

Evaluating Age Determination and Spatial Patterns of Growth in Red Sea Urchins in Southeast Alaska

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Abstract.—The goals of this study were to characterize growth of the commercially harvested red sea urchin *Strongylocentrotus franciscanus* in southeastern Alaska and test the validity of an aging technique. We aged urchins by counting growth rings on a part (rotula) of the Aristotle's lantern complex from urchins collected at three sites. A subset of collected urchins had three or more years of size measurements from passive integrated transponder (PIT) tag data, allowing us to fit and compare PIT tag and ring-derived growth curves and test the assumption that rings were formed annually. Growth from PIT-tagged individuals approximated the growth derived from ring counts for two of three sites. The third site deviated slightly from predicted growth, providing support for our aging technique. However, we failed to detect any extremely old urchins, suggesting that this technique is not appropriate for assessing the longevity or growth trajectory of very large urchins. An additional five sites without PIT-tagged urchins were sampled to examine spatial variation in growth. Estimates of time to fishery entry varied substantially among sites, but four nonlinear growth functions produced similar estimates at individual sites. Time to fishery entry was positively correlated with an index of food availability, which suggests that the technique revealed true variation in growth rates.

Commercial harvest of red sea urchins *Strongylocentrotus franciscanus* throughout their range has spurred the development of techniques to accurately estimate urchin life history variables for fisheries management. Recent studies have recognized the red sea urchin's extreme longevity (Ebert et al. 1999; Ebert and Southon 2003) and the importance of selecting appropriate growth models (Ebert et al. 1999; Rogers-Bennett et al. 2003) and fishing strategies (Pfister and Bradbury 1996; Morgan et al. 2000; Lundquist and Botsford 2004) to understand the effects of fishing on populations of this species. Accurately determining and modeling urchin age and growth remain a challenge, and spatial patterns in growth remain understudied. Here, we test the validity of an age and growth determination technique for the red sea urchin in

southeast Alaska, assess the efficacy of a variety of growth models fit to the aging data, and begin to compare patterns of growth among locales.

Most studies of urchin growth have relied upon mark-recapture methods with tetracycline (Ebert 1977; Rowley 1990; Kenner 1992; Ebert and Russell 1992, 1993; Ebert et al. 1999). Passive integrated transponder (PIT) tags, electronic tags injected inside the test of the urchin, have been used to provide direct, multiyear monitoring of individuals (Rogers-Bennett et al. 2003). Both techniques are time consuming and labor intensive.

Determination of age without tagging has been less successful. Jensen (1969) suggested that portions of urchin tests produce growth lines that might be used to determine age. Breen and Adkins (1976) and Ebert (1988) demonstrated that test plates and spines were unreliable indicators of age. Robinson and MacIntyre (1997) documented a positive correlation between test diameter and growth rings found on a part (rotula) of

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the Aristotle's lantern complex in green sea urchins *Strongylocentrotus droebachiensis*. Brey et al. (1995) documented that growth lines could be accurately used for Antarctic sea urchins *Sterechinus neumayeri*, while Russell and Meredith (2000) compared tetracycline marking with growth lines on urchin plates and rotulae (see also Gage 1991, 1992). Russell and Meredith (2000) concluded that growth lines on both plates and rotulae were formed annually in some individuals, while more than one band was created in some and less than one complete band was observed in others.

We studied red sea urchins by use of PIT-tagging and rotula ring counts. By standardizing the ring-counting technique and comparing average growth curves generated using this method with those from multiple years of PIT tag-recapture data, we provide evidence that rotula ring counts can, for a range of ages, reasonably approximate age and past growth. Further, our method suggests that growth varies substantially among sites and is correlated with an indicator of food availability. Thus, the age at which red sea urchins recruit to the fishery is highly variable over relatively small spatial scales. However, our ability to accurately describe growth of large, old urchins with this technique is extremely limited.

Methods

Study area and field sampling.—The study area consisted of a total of eight ocean-exposed and fjord sites in the southern portion of southeastern Alaska (Figure 1). Six sites were located along Clarence Strait, a north-south-oriented fjord, while the other two were located at ocean-exposed sites west of Clarence Strait. All urchins used in this study were collected during July and August 2001. Nearshore subtidal habitat in the study area is primarily bedrock, boulder, or cobble substrate dominated by large brown algal species, including *Macrocystis integrifolia*, *Nereocystis luetkeana*, and *Laminaria* spp.

Three sites (Bob's Bay, Diver Point, and Blank Island) were located at PIT-tagging sites established by the Alaska Department of Fish and Game (ADFG). Urchins from these sites were sampled to compare growth curves derived from counting rotula rings and curves from multiple years of PIT tag-recapture data. The PIT tags do not significantly affect urchin growth in the laboratory (Hagen 1996). The PIT-tagged individuals contained 3–5 years of consecutive test diameter measurements spanning the years 1997–2001. The five remaining sites were spaced along the shores of Clarence Strait adjacent to ADFG urchin survey sites and were selected solely to examine variation in growth along the length of Clarence Strait. Sample

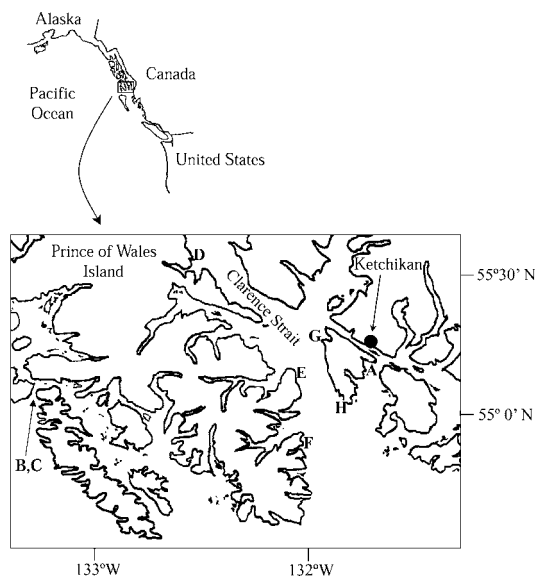


FIGURE 1.—Map of the locations of red sea urchin sampling in southeast Alaska. Sites are denoted by letters: (A) Blank Island; (B) Bob's Bay; (C) Diver Point; (D) site 102–70; (E) site 102–50; (F) site 102–20; (G) site 101–29N; and (H) site 101–29S.

sizes ranged from 75 to 120 urchins at PIT tag sites and 52–77 urchins at non-PIT tag sites (Table 1). All sites were relatively homogeneous in slope and habitat and were sampled at a standard depth of between 4 and 8 m below mean low water.

The urchins sacrificed for age determination via ring counts were selected to represent the range of urchin sizes present at each site. All urchins collected were measured three times along distinct diameters with Vernier calipers to obtain a consensus test diameter to the nearest 0.1 cm. To maximize the resolution in sizes previously documented to have high and variable growth rates elsewhere (Ebert et al. 1999), small urchins (1.0–8.0 cm in test diameter) were sampled at a higher proportion relative to their abundance than other sizes. All sampled urchins were sacrificed for rotula ring counts. The subsamples that were PIT-tagged allowed us to test the assumption that rings are produced annually and to evaluate efficacy of our age determination technique. Blank Island, Bob's Bay, and Diver Point samples included 18, 35, and 20 PIT-tagged urchins, respectively.

Age determination with rotula rings.—After collection and test measurement, the Aristotle's lantern complex was removed from each urchin. Lanterns were dissected to retrieve the five rotulae. Rotulae are sturdy, dog-bone shaped components of the Aristotle's lantern complex that connect the five demi-pyramids of

TABLE 1.—A comparison of model selection criteria for four red sea urchin growth functions at eight sites in southeast Alaska (n = number of red sea urchins sampled; AIC_c = Akaike's information criterion). Combined data includes 11 data from all sites. The number of parameters used in each model is indicated in parentheses.

Site	n		Tanaka (4)	Jolicoeur (3)	Richards (3)	Brody-Bertalanffy (2)
Blank Island	120	R^2	0.97	0.96	0.96	0.96
		AIC_c	269.2	275.6	278.9	282.3
		AIC_c weights	0.95	0.04	0.01	0.00
Bob's Bay	92	R^2	0.96	0.96	0.96	0.95
		AIC_c	205.8	203.6	202.1	219.5
		AIC_c weights	0.10	0.29	0.61	0.00
Diver Point	75	R^2	0.95	0.95	0.95	0.94
		AIC_c	156.3	155.8	156.1	162.6
		AIC_c weights	0.29	0.37	0.32	0.01
101-29N	77	R^2	0.94	0.94	0.94	0.94
		AIC_c	187.2	185.9	185.7	185.5
		AIC_c weights	0.14	0.26	0.29	0.31
101-29S	54	R^2	0.95	0.95	0.95	0.95
		AIC_c	116.0	115.5	116.7	117.4
		AIC_c weights	0.29	0.36	0.20	0.15
102-20	58	R^2	0.88	0.88	0.89	0.88
		AIC_c	123.9	122.7	122.4	120.3
		AIC_c weights	0.09	0.17	0.19	0.55
102-50	52	R^2	0.96	0.96	0.95	0.95
		AIC_c	127.7	125.4	124.4	122.2
		AIC_c weights	0.04	0.13	0.21	0.62
102-70	53	R^2				
		AIC_c	107.1	109.2	111.9	111.8
		AIC_c weights	0.65	0.23	0.06	0.06
Combined	581	R^2	0.93	0.93	0.93	0.93
		AIC_c	1,467.4	1,473.7	1,474.2	1,505.1
		AIC_c weights	0.93	0.04	0.03	0.00

the lantern. Rotulae were physically cleaned of soft tissues, air dried, and taken to the laboratory for microscopic analysis.

In the laboratory, each rotula was broken in half along the short axis; both halves were charred over a low-temperature alcohol flame and observed in cross section (Robinson and MacIntyre 1997). Burning is required to observe rings. The rings are seen as alternate dark (maroon to black) and light (light gray or off-white) phases. One pair of rings, consisting of one dark and one light band, was putatively considered to represent 1 year of growth. For this study, dark rings were counted because rotulae that are burned excessively begin to turn to ash and produce white or off-white areas that may confuse ring counts.

Several conventions were adopted to standardize ring counts. If the first dark ring on a rotula was larger than 0.1 cm in diameter, it was assumed to represent more than 1 year of growth. A 0.1-cm-diameter threshold was chosen because the smallest urchins

sampled (1.0–1.5 cm in test diameter), which were assumed to be 1 year old, possessed rotulae that were greater than 0.1 cm wide and that lacked rings. Red sea urchins are known to have a test diameter of approximately 0.05 cm at settlement (Ebert et al. 1994). All urchins were collected in late July and August 2001. Based on (1) the latitudinal shift in spawning season from winter and spring south of Point Conception, California, to later in the summer and fall in more northerly areas (Ebert et al. 1994), (2) the observation of a fall-spawning peak in British Columbia (Bernard 1977), and (3) an estimated larval pelagic period of between 2 and 4 months (Strathmann 1978), our sampling occurred approximately 6 months after the probable peak urchin settlement period for southeast Alaska. Because water temperatures and the availability of kelp forage does not reach a maximum until at least early August (ADFG unpublished data), it is unlikely that 6 months is long enough for over a centimeter of growth to occur under less-than-ideal

growing conditions. Therefore, these small urchins are presumed to be at least 1 year old, and 0.1 cm seems a reasonable maximum width for a first year's growth ring in a rotula.

For all urchins, the edge of the rotula was counted as the current year's growth. Because urchins were collected during the peak growing season (approximately 6 months after peak settlement), we assumed that each individual had experienced half of their growth for the year.

Modeling growth.—As Ebert and Russell (1993) remarked, an ideal growth model for the red sea urchin has yet to be developed. We therefore fitted and compared four models that have been used for urchin growth: Brody–Bertalanffy (Fabens 1965; Ebert and Russell 1992); Richards (1959); Jolicoeur (1985; Ebert and Russell 1993); and Tanaka (1982, 1988; Ebert et al. 1999). For each site, a scatter plot of rotula ring number versus test diameter for all collected urchins was constructed. Each function was fitted by use of nonlinear regression (JMP version 5.1 for Macintosh, SAS Institute, Cary, North Carolina).

The Brody–Bertalanffy model is probably the most commonly used growth model in fisheries and conservation biology. This model is described as:

$$S_t = S_\infty(1 - be^{-Kt}) \quad (1)$$

where S_t is urchin test diameter at age t , S_∞ defines the maximum urchin test diameter, e is the base of natural logarithms, and K is the Brody growth parameter; S_∞ and K are fitted parameters. The parameter b was not fitted and was assumed to equal 1 because it is calculated as $(S_\infty - S_{\text{settlement}})/S_\infty$ and because the settlement size of red sea urchins is very small (~ 0.05 cm), much less than S_∞ (Rogers-Bennett et al. 2003). In the Brody–Bertalanffy model, the growth rate attains a maximum at very small sizes and declines linearly with age.

The Richards function is an extension of the Brody–Bertalanffy model and has an additional shape parameter n , which allows for an inflection in the curve of S versus t as follows:

$$S_t = S_\infty(1 - be^{-Kt})^{-n} \quad (2)$$

Otherwise, the parameters are the same as the Brody–Bertalanffy model. See Rogers-Bennett et al. (2003) for a discussion of the effects of each parameter on the shape of the growth curve.

The Jolicoeur function is:

$$S_t = S_\infty(1 - bt^{-K})^{-1} \quad (3)$$

where S_∞ , b , and K are fitted parameters. This function

has been used to model urchin growth previously (Ebert and Russell 1993).

The Tanaka equation is:

$$S_t = \frac{1}{\sqrt{f}} \log_e |2f(T - c) + 2\sqrt{f^2(T - c)^2 + fa}| + d \quad (4)$$

where S is urchin size (cm); f , d , a , and c are fitted parameters; and T is age at time t (Tanaka 1982). The vertical lines inside the logarithm indicate an absolute value. For a discussion of the effect of each parameter on the growth curve's shape, see Ebert et al. (1999). A valuable feature of the Tanaka function is that fitted curves lack an asymptote, implying the potential for an urchin to grow throughout its life.

The Akaike information criterion (AIC) (Burnham and Anderson 2002) was used to identify the most parsimonious growth model for each site. Because having more parameters in a function will almost always allow a closer fit to the data, AIC discounts the increase in goodness of fit by the additional number of parameters to identify the preferred model given the data. We used the corrected index (AIC_c) because it provides more accurate results when sample sizes are small (Morris and Doak 2003). The AIC_c is expressed as:

$$AIC_c = \log_e |L| + \frac{2pq}{q - p - 1} \quad (5)$$

where L is the maximum likelihood estimator of the best parameter set for the growth equations, q is number of data points, and p is the number of parameters. For the likelihood calculations, normally distributed deviations were assumed.

From AIC_c , Akaike weights (range = 0–1) were calculated. Akaike weights indicate the probability that the model is the best among the set of candidate models considered. For example, a model with an Akaike weight of 0.60 indicates that there is a 60% chance that it is the best model given the set of competing models.

Estimates of age at fishery entry were calculated for each model at each site to explore the effect of model choice on this parameter. Although Alaska has no minimum harvest size limit, port sampling indicates that urchins are not harvested until they reach at least 8.0 cm in test diameter (ADFG, unpublished data). We calculated time to fishery entry (8.0 cm in test diameter) for each model at each site.

Residual analyses.—Once the best growth function was selected, data from the three PIT-tagging sites (Blank Island, Bob's Bay, and Diver Point) were used to test the hypothesis that the ring counts represented yearly increments. We began by assuming that ring

counts represented years. The rotula ring count therefore provided each urchin's age in 2001; together with the test diameter for 2001, the ring count positioned each urchin relative to the fitted growth curve for 2001. Sizes of PIT-tagged urchins that were recaptured multiple times were compared with the best-fit growth curve fitted to all non-PIT-tagged urchins. For example, a single PIT-tagged urchin with a ring count of 6.5 in 2001 was assumed to have ring counts of 5.5 in 2000 and 4.5 in 1999 and known test diameters of 8.5 cm in 2001, 7.6 cm in 2000, and 6.5 cm in 1999. Data on size at ring number were then compared with predicted size-at-age data from the growth models to produce a residual for 1999, 2000, and 2001.

Residual plots of observed (PIT tag recapture) minus predicted (growth model) size were constructed for each year for each size of PIT-tagged urchins. If the growth model represents average growth for the population, the fitted growth curve should be mirrored by each urchin's growth, and residual distributions for PIT-tagged individuals from 2000, 1999, and previous years should not shift up or down over time. Residual distributions that tend to move away from the initial (2001) residual distribution would indicate that the growth model did not faithfully represent the population, indicating that annual ring formation is not a valid assumption. Specifically, residual distributions that became more positive over time would indicate that actual growth is slower than predicted by the growth model, while residuals that shifted negatively would indicate that growth is faster than the model predicts.

We used repeated-measures analysis of variance (ANOVA) to compare the trend of residuals at the three PIT-tagging sites over the period 1999–2001. Repeated-measures ANOVA is appropriate because individuals were recaptured in multiple years, and therefore the residual for an individual cannot be considered independent between years. Trends in residuals were analyzed with each site treated independently and with pooled values using site as a blocking factor. Both analyses produced nearly identical results; thus, for simplicity only the analysis of sites treated independently are presented here. Repeated-measures ANOVA required the omission of individuals that lacked size data for any of the 3 years of interest (1999, 2000, and 2001). This reduced our sample size because several tagged individuals were not recaptured every year. Because we wanted to include those urchins with missing data to increase our sample size and to look for longer trends (i.e., 1997–2001 instead of 1999–2001), we visually checked the residual trends of individual urchins for consistent negative or positive trends. Finding no obvious pattern in individual residual

trends, we used linear regression with this expanded data set to compare the mean trend of residuals at each site from 1997 to 2001.

Aristotle's lantern index.—Aristotle's lantern demi-pyramids were also collected from each urchin sampled for rotulae at every site to test for a relationship between growth and food availability. The ratio of demi-pyramid length to test diameter has been shown to be an indicator of food availability in urchins (Ebert 1980, 1996; Black et al. 1982, 1984; Edwards and Ebert 1991). Relatively longer pyramids indicate lower food availability. We measured demi-pyramid lengths in each urchin and used linear regression to relate demi-pyramid length and test diameter (Ebert 1980). After both variables were log transformed, we followed Ebert et al. (1999) in standardizing the regression intercept to the test diameter of the red sea urchin at settlement (0.05 cm; Ebert et al. 1994) at each site as follows:

$$\log_e L = \log_e C + \beta[\log_e D - \log_e(0.05)] \quad (6)$$

where L is the demi-pyramid length, C is the initial lantern length shortly after settlement, and D is the test diameter. This approach is justified because the Aristotle's lantern complex is formed shortly after settlement, and size should be similar for all urchins. Subsequently, we calculated an unweighted mean intercept for all sites ($\log_e C$) and used this as a fixed intercept to fit equation (6) again, producing a slope β at each site.

This allowed us to compare estimates of β between sites. Because larger β -values should indicate poorer food conditions (Ebert et al. 1999), we estimated the pairwise correlations between β and the time to fishery entry at all sites.

Results

Age Determination with Rotula Rings

Rotula ring counts ranged from 0.5 to 31.5, and urchin test diameters ranged from 1.3 to 16.0 cm. Larger individuals tended to have more rings (Figure 2).

Growth functions were fit to data from all sites by assuming that the number of rings was a good proxy for urchin age. The R^2 -values for all models and sites were high (all sites > 0.88 ; Table 1). Visually, growth from PIT-tagged individuals closely matched the predicted growth (Figure 3). Comparison of the residual sums of squares and AIC_c weights for the four fitted functions at each site suggested that different growth models were preferred at different sites, but often several models fitted the data equally well (Table 1). However, when all sites were combined to fit an average growth curve, the Tanaka function was

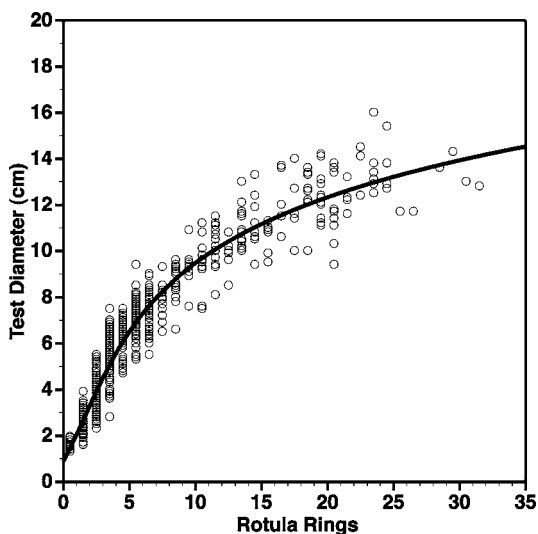


FIGURE 2.—The relationship between the number of rotula rings and test diameter for red sea urchins collected in southeast Alaska. Each point represents an individual urchin ($n = 581$). The line is the Tanaka function (fitted parameters: $f = 0.731$, $d = 6.116$, $a = 0.630$, $c = 1.749$).

approximately 75% likely (Table 1; Figure 2). Because of this uncertainty in model selection, we conducted residual analyses using the Tanaka, Jolicoeur, and Richards functions. Each function produced similar results, so we present only the analysis based on the function favored by AIC_c at each site.

Repeated-measures ANOVA tested for trends in residuals of individual size at each site compared over 3 years (1999–2001). Tests for sphericity indicated homogeneity of treatment difference variances, allowing for examination with an unadjusted, one-way repeated-measures ANOVA (Table 2; Stevens 1996). Bob's Bay and Diver Point showed no significant trend in residuals over time, but Blank Island exhibited a significant trend ($P = 0.021$; Table 2).

Linear regression similarly suggested no trend in the residuals for 1997–2001 at Bob's Bay, and 1999–2001 at Diver Point (Table 2; Figure 4). However, Blank Island again showed a marginally significant trend from 1997 to 2001 (slope = 0.216, $P = 0.021$, Figure 4A) with residuals in 1997 tending to be greater than those in 2001 indicating that the growth model predicted greater growth than was evinced by the PIT-tagged urchins (Figure 4). The two metrics suggest ring counts approximate years at Bob's Bay and Diver Point, but indicate a significant trend in residuals at Blank Island.

Urchins containing PIT tags had ring counts between 3 and 21, but the vast majority had counts between 3 and 15. Because the number of rings increased with urchin size, few data were available for the largest

urchins. The 1.15-cm-long PIT tags are too large to use on urchins smaller than about 2.5 cm in test diameter (ADFG, unpublished data). Since red sea urchins are predicted to take 1–3 years to reach this size, urchins with three or more years of recapture data (as in this study) should have a minimum of four rings. The single urchin with three rings in 2001 was tagged at a size of 2.8 cm in 1999 at Diver Point (data not shown). Its residuals increased from 2001 to 1999 (0.88 cm for 2001, 1.01 cm for 2000, and 1.51 cm for 1999) indicating that the urchin grew less than expected. The most likely explanation for this pattern is that the urchin was judged to be 3 years old based on its rotula rings, when in fact it was 4 years old.

Only four PIT-tagged urchins had more than 15 rings, and we therefore lack the data to comment on the reliability of ring counts for determining age over the entire spectrum of urchin ages. Thus, rings appear to reasonably estimate age in years at the three PIT-tag sites, but our data can only support this conclusion for ring counts of 2–15.

Time to fishery entry did not vary substantially with the growth model used (range = 0.1–0.5 years; Table 3). Differences among growth models were dwarfed by variation among sites. Using the Tanaka function, fishery entry times ranged from 5.8 (Blank Island) to 9.7 (site 102–50) years, a difference of 3.9 years (Table 3). The combined Tanaka function that was fitted based on all data from all sites predicted a time to fishery entry of 7.1 years.

Aristotle's Lantern Index

The slope β of regression between test diameter and demi-pyramid length varied substantially among sites (Table 4). Slopes were generated using a common intercept ($\log_e C$) of -3.50 , which was the best estimate of demi-pyramid length immediately after settlement (equation 6; Table 4). This results in a lantern length of 0.030 cm in a postsettlement urchin of 0.05-cm test diameter, which is slightly larger than the 0.023 cm calculated by Ebert et al. (1999). The correlation between β and time to fishery entry as predicted by the Tanaka function was positive and highly significant (pairwise $r = 0.873$, $P = 0.0046$; Figure 5), suggesting that areas with relatively larger demi-pyramids (therefore implied lower food availability) had longer times to fishery entry. Correlations using time to fishery entry as calculated by the Richards, Jolicoeur, and Brody–Bertalanffy functions all showed similar positive and significant relationships.

Discussion

All four growth functions provided good fits for the relationship between rotula ring number and test

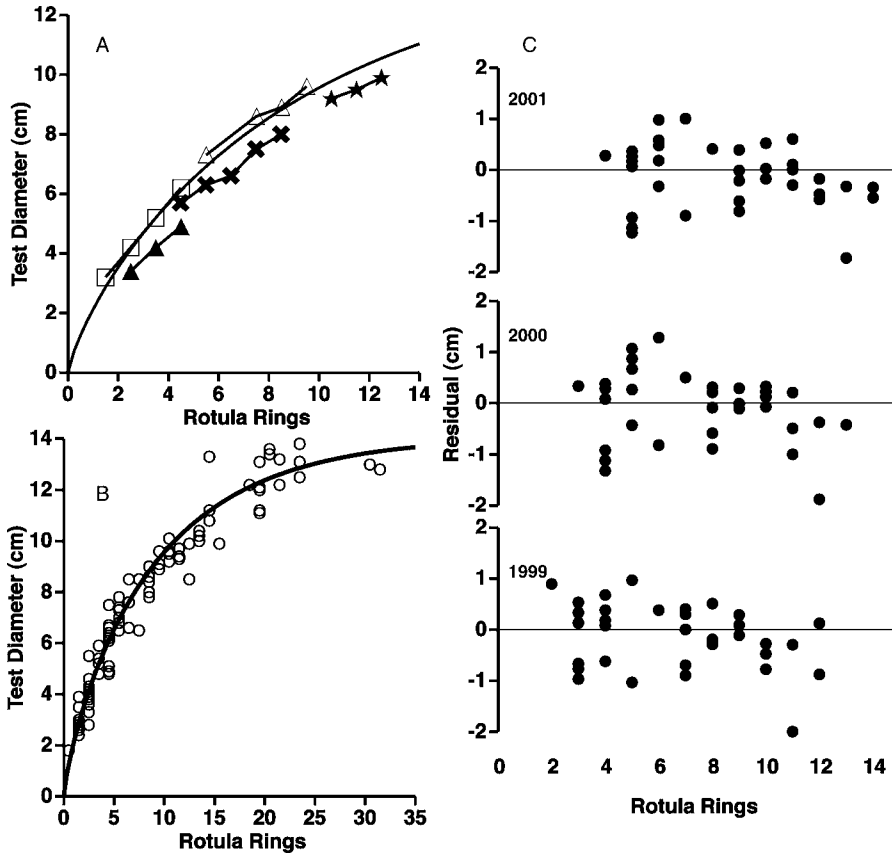


FIGURE 3.—(A) Growth increments of five PIT-tagged red sea urchins from Bob’s Bay, Alaska, overlaid with the fitted Tanaka function. The rightmost point of each data series corresponds to the size and rotula ring count for 2001. (B) Relation between ring count and test diameter for red sea urchins at PIT-tagging sites is fitted with the Richards model best-fit line for Bob’s Bay ($R^2 = 0.96$). (C) Residual values (PIT tag–Richards relation) for rotula ring counts of urchins collected at Bob’s Bay, 2001–1999, are depicted. Residuals do not shift over time.

TABLE 2.—Summary of results for tests of trends in PIT-tagged Alaskan red sea urchin residuals: tests for the assumptions of sphericity; repeated-measures ANOVA of residual trends over 3 years (1999–2001) (univariate F statistic is shown); and linear regression of residual trends over 5 years (1997–2001) at Blank Island and Bob’s Bay and 3 years (1999–2001) at Diver Point. See text for details.

Test or parameter	Blank Island	Bob’s Bay	Diver Point
Test for sphericity			
Mauchly criterion	0.77	0.83	0.76
χ^2	2.37	5.88	4.06
df	2	2	2
P	0.306	0.053	0.131
Repeated-measures ANOVA			
df	2, 20	2, 66	2, 32
F	4.71	1.13	2.03
P	0.021	0.328	0.148
Linear regression			
df	1, 53	1, 120	1, 55
F	5.66	0.32	0.18
P	0.021	0.573	0.675

diameter (Table 1). No growth model was favored across all sites. Comparisons of AIC_c within a site identified different preferred functions at the different sites, and models often had approximately equal likelihood (Table 1). The Tanaka, Jolicoeur, and Brody–Bertalanffy models were preferred at two sites each and the Richards function was preferred at one site (Table 1). This result differs substantially from previous studies of urchin growth that have found preferences for certain growth functions (e.g., Ebert and Russell 1993; Rogers–Bennett et al. 2003; but see Lamare and Mladenov 2000). This difference may be attributed to the different methodologies used to determine the growth curves. Virtually all other studies have relied primarily on tetracycline tagging over 1 year to produce estimates of growth and then have extrapolated growth from the observed year to the lifetime of the urchin (but see Lamare and Mladenov

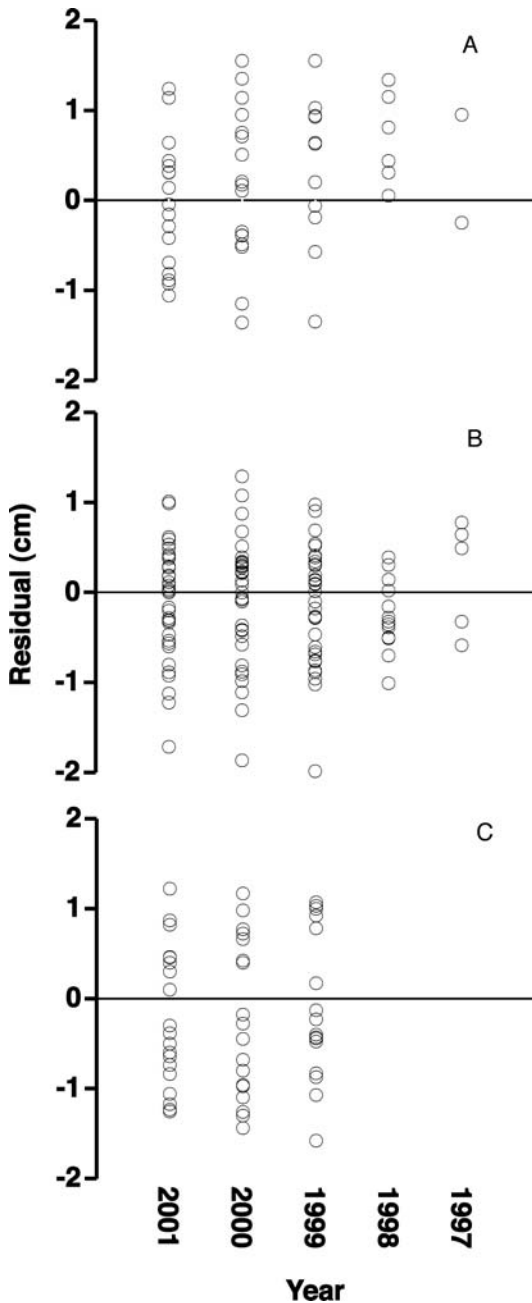


FIGURE 4.—Linear regression of residual size and year for red sea urchins collected at three sites in southeast Alaska: (A) Blank Island ($P = 0.021$, slope = $0.216 \times \text{year}$), (B) Bob's Bay ($P = 0.573$), and (C) Diver Point ($P = 0.675$).

2000). Small differences in fitted growth over 1 year stemming from characteristics of the growth models—the linearly declining growth rate with age of the Brody–Bertalanffy function or the initial lag and

asymptotic growth of the Tanaka function, for example—are exaggerated when extrapolated and therefore generate large discrepancies in estimates of age at fishery entry (Rogers-Bennett et al. 2003). We fit growth curves to size-at-age data, which avoids the issues of extrapolating individual years, and as a result the different growth curves predict very similar times to fishery entry at individual sites (Table 3). As might be expected from a suite of models that produce very similar curves, models with more parameters tend to be favored in situations with more data. Thus, the four-parameter Tanaka model is favored at Blank Island and when all sites are combined. Based on AIC_c , models with fewer parameters are preferred at sites with fewer data points (Table 1).

Size-at-age data are only useful if urchins can be accurately aged. We tested the accuracy of our aging technique by comparing curves derived from our size-at-age data with growth from individual PIT-tagged urchins and examining the trends in the residuals. At two sites, residuals showed no trend over time, suggesting that our aging technique is accurate (Table 2; Figures 3, 5). At the third site, Blank Island, there was a significant relationship, indicating that the fitted growth curve overestimated actual growth. This could happen for three main reasons: (1) statistical chance wherein the small number of PIT-tagged individuals at Blank Island in 1997 and 1998 (Figure 3; Table 3) combined with random fluctuations in sizes to produce a marginally significant trend (Table 2); (2) no ring was formed during some years, and therefore age was underestimated while growth rate was overestimated; (3) growth estimates from age and size data necessarily produce average growth curves over the age of each urchin, thus smoothing yearly variation in growth. As a result, several consecutive years of poor growth would yield the same pattern as an errant growth curve. Given the documented difficulty in urchin age determination (Breen and Adkins 1976; Russell and Meredith 2000; but see Brey et al. 1995), the second possibility must be considered the most likely, but the third option can be examined with more annual growth data from these sites (ADFG, unpublished data).

Linear regression suggested that growth at Blank Island was overestimated by 0.216 cm/year, averaged across all PIT-tagged urchins. This number is within the range of measurement error for urchin test diameters (Smith et al. 1998) but results in growth overestimation by more than 1 cm over a period of 5 years, which could have a profound effect on estimates of time to fishery entry.

The nonsignificant residual trends for Bob's Bay and Diver Point do not indicate that error is absent in the growth curve generated by the aging technique but

TABLE 3.—Time (years) to fishery entry for red sea urchins (80 mm in test diameter) at eight sites in southeast Alaska as calculated by four growth functions.

Site	Tanaka	Jolicoeur	Richards	Brody-Bertalanffy
Blank Island	5.8	6.0	6.1	5.9
Bob's Bay	7.3	7.4	7.5	7.1
Diver Point	7.0	7.1	7.0	6.4
101-29N	6.7	6.9	6.9	6.7
101-29S	7.5	7.4	7.5	7.1
102-20	7.4	7.5	7.5	7.6
102-50	9.7	9.7	9.5	9.6
102-70	6.9	6.9	7.0	6.9
Combined	7.1	7.2	7.2	6.9

rather than any error is low enough to avoid detection (i.e., is sufficiently less than individual growth variation and measurement error). It is always possible that with more data points and longer time series, deviations of growth would have been detected, but any trends present were certainly very weak.

Our results suggest that at Blank Island, urchins may form rings at a rate different from 1 ring/year; this result is analogous to the findings of Russell and Meredith (2000). In Maine, they tagged *S. droebachiensis* with tetracycline in tide pools, collected all urchins after a year, and examined the rotulae to see if a complete cycle of rings (one light and one dark) occurred after the tetracycline mark. They found that although some urchins showed one full cycle, small urchins tended to exhibit more than one cycle whereas large urchins tended to produce less than one. Russell and Meredith (2000) concluded that ring patterns were not sufficiently consistent to justify their use in determining age. Given that red urchins are thought to have a maximum age of over 100 years (Ebert et al. 1999; Ebert and Southon 2003), our failure to observe large urchins with more than 35 rings suggests either that old urchins are relatively rare and did not occur in our sample or that rings become more erratically deposited with increased age, resulting in age underestimation (Brey et al. 1995). The compres-

sion of many rings into a narrow region along the outer edge of the rotula was frequently observed in large urchins and increased the difficulty of detecting individual rings (A.O.S., personal observation).

Accordingly, the major difference between our growth curves and previous work is the shape of the curve for old urchins. Researchers agree that at large sizes, urchins grow slowly. Modeling growth with the Tanaka function, Ebert and Russell (1993) and Ebert et al. (1999) suggested that the annual rate of increase was much less than 0.1 cm/year in California. In this study, we predict that average growth for very large urchins could be as much as 0.12 cm/year. Either way, measurement error and irregularities in the test diameters of large urchins could obscure observation of actual growth and hinder comparisons of PIT tag derived growth and predicted growth. This problem does not arise to the same extent in small urchins because of their greater growth rates and a smaller potential for measurement error. Because ring formation cannot be verified for large urchins, a different technique is needed to determine maximum age (Ebert and Southon 2003). Understanding of the maximum and average longevity of adult urchins and the relation between longevity or reproductive output and the documented high temporal and spatial variability in juvenile recruitment for this genus remains an issue of practical importance for fisheries managers and marine ecologists (e.g., Tegner and Dayton 1977; Schroeter et al. 1996; Morgan et al. 2000).

Our estimates of age at fishery entry are very similar to previously published estimates on this species (e.g., Ebert et al. 1999; Rogers-Bennett et al. 2003). Using a fishery entry size of 8.9 cm in northern California, Rogers-Bennett et al. (2003) found an average time to fishery entry of 7.2 years, while Ebert et al. (1999) documented an age to 8.0 cm of slightly more than 6 years using a combination of data from 18 sites from southern California to southeastern Alaska. Both estimates are comparable to our estimate of 7.1 years to fishery entry using the best-fit Tanaka function for

TABLE 4.—Results of regressions between demi-pyramid length and test diameter (Aristotle's lantern index; equation 6) in Alaskan red sea urchins. Underlined values are for samples whose 95% confidence intervals (CIs) lie outside of the common intercept ($\log_e C$) of -3.501 . Regression slopes (β , and CIs were determined based on the common value for $\log_e C$).

Site	<i>n</i>	$\log_e C$	95% CI	β	95% CI
Blank Island	119	-3.264	-3.159 to -3.369	0.839	0.837 to 0.841
Bob's Bay	91	-3.562	-3.406 to -3.717	0.845	0.844 to 0.847
Diver Point	73	-3.778	-3.588 to -3.967	0.846	0.844 to 0.848
101-29N	75	-3.247	-3.091 to -3.402	0.849	0.847 to 0.851
101-29S	54	-3.556	-3.298 to -3.814	0.849	0.847 to 0.851
102-20	57	-3.687	-3.294 to -4.079	0.854	0.851 to 0.858
102-50	51	-3.571	-3.397 to -3.746	0.859	0.857 to 0.861
102-70	53	-3.345	-3.112 to -3.578	0.847	0.845 to 0.849

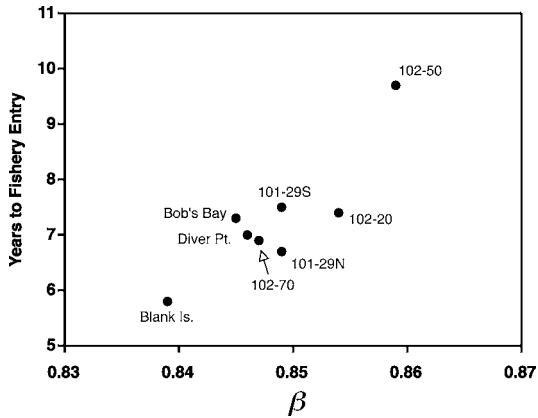


FIGURE 5.—Relationship between red sea urchin age (years) at fishery entry in southeast Alaska and the slope of the Aristotle's lantern-test diameter regression (β). Pairwise correlation was highly significant ($r = 0.873$, $P = 0.0046$).

the combined data from all sites (Table 4). The strong correlation between age at fishery entry and demi-pyramid length (a proxy for food availability) further supports the estimated growth curves as reasonable and responsive to environmental conditions. Use of the demi-pyramid index may ultimately potentially provide an easy method for assessing habitat quality for urchins, but first it must be compared with growth rates at more sites over a larger geographic range. An intriguing possibility for future work is the development of a technique for producing growth curves using tagging or aging studies for small to medium sizes and radiocarbon aging for larger urchins.

Before ring counts can be used widely in determining growth, rotula ring counts must be shown to be reliable for age estimation of urchins in a variety of growth environments, including those where growth is slow or erratic. It is possible that all sites sampled in this study were conducive to high growth. All were on rocky substrate, had available macroalgal species for forage, and occurred in areas with moderate to high water flow. The three sites for which we compared the rotula method with PIT tag data were classified as moderate- to high-growth sites based on the demi-pyramid index (Table 3; Figure 5).

Rotula ring counts appeared to approximate age well at two sites and estimated age with fairly small error at a third. Given the clear differences in urchin growth documented by Ebert et al. (1999) and Lamare and Mladenov (2000), we argue that a technique allowing relatively fast and inexpensive assessment of growth over many sites and that involves some error may sometimes be preferable to the expensive, time-consuming, accurate documentation of growth at one

or two sites by use of tetracycline or PIT tags. With further study of its accuracy at other sites, rotula ring counts may allow wide investigation of growth and age structure and could be particularly helpful in understanding spatial patterns in growth.

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