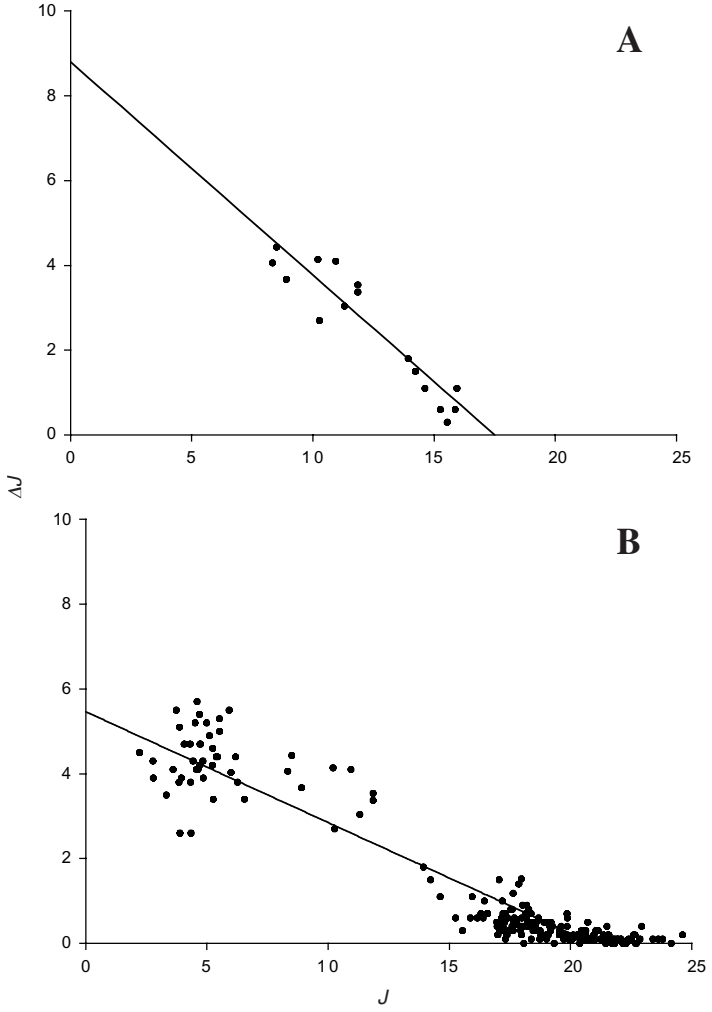

Figure 1

(**A**) Linear function fitted to the middle portion of the urchin growth data set. (**B**) Linear von Bertalanffy function superimposed on the entire data set. J = jaw length (mm); ΔJ = change in jaw length (mm).

The von Bertalanffy model

For many organisms, annual growth rate decreases as size (age) increases. This process is frequently modeled by using the von Bertalanffy equation (von Bertalanffy, 1938)

$$J_{t+1} = J_t + J_\infty(1 - e^{-K}) - J_t(1 - e^{-K}) \quad (2)$$

or

$$J = J_\infty(1 - e^{-Kt}), \quad (2a)$$

which leads to a linear decrease in growth rate as a function of size. We make the point here, that J_{t+1} and J_t refer to a discrete data set, whereas J is a smooth, continuous function of t.

Our data and, quite possibly, much of the data collected in similar studies, are not well represented by the von Bertalanffy equation. How is it then that the deficiencies of this well used equation have not come to light? The answer, not surprisingly, lies in the cancellation of errors within data sets that only incompletely cover the critical growth period.

Our data (Figs. 1B and 2) show three features of sea urchin growth that are inconsistent with the von Bertalanffy model: 1) annual growth, $\Delta J = J_{t+1} - J_t$, for juveniles that is lower than anticipated from the model; 2) a maximum or plateau in the growth function, $\Delta J = f(J_t)$, for urchins near jaw size J_t = 5 mm (test diameter 20 mm); and 3) an asymptotic approach of ΔJ to zero (Figs. 1B and 2), which may be ascribed to indeterminate growth for adults of all sizes or to dispersion of final adult urchin sizes (Sainsbury, 1980).

There is a good deal of individual variation in growth rate as a function of J_t, which prevents unequivocal selec-

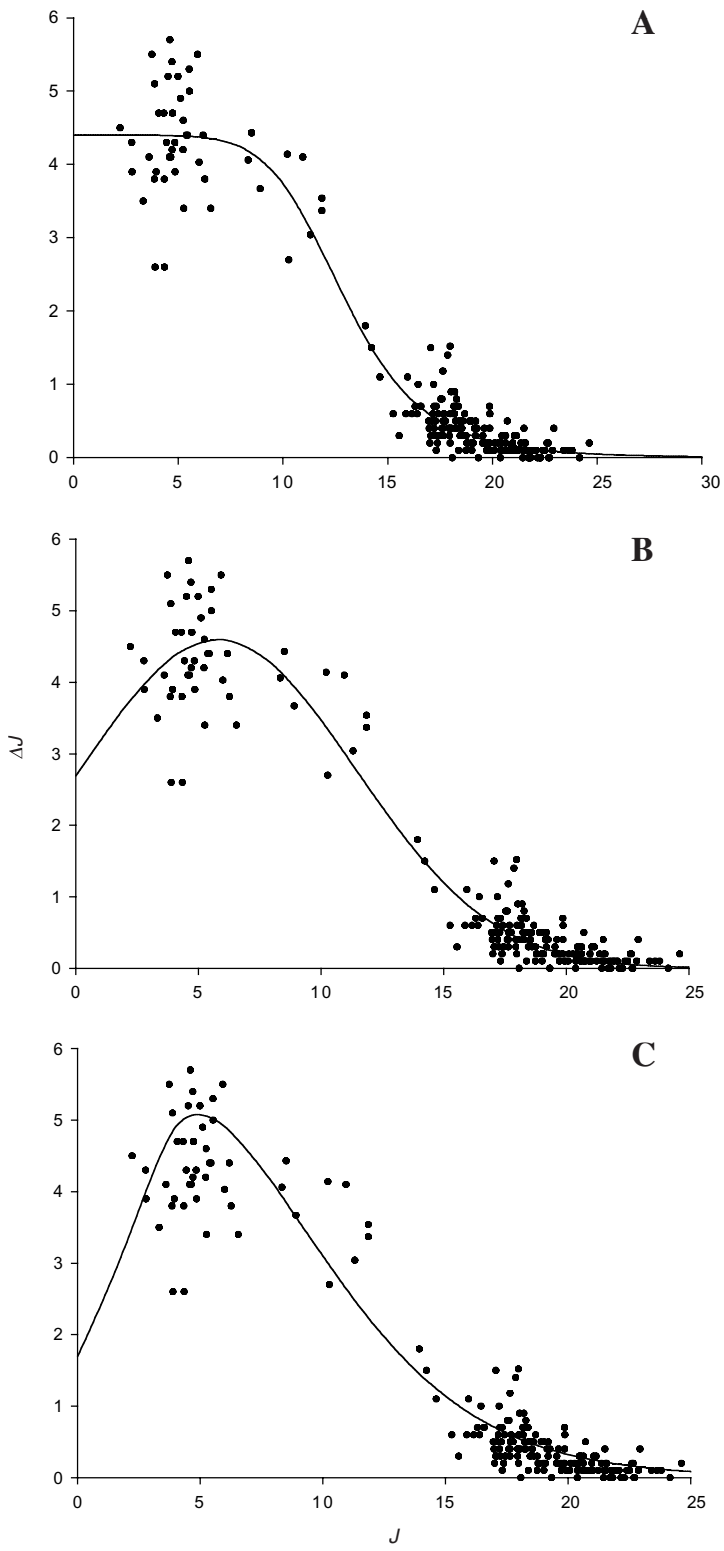

Figure 2

Annual growth as a function of jaw size for six models: logistic dose-response, Gaussian, Tanaka, Ricker, Richards, and von Bertalanffy models. J = jaw length (mm); ΔJ = change in jaw length (mm).

tion of one model. Nevertheless, it is clear that the von Bertalanffy model does not represent the data well over the full range of urchin sizes (J_t). To investigate this point further, we divided our data set into three groups over the range of of J_t . The groups are

1 Juveniles (J_t < 8 mm) that do not fall on the linear descent of ΔJ versus J_t characteristic of von Bertalanffy growth.
2 Sublegal, actively growing adults (8 mm< J_t<16 mm) that do follow von Bertalanffy kinetics.
3 Adults (16 mm< J_t < 24 mm) that appear to grow to large J_t but only very slowly, and do not conform to the von Bertalanffy model.

If the data were fitted to the von Bertalanffy equation, all three groups should give the same slope $\Delta J / J_t$ because three segments of the same straight line all have the same slope. Instead, group 1 gives a small positive slope, group 2 gives a negative slope that leads to unrealistic conclusions for early growth rate and time-to-fishery estimates shown in (Fig. 1A), and group 3, excluding growth information from sublegal urchins, yields a plausible mean final jaw size of 22.6 mm but gives a growth rate constant that indicates very slow growth for adults and many decades for time-to-fishery.

In the present study we fitted a decreasing, linear von Bertalanffy function only to the sublegal (group 2) urchins (Fig. 1A) which did conform to von Bertalanffy growth. The von Bertalanffy function for the partial data set of actively growing urchins in (Fig. 1) has a slope of −0.504/yr, a ΔJ intercept of 8.7 mm/yr, and a J_t intercept of 17.3 mm. These results lead one to predict that final grow to 90% of their final size in 3.5 years and that mean final size will be less than the legal size (89 mm test diameter), which is obviously false. We also show the same function superimposed on the entire data set (Fig. 1B) where discrepancies between the von Bertalanffy function and data groups 1 and 3 above are evident. For our data set (Fig. 1) and, we suggest, for urchin growth in general, the von Bertalanffy curve does not represent early growth, and a transition curve or a peaked function reflects actual growth better. For our data set, the von Bertalanffy model gives an overestimate of the rate of urchin growth and an underestimate of the time to enter the fishery.

The slopes of these three line segments give an indication how the von Bertalanffy model, despite its implausible fit to the complete data set, can give plausible growth parameters. Errors in fitting a von Bertalanffy curve to a data set resembling ours lie in opposite directions

for groups 1 and 3 of the growth; consequently they cancel, in whole or in part. In fact, all reported data sets have many more observations falling into group 3 than into group 1, which is either swamped out by group 3 or does not appear at all. This leaves groups 2 and most or all of group 3 to determine the slope of the von Bertalanffy linear function. The average of these two erroneous slopes may or may not be a realistic approximation for urchin growth, depending on the number of measurements in each group.

Alternative growth models

Curves that rise to a maximum and then decay asymptotically are very common in the physical sciences and have been successfully modeled for more than a century (e.g. Wien, 1896). Any rising function multiplied into an exponential decay, e.g. $(x)\ \exp(-x)$, models such a curve more or less well. The problem is not in finding a model but in selecting from among many possibilities. We compared several models in our study and included a Gaussian model for this data set because it has a small sum of squared residuals and because it has well-defined parameters in the arithmetic mean and standard deviation. Here the arithmetic mean merely serves to fix the position of the maximum on the J_t axis and the standard deviation from μ gives the range, in units of J_t, of actively growing animals. The model is descriptive only; it does not imply a mechanism of growth.

We present results from six growth models, the logistic dose-response, Gaussian, Ricker, Tanaka, Richards, and von Bertalanffy models, in order of quality of fit (Fig. 2). Each model is characterized by a different $\Delta J = f(J_t)$, where $f(J_t)$ is a function of annual growth ΔJ versus size at tagging, J_t. Equations 3–8 were input as user-defined functions into a curve-fitting program (TableCurve, Jandel Scientific, now SPSS, Chicago, IL), either as $f(J_t)$ or the equivalent $J_{t+1} - J_t$. In certain cases, additive parameters that make a negligible contribution to the final fit were dropped. This curve-fitting program uses the Levenburg-Marquardt procedure for finding the minimum of the squared sum of deviations. During the least-squares minimization, local minima are occasionally found and must be discarded in favor of the global minimum. Matrix inversion is performed by the Gauss-Jordan method (Carnahan et al., 1969).

We present these models ranked by the fitting criterion of the sum of squared residuals, called "Error Sum of Squares" in the output from the TableCurve fitting program, which we have given the abbreviation RSS. Several

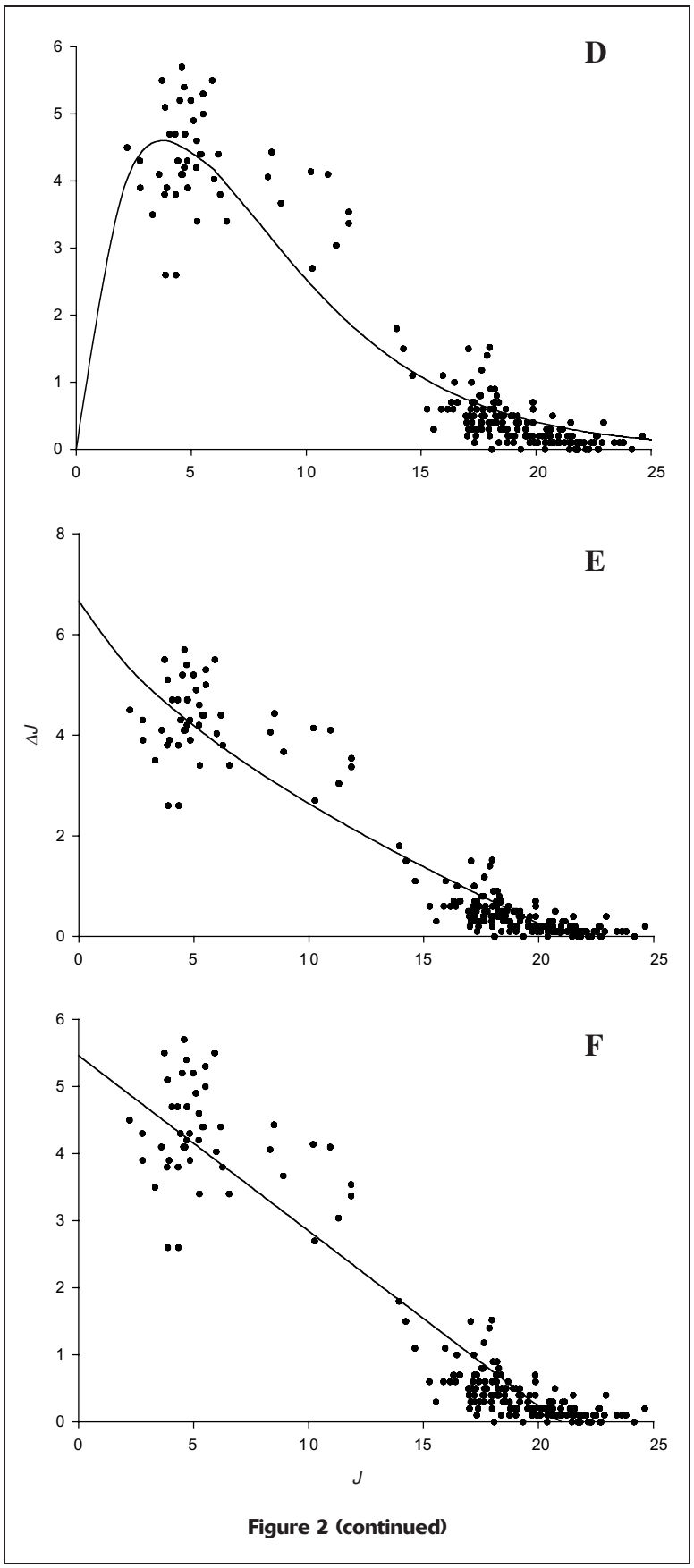

Figure 2 (continued)

Table 2

A comparison of the fitting criteria for six red sea urchin growth functions. r^2 = the coefficient of determination; RSS = the error sum of squares; AIC = Akaike's information criterion; SBC = Schwartz-Bayesian criterion.

	r^2	SE	RSS	AIC	SBC	No. of parameters
Logistic	0.946	0.392	31.9	–393	–383	3
Gaussian	0.945	0.397	32.8	–387	–377	3
Tanaka	0.933	0.436	39.6	–347	–337	3
Ricker	0.918	0.483	48.7	–305	–299	2
Richards	0.900	0.534	59.4	–262	–251	3
von Bertalanffy	0.895	0.545	62.1	–254	–247	2

other fitting criteria are also given in Table 2. We used both the AIC information criterion, $AIC = K\ln(RSS) - K\ln K + 2m$, and the Schwartz-Bayesian criterion $BIC = K\ln(RSS) - (K-m)\ln(K)$, where K is the number of data points, and m is the number of parameters in the fitting equation (Akaike, 1979). These tests of curve-fitting quality were used to bring out any substantive difference between the 2-parameter and 3-parameter equations. The results show that differences between the 2- and 3-parameter cases are swamped out by the data, as might have been anticipated from the disparity between the number of points (K=211) and the number of parameters. For the present data set, in applying either of these criteria, one is essentially seeking the smallest RSS.

Individual models

Logistic dose-response The logistic dose-response curve (time-to-fishery estimate: 6.6 yr)

$$f(J_t)=a/(1+(J_t/b)^c) \quad (3)$$

(Hastings, 1997) fits our data the best of all the models examined here. The curve fit (a=4.4, b=12.9, c=6.8) with RSS = 31.9, is a sigmoidal transition function (TableCurve Windows, vers. 1.0, Jandel Scientific Corp., SPSS, Chicago, IL). There is a transition between a fast-growing group of sea urchins, which maintain a constant growth rate ($f(J_t)$=annual $\Delta J \cong 4.4$ mm/yr up to about J_t=8 mm), to sea urchins growing slowly at a rate that diminishes as J_t increases beyond 16 mm. The inflection point is at $J_t \cong$ 13 mm. There is considerable individual variation in both data groups, but more in the fast-growing group than in the larger slow-growing group.

Gaussian The Gaussian function (time-to-fishery estimate: 6.9 yr), although rarely if ever used in this context,

$$f(J_t) = Ae^{-(J_t-\mu)^2/2\sigma^2} \quad (4)$$

fits the data about as well (RSS=32.8) as the logistic dose-response model. It is a three-parameter model (Rogers, 1983) for which the parameters are maximum growth (A=4.6 mm/yr), size at maximum growth (μ=5.8 mm), and standard deviation (σ=5.6mm) of the distribution of maximum growth versus size. Applied to the present data set, the Gaussian function yields an initial annual growth rate ΔJ=2.8 mm/yr, and a time of entry into the fishery of about 7.0 yr. A strength of the Gaussian model aside from its good fit is that it provides a plausible growth model with maximum ΔJ, not at settlement, but at a jaw size about one third that of adults, and that the parameters are well defined. In this model, annual growth is randomly distributed, according to jaw size, about the maximum in ΔJ.

Tanaka The Tanaka equation (time-to-fishery estimate: 8.2 yr)

$$f(J_t) = \frac{1}{\sqrt{f}}\ln\left|2G + 2\sqrt{G^2+fa}\right| + d - J_t, \quad (5)$$

where

$$G = \frac{E}{4} - \frac{fa}{E} + f \text{ and } E = \exp\left(\sqrt{f}(J_t - d)\right),$$

can be obtained from its differential form (Tanaka, 1982; Ebert, 1999)

$$\frac{dJ}{dt} = \frac{1}{\sqrt{f(t-c)^2 + a}} \quad (5a)$$

by using a standard integral (Barrante, 1998). The parameters are a=0.0330, d=15.7, and f=0.0773.

The Tanaka model shows an asymptotic approach to zero growth at large J_t, allows for an early lag in growth, and does not force a maximum growth rate on juvenile urchins. The fit to our data set (RSS=39.6) requires three parameters (the parameter c in Eq. 5a drops out). This function has been used to model red sea urchin growth (Ebert and Russell, 1993).

Ricker The Ricker function (time-to-fishery estimate: 9.2 yr) for population growth (Hastings, 1997) translated into terms of urchin growth is

$$f(J) = BJ_t\, e^{-KJ_t} \quad (6)$$

(Ricker, 1954). This model yields a maximum in the growth function and an asymptotic approach to zero that characterize the data set (Fig. 2D). The empirical fitting parameters are maximum growth rate constant (B=3.15/yr) and K = 0.252 /mm, a constant that controls decrease in growth rate as the animal matures. Fitted to the present data set, it gives RSS = 48.7. Initially, J_t is small and $\Delta J = BJ_t$. At larger J_t, annual ΔJ passes through a maximum as the negative exponential becomes important. Growth, though never zero, will eventually be too small to measure over a one-year period. This model requires an arbitrary specification of the jaw size at settlement which is not well known and to which the resulting $f(J_t)$ curve is quite sensitive.

Richards The Richards function (time-to-fishery estimate: 6.1 yr) incorporates the von Bertalanffy and logistic (as distinct from the "logistic dose-response") models

$$f(J_t) = \left[J_\infty^{-1/n}(1-e^{-K}) + J_t^{-1/n}e^{-K}\right]^{-n} \quad (7)$$

and has an additional "shape parameter" n allowing for an inflection in the curve of J versus t (Richards, 1959; Ebert, 1980a)

$$J = J_\infty(1 - be^{-\mathrm{Kt}})^{-n}. \quad (7a)$$

When n = −1, this equation is the von Bertalanffy model, and when n = 1, it is the logistic model. Minimization of the fitting parameters leads to J_∞ = 21.2 mm, K = 0.239/yr, and n = −0.747 (unitless) with RSS = 59.4. In general, there is another parameter, b, to be determined:

$$b = \frac{(J_\infty - J_{settle})}{J_\infty},$$

where J_{settle} is the jaw size at settlement. In the present case, J_{settle} is very small in relation to J_∞; therefore b is essentially 1.

Minimization can be difficult owing to the singularity at n = 0. Minimization of the Richards function from small negative values of n and reasonable guesses as to J_∞ and K leads to a pseudo von Bertalanffy curve with diminishing slope as J_t increases (Fig. 2E). The SSE is better than it is for the true von Bertalanffy model (Fig. 2F) because there is one more fitting parameter. Approaching the n = 0 singularity from positive values of n does not produce the desired logistic curve. Rather the fitted n value becomes very large, leading to the Gompertz case (see also Ebert, 1999, chapter 11). The equation with n tending to ∞ does not appear to represent any real case and will not been considered further.

Von Bertalanffy Currently, the most widely used growth model is the von Bertalanffy or Brody-Bertalanffy model (time-to-fishery estimate: 5.9 yr)

$$f(J_t) = J_\infty(1 - e^{-K}) - J_t(1 - e^{-K}) \quad (8)$$

(Brody, 1927; von Bertalanffy, 1938), which produces a decreasing linear function of ΔJ vs. J_t (Walford, 1946) with a slope of $-(1 - e^{-K})$ and

$$J(t) = \mathrm{J}_\infty(1 - e^{-Kt}), \quad (8a)$$

where J_∞ = the limiting jaw size at long time t.

The model predicts that the smallest individuals have the fastest growth and yields the shortest time-to-fishery (however, see "Discussion" section). Fitting parameters (ΔJ=5.45 − 0.261 J_t) for the present data set yield J_∞ = 20.9 mm and K = 0.303/yr, and an RSS = 62.14 mm.

Growth curves $\Delta J = f(t)$

Having $\Delta J = f(J_t)$, one can assume a small (essentially zero) initial size at settlement and determine the size 1, 2, 3, . . . years after settlement by a recursive calculation. Six growth curves $J = f(t)$ can be generated from our six models from different functions for $\Delta J = f(J_t)$. We provide a single function

$$J = A(B - e^{-Ct}) + Dt \quad (9)$$

encompassing the entire group of six models, which differs only in the fitting constants A, B, C, and D given in Table 3. Parameters A and C, with B = 1.0, lead to a first-order growth curve familiar from chemical kinetics (Atkins, 1994). When $B \neq 1.0$, the curve is no longer first order but shows deviation near t = 0, typically a short delay or induction time. Parameter D indicates growth after "final" growth is achieved (indeterminate growth); in our study it is approximated by a small increase of constant slope. This is used to add growth during the indeterminate growth phase.

Sensitivity to changes in the parameters

We examined the robustness of each of the parameters in the six models by changing them ±10%, then noting the behavior of the model. Results are given in the last two columns of Table 3. In the first two models, ±10 % variation in the parameters yields a change in the estimate of years to fishery of less than 1 year. Other models gave estimated time-to-enter-the-fishery variations over the range shown. See Schnute (1981) and Ebert et al. (1999) for discussions of parameter sensitivity.

Discussion

Our results show that red sea urchins in northern California are slow growing animals. The six models we used to generate growth predictions yielded estimates of the time to enter the fishery (89 mm test diameter) averaging 7.2 ±1.3 years and a range of estimates from 5.9 to 9.2 years. The robustness of this result is important for its use in fishery management. These six growth models, applied to the same data set, give similar growth curves, J versus. t (Eq. 9, Fig. 3) differing mainly at small J. Ranking these diverse models according to goodness of fit with our large data set shows that three models represent the data well, but that the von Bertalanffy model, the most widely used model, describes the data least well (Table 2).

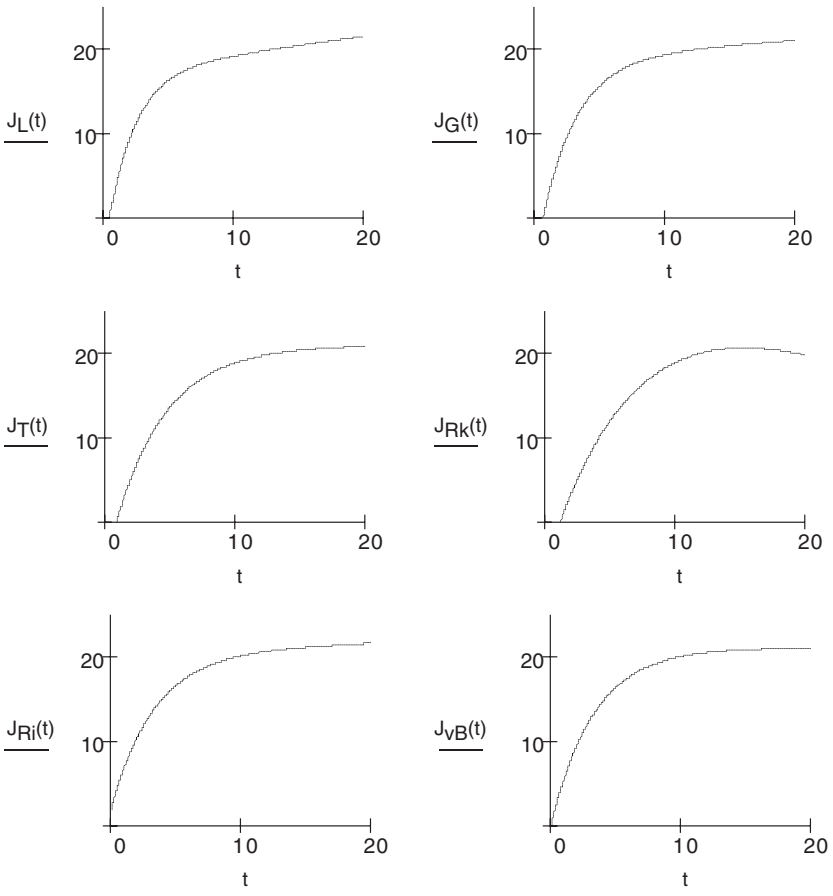

Figure 3

Jaw size (mm) versus time (y) obtained with J_{t+1} $J_t = J = f(J_t)$ onto $J = f(t)$. J_L = logistic dose response, J_G = Gaussian, J_T = Tanaka, J_{Rk} = Ricker, J_{Ri} = Richards, J_{vB} = von Bertalanffy. Note: *A, B, C*, and *D* in Equation 9 characterizing these curves are constants of the model and are not equal in number to the fitting parameters of the curves in Figure 2.

Our results suggest another important caveat: gaps in the data influence parameter estimates and time-to enter-the-fishery estimates. Many studies of sea urchin growth are based on a limited range of urchin sizes, primarily those of slow growing adults. Growth information from juveniles is difficult to obtain because recapturing tagged juveniles is problematic owing to high movement or mortality rates (or both). If growth information from adult urchins is used exclusively, inappropriate models can be fitted to the data ΔJ vs. J_t ($J_t \geq 16$ mm, Figs. 1 and 2) because there is no information at smaller J_t. In our example, lack of growth information from juveniles produced an overestimate of early growth and, as a consequence, an underestimate of the time to enter the fishery (Fig. 1A). Bias toward faster growth rates could lead to more liberal fishing policies and less precautionary management compared with bias toward slower growth rates. This problem has been noted by other researchers (Yamaguchi, 1975; Rowley, 1990; Troynikov and Gorfine, 1998).

Model selection

Model selection has always been an important aspect in applying growth modeling. In our case, with a data set from a broad range of size classes, we find that the six models yield similar growth curves, J versus t, indicating that our results of time to enter the fishery are robust to model selection. The unique features of the models show why the estimates are either longer or shorter than the mean we derive from all six models. Our composite model (Eq. 9) allows for the prediction of the most probable growth trajectory. The error terms (Table 2) describe dispersion about the most probable trajectory.

Both the logistic dose-response and the Gaussian functions qualitatively fit our sea urchin growth data better than the von Bertalanffy or Richards functions (Fig. 2). A comparison of the sum of the squared residuals (RSS) confirms this observation, ranking these models first and second, respectively. We use RSS as our primary criterion

Table 3

Parameters *A, B, C,* and *D* for the size versus time curves. Models are ordered according to goodness of fit. "Sensitivity" is the sensitivity to a parameter in estimated years to fishery.

Model	*A*	*B*	*C*	*D*	Years to fishery	Sensitivity	Parameters that varied
Logistic	21.3	0.80	0.48	0.22	6.6	<1	*a, b, c*
Gaussian	23.8	0.78	0.38	0.12	6.9	<1	A, μ, σ
Tanaka	25.6	0.80	0.26	0.02	8.2	1.5	*b*
Ricker	41.1	0.87	0.14	–0.68	9.2	–2.4, 3.5	J_∞, K
Richards	18.5	1.1	0.30	0.06	6.1	1.3, 2.7	J_∞, K
Bertalanffy	21.0	1.01[1]	0.30	0.01[1]	5.9	0.7, 0.6	J_∞, K

[1] These values are forced by the model.

for model selection; however both the AIC information criterion (Akaike, 1979) and the Schwartz-Bayesian criterion confirm the ranking of the models (Table 2). Model selection is discussed in detail elsewhere (Burnham and Anderson, 1998; Quinn and Deriso, 1999).

The Gaussian, Tanaka, and Ricker models yield both ΔJ vs. J_t and J_{t+1} vs. J_t curves that are concave downward and that visually conform with the data. These models are preferred over the Richards curve, which is concave upward, and the von Bertalanffy function, which is linear. The logistic and Gaussian models fit our data better (Table 2) than the other models examined. It is not surprising that the logistic and Gaussian models fit our data well, given the maximum or plateau visible in the data set for ΔJ vs. J_t. The Gaussian mean at J_t = 4.6 mm, with a standard deviation of 5.7 mm shows that a data set with $J_t > 4.6 + 5.7 =$ 10.3 mm represents urchins that are one standard deviation (σ) above the mean of the growth curve, i. e., 16% of the growing population. Urchins with $J_t > 17.0$ mm, are greater than 2σ above maximal growth, i. e. 2.5% of the growing population. Therefore, a growth curve fit only to adult urchins with $J_t > 17.0$ mm represents only small subset of the total growing population and is not representative of the total population. This demonstrates that data from a limited size range can generate erroneous growth parameters and shorten estimates of time to enter the fishery.

Variation in growth

The plateau in growth rate implied by the logistic dose-response curve or the maximum in growth rate for juvenile urchins well after settlement implied by the Gaussian curve suggests that urchin growth is not at its maximum when sea urchins first settle. It is realistic to imagine that a sea urchin will be at its maximum growth rate sometime after the first year or two.

In this study we found high individual variation in sea urchin growth. Growth in juveniles was especially variable, despite the fact that the juvenile urchins that were stocked were full siblings. We found no evidence for an increase in dispersion as sea urchins grow larger. Data from many sources suggest individual variation in juvenile growth is high. Full sibling red urchins (n=200) reared in the laboratory under identical food, temperature, and light regimes varied in test diameter from 4 to 44 mm at one year (Rogers-Bennett, unpubl. data). Similarly, cultured purple urchins (*S. purpuratus*), varied from 10 to 30 mm at one year (Pearse and Cameron, 1991)—a trend observed in other commercially cultured marine invertebrates (Beaumont, 1994) and fishes (Allendorf et al. 1987).

Our data contain broad distribution in the region of the small size classes, which is consistent with high individual variation in growth (K). Varying the growth constant, K, e.g. in the Ricker model (cf. Sainsbury, 1980), produces dispersion at the smaller size classes. Our urchin growth data also show a wide array of large sizes as well. Models have been used to examine the impact of this type of individual growth variation. In the von Bertalanffy model, if final size, J_∞, is varied 10%, this results in a broad distribution of the largest size classes (Botsford et al., 1994). We see a broad distribution in the largest size classes in our data, with animals larger and smaller than the estimated final size J_∞. Many of the animals smaller than J_∞ could be at their final size. The biological interpretation of this broad distribution at the largest sizes is an open question. There may be a wide array of final sizes because of independent values of K and J_∞ (cf. Sainsbury, 1980) and each individual hits its own final size abruptly or at an asymptotic approach to final size (cf. Beverton, 1992) also known as indeterminate growth (cf. Sebens, 1987).

We suggest that the composite model presented in the present study (Eq. 9) may be useful for a wide array of invertebrates and fishes especially those with a broad array of final sizes.

Spatial patterns in growth

In our study, we found no evidence for spatial patterns in growth. To observe spatial patterns this would have to be detectable above the background of individual variation. Sea urchins from the shallow and deep sites at Salt Point had measurable differences in gut contents, food availability, and oceanographic conditions; however these did not translate into significant differences in growth between

the depths over the year examined. Similarly, no latitudinal differences in red sea urchin growth were found in a large-scale growth study at 18 sites ranging from Alaska to southern California where growth varied between neighboring sites as between much as distant sites (Ebert et al., 1999).

Future studies could be longitudinal and examine temporal patterns in sea urchin growth, for example during and after warm water El Niño years, as has been examined for abalone in southern California (Haaker et al., 1998); however these temporal patterns too would have to be greater than individual variation to be detectable.

Implications for fishery management

Large old sea urchins (>125 mm test diameter) are fished in California despite fishermen receiving lower prices for these sea urchins compared with mid-size animals (Rudie[2]). Many of the large, old urchins have high gonadal weights (>100 g) (Carney, 1991; Rogers-Bennett et al., 1995), thereby potentially contributing more to reproduction than smaller urchins (Tegner and Levin, 1983; Tegner, 1989; Kalvass and Hendrix, 1997). Similarly, large coral-reef fish also have the potential to contribute more to reproduction than smaller fish (Bohnsack, 1993).

In fished areas, size-frequency distributions are heavily skewed to smaller urchins indicating that the larger size classes are absent (Kalvass and Hendrix, 1997). If the abundance and density of red sea urchins is decreased during fishing, this will decrease the chances of fertilization success significantly (Levitan et al., 1992). Sufficient numbers of large broodstock are critical because recruitment does not appear to be successful every year (Ebert, 1983; Pearse and Hines, 1987; Sloan et al., 1987). In addition, fishing can impact recruitment success because the spines of large urchins provide canopy shelter for juveniles; therefore an Allee effect may be present (Tegner and Dayton, 1977; Sloan et al., 1987; Rogers-Bennett et al., 1995). Size-structured red sea urchin models that include variable recruitment or an Allee effect (positive density dependence) resulted in a >50% decrease in estimated population size even at low fishing mortality levels (Pfister and Bradbury, 1996).

Harvest experiments conducted in northern California have shown that management strategies that protect large urchins (upper size limits and harvest reserves) improve recovery and recruitment after six years compared with strategies in which large urchins are harvested (lower size limits only) (Rogers-Bennett et al., 1998). Upper size limits and reserves have been used in the management of the sea urchin fishery in Washington state (Bradbury, 2000) and are currently being considered for California's red sea urchin fishery (Taniguchi[3]).

In conclusion, our work and that of others (Ebert and Russell, 1992, 1993; Ebert et. al., 1999) suggest that red sea urchins are slow growing, long-lived animals. Intense harvest rates may have serious consequences because red sea urchins require seven years to reach harvestable size in northern California. Declines in red sea urchin landings in northern California of more than 80% from the peak of 13,800 t in 1988 (Kalvass, 2000) demonstrate that harvest rates are high. Our growth results suggest that proposed alternative management strategies that would protect large, slow growing broodstock inside reserves or upper size limits for the fishery could be beneficial, in addition to existing regulations, for sustaining the fishery.

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