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Estimating survival in echinoid populations

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Abstract

Estimating survival rate is a basic part of population studies. Generally it is assumed that populations being studied are both stable and stationary. This probably is seldom the case although as a long-term average populations may persist at a mean density. Estimating survival in short-term studies may fail to capture average rates. A long-term study of the purple sea urchin *Strongylocentrotus purpuratus* at Sunset Bay, OR, USA from 1964–2009 is used to demonstrate methods for estimating survival based on the coefficient of variation of size distributions, the fraction of new recruits in a population, means of size data coupled with estimates of growth, and a method that uses rates of flow through size categories. A short-term study of just a few years may by chance sample when an unusual recruitment event drives a population far from stationary structure and so distorts the estimate of mean survival. The best solution, as shown for *S. purpuratus,* is a long time series but in advance it cannot be determined how long this should be. If a study of three years shows no substantial change in population size structure it may be reasonable to accept estimates of survival.

key words: survival, mortality, coefficient of variation, Tanaka growth function, Gamma model, Van Sickle's method, *Strongylocentrotus purpuratus*

Introduction

Estimating survival is a vital part of understanding the present and future development of a population. Different species present different problems in obtaining estimates and here we focus on sea urchins in natural populations. The easiest data to gather are individual size measurements usually diameters determined using calipers. Dissection of size-frequency distributions into components has been a focus of echinoderm researches for decades (e.g. Crozier 1920; Moore 1935).

For many organisms, size data are easy to gather and so distributions are common in the literature. In many cases, they provide the only clues to the underlying dynamics of growth, survival, and recruitment and so it is understandable that an extensive literature exists concerning their analysis. One general research approach has focused on the separation of size distributions into components (e.g. Harding 1949; Cassie 1954; Bhattacharya 1967; Macdonald & Pitcher 1979). Size data have been used to estimate mortality with known growth parameters (e.g. Beverton & Holt 1956; Van Sickle 1977; Sainsbury 1982) or both growth and mortality parameters have been estimated (e.g. Green 1970; Ebert 1973; Pauly 1987; Fournier *et al.* 1990; Gayanilo *et al.* 2005). A third approach has focused on modeling size distributions to gain insight into the underlying processes that give rise to observed distributions (e.g. Craig & Oertel 1966; Barry & Tegner 1990; Hartnoll & Bryant 1990; Ebert *et al.* 1993). Simulations of size distributions are metaphors of the dynamic processes that give rise to actual size distributions. Methods to estimate annual survival or mortality all have assumptions that may not be made explicit when size data are used. A consequence is that estimates may misjudge actual loss rates.

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The major assumption is that the population being studied is stationary. Sometimes this is expressed in two steps: stable and stationary or stable with stationary structure. For organisms with seasonal reproduction, one can expand the definition to seasonally stable and stationary. Seasonally stable means that if you sample at the same time of year there will be a fixed fraction of individuals in each age or size class; the population, however, may be growing or declining. A stationary population is not only stable but also is not growing or declining. This assumption is important for estimating survival.

We present an analysis of the purple sea urchin *Strongylocentrotus purpuratus*. Although this species occurs in the subtidal, all data here are intertidal and from the exposed outer coast. A major portion of data presented here are from Sunset Bay, Oregon, USA, parts of which have appeared in various analyses dating back to the 1960s (Ebert 1968). Data have been selected from a site referred to as the "Surfgrass Area", which was called the "Eelgrass Area" in, for example Ebert (1968). Size data gathered in 1985 from the Surfgrass Area were used in Ebert & Russell (1988) and data from 1985 and 1987 in Ebert (2010) but otherwise data from this site have not been presented previously. Some data from other sites within Sunset Bay have been analyzed elsewhere (Ebert 1975, 1983, 2013a). All raw data are in Ebert *et al.* (2018). The point of the analysis of size and growth data for *S. purpuratus* is to call attention to the problem in assuming that the population being studied has stationary structure.

Methods

Some samples between the US-Mexico border and Point Conception in southern California were gathered on gravel/cobble but all others were on rock substrate in tide pools or channels where sea urchins are sedentary. Collection was by hand and an attempt was made to find all sea urchins. The size limit where individuals can be found in proportion to their actual abundance is about 0.5cm and all those collected were measured to avoid bias in measuring just a subsample.

Four general approaches for describing survival are presented: (1) shape of size-frequency distributions; (2) fraction of individuals ≤ age 1; (3) growth and mean size; and (4) growth used to determine flow through size classes.

1. Shape of size-frequency distributions

The shapes of a size-frequency distributions can be used to compare samples but without obtaining explicit estimates of survival. Samples drawn from a population that has size measurements spanning the range of possible sizes from smallest to largest can be judged to have higher recruitment and lower survival compared with samples where there are large individuals concentrated at a narrower range. The coefficient of variation of size, standard deviation divided by the mean, is a measure of the spread and so is a simple metric for sample comparisons (e.g. Ebert & Russell 1988). No estimates of either recruitment or mortality can be made but because the calculation is simple, large numbers of samples can be arranged to show general patterns. Application of the coefficient of variation is shown using data from a broad survey from Mexico to Canada conducted in the 1980s (Ebert 2010) and again in 2007–2009 (data in Ebert *et al.* 2018).

2. Fraction of individuals ≤ Age 1

The fraction of a population that is Age ≤1year old can be used to estimate survival (Caughley 1967). The idea is very simple: if a population is seasonally stationary, that is, with a fixed number of individuals in each size class when sampled at the same time of year, the fraction of new individuals must be equal to the fraction dying. This method occasionally has been used in sea urchin studies (e.g. Ebert 1982; Uthicke *et al.* 2016) but is very sensitive to annual variation in settlement. The Surfgrass Area was visited a total of 20 times from 1964 to 2009 and components of size distributions separated using Mixdist in R (Macdonald & Du 2018) to obtain estimates of the fraction ≤ Age 1, or annual mortality, M yr^{-1}. Annual survival is exp(-M).

3. Growth and mean size

Growth parameters from tagged individuals can be used with mean size in a sample (e.g. Ebert 2013b) to estimate M, the instantaneous mortality coefficient. The mean size of individuals, $\overline{D_T}$, in a sample is

$$\overline{D_T} = \left(1 - e^{-M}\right) \sum_{t=0}^{\omega} e^{-Mt} F(\Phi, t), \tag{1}$$

where F(Φ,t) is some growth function with F parameters and time, t. With parameters estimated from tagging, the only unknown is M, instantaneous mortality. The examples given here use the Tanaka and Gamma models (Tanaka 1982; Ellers & Johnson 2009, Ebert 2013b) and so parameters F, are f, d, and a for Tanaka and κ, λ, and α for the Gamma model. Unlike the Tanaka function, the Gamma model does not include an explicit time term, t, and so growth was modeled iteratively. Obtaining an estimate of M was by Newton's Method (Ebert 2013b) with programs written in BASIC (S1).

To measure growth, sea urchins were tagged in pools on a bench called the Surfgrass Area (43° 20' 02.3”N; 124° 22' 38.7”W). On 15 May, 2007, tagging was done in two pools (pool #1 N = 168 and pools #2 N = 43) using the chemical calcein (Diehl & Ellingboe 1956; Lamare & Mladenov 2000; Ellers & Johnson 2009) and on 6 May, 2008, (pool #3 N = 121), tagging was with tetracycline (Bevelander *et al.* 1960; Weber & Ridgway 1962; Kobayashi & Taki 1969; Ebert 1982). Those tagged in 2007 were collected on 6 May, 2008, and those tagged in 2008 were collected on 9 May, 2009 so Δt = 1 year. In pool #1 in 2008, 155 were collected and of these 103 showed a calcein mark. In pool #2, 36 were collected and 26 shown a mark. In 2009, 107 were collected in pool #3 and of these 92 showed a tetracycline mark.

4. Growth used to determine flow through size classes

Growth determines the flow of individuals through size categories of a size distribution. The difference between transfer from one size class to the next is the loss rate (Van Sickle 1977).

$$M_i = \frac{1}{W_i N_i}\left(\Delta D_i N_i - \Delta D_{i+1} N_{i+1}\right) \tag{2}$$

Mi = instantaneous mortality rate.

Wi = width of the interval in the size distribution being analyzed e.g. 0.5, 1.0cm etc.

ΔDi = growth rate at the lower size of the size interval using a growth model with ΔDi as a function of Di at time of tagging.

Ni = number at lower size of the size interval.

Pi = annual survival, e-Mi

Application of Eq. 2 used the sum of all 20 size distributions from the Surfgrass Area (total N = 4097) and broke the data into size categories with a width, Wi, of 0.5 centimeters. Values of ΔD used Tanaka parameters.

Results

1. Shape of size-frequency distributions

The use of the coefficient of variation of size at sites from Mexico to Canada shows a pattern (Fig. 1) present at both time periods. Larger values of the coefficient, greater spread of the size data, indicate some combination of high recruitment and mortality. The largest CV values were found in Central California generally bounded by Cape Mendocino in the north and Point Conception in the south. Within this central region there was substantial spread of CV values, which may represent local effects of recruitment and mortality as well as annual variation. There also is a hint of a slight northward shift of the distribution of CV values from latitude 37.8° in 1985–87 to 38.3° in 2007–09 ($F_{1,137}=3.123$, $P=0.079$), which may or may not have biological significance. The overall pattern of recruitment and mortality across the entire range that was sampled in 1985–87 was also present 20 years later. The mechanisms causing this pattern are uncertain.

2. Fraction of individuals ≤ Age 1

The long time series of size data gathered at the Surfgrass Area, (Fig. 2) shows variation in recruitment of individuals centered at approximately 1.5cm. The greatest number of small sea urchins was at the start of the study, 1964. The fraction of individuals Age ≤1 year shows that in most years there were very few and sometimes there were none. In such cases the estimate of annual survival is 1.0. The pattern from 1964 to 2009 (Table 1) shows that estimates of annual survival in general are >0.9 yr-1.

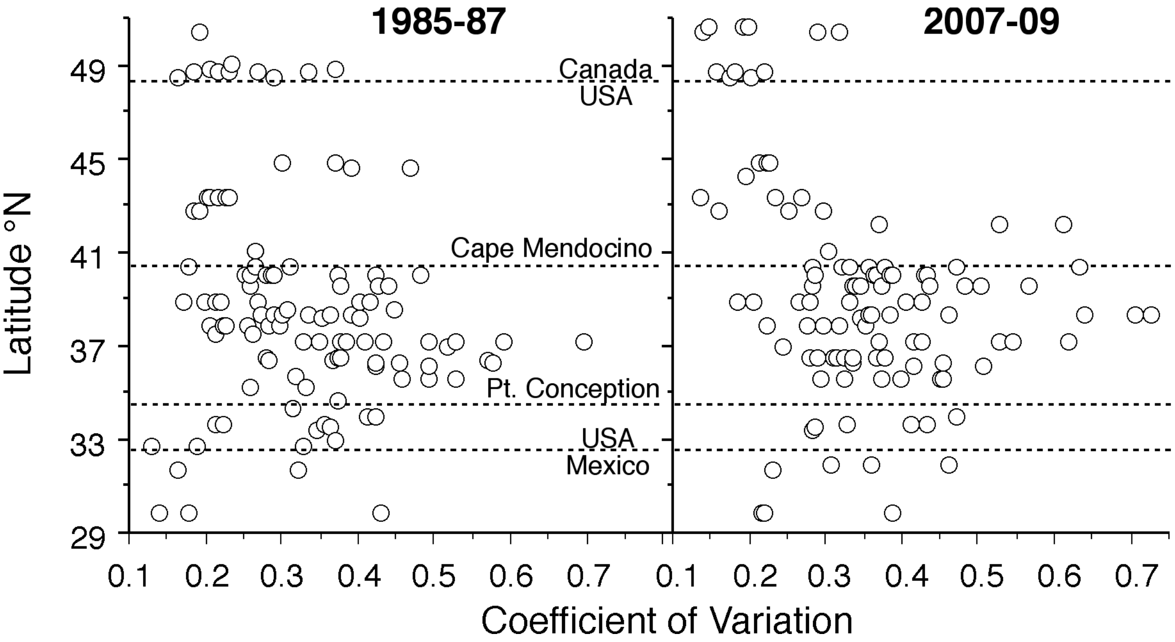

FIGURE 1. Changes in the coefficient of variation, CV (standard deviation/mean), of *Strongylocentrotus purpuratus* test diameter associated with latitude along the Pacific coast of North America at two time periods, 1985–87 and 2007–09; large values of the CV occur when the spread of sizes includes many small and medium individuals indicating frequent recruitment and high mortality compared with small CV values with concentration at large sizes indicating both low recruitment low mortality.

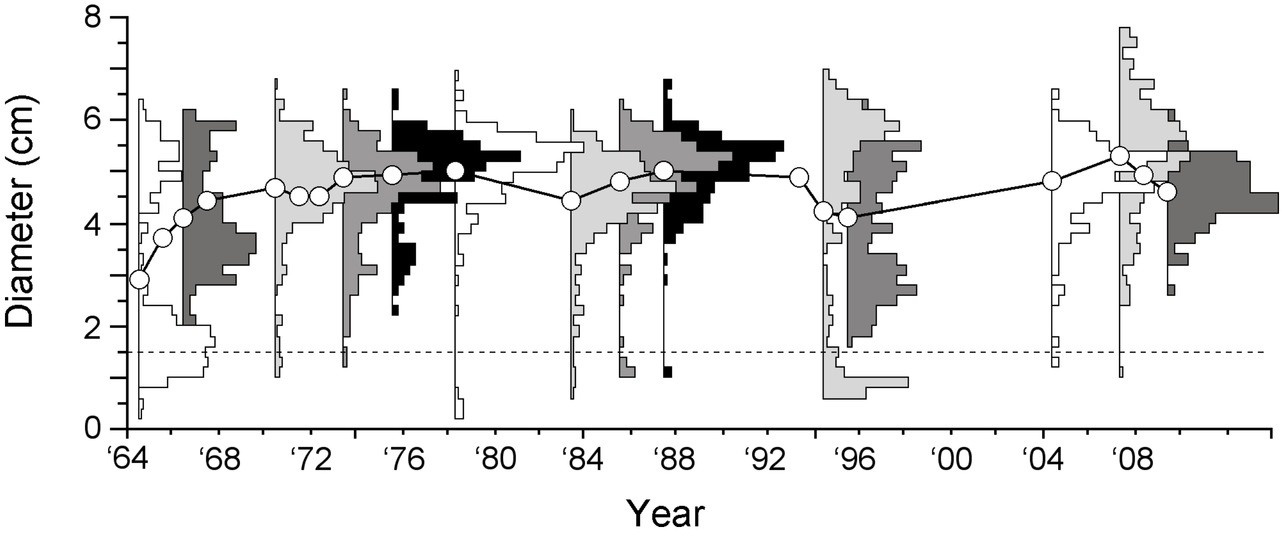

FIGURE 2. *Strongylocentrotus purpuratus* size-frequency distributions 1964–2009 Surfgrass Area, Sunset Bay, Oregon, USA; dashed line at 1.5cm is approximate size of individuals in summer that settled the previous year; not all distributions are plotted because of extensive overlap; sample sizes averaged 200 individuals; open circles are means of distributions, which varied across the 55 year period but without an increasing or decreasing trend.

TABLE 1. *Strongylocentrotus purpuratus*, Surfgrass Area, Sunset Bay, Oregon, USA; CV is the coefficient of variation of diameter; Fraction ≤1 yr is individuals approximately Age 1 year old; Survival(1) is 1- Fraction≤1 yr; Survival(2) is from Mean test diameter and Tanaka growth parameters (Eq. 1).

DATE	N	CV	FRACTION≤1YR	SURVIVAL(1) YR-1	MEAN	SURVIVAL(2) YR-1
9-AUG-64	311	0.610	0.450	0.550	2.885	0.683
9-JUL-65	238	0.458	0.069	0.931	3.717	0.833
6-JUL-66	112	0.252	0.009	0.991	4.102	0.881
8-JUL-67	221	0.193	0	1.000	4.428	0.913
23-JUN-70	310	0.198	0.042	0.958	4.687	0.934
24-JUN-71	224	0.268	0.085	0.915	4.536	0.923
12-JUN-72	199	0.213	0.009	0.991	4.522	0.921
28-JUN-73	148	0.142	0	1.000	4.884	0.947
26-JUN-75	127	0.164	0	1.000	4.919	0.949
24-MAY-78	189	0.196	0.026	0.974	5.021	0.955
12-JUN-83	291	0.212	0.020	0.980	4.448	0.915
5-JUN-85	203	0.198	0.039	0.961	4.826	0.944
16-MAY-87	192	0.145	0.022	0.978	5.026	0.955
5-JUN-93	152	0.186	0	1.000	4.891	0.948
24-JUN-94	244	0.490	0.151	0.849	4.227	0.894
16-JUN-95	189	0.313	0.000	1.000	4.087	0.880
5-JUN-04	116	0.174	0.017	0.984	4.819	0.943
15-MAY-07	212	0.217	0.009	0.991	5.320	0.969
6-MAY-08	312	0.212	0.009	0.991	4.920	0.949
9-MAY-09	107	0.130	0.000	1.000	4.619	0.929
MEAN	205	0.249	0.048	0.952	4.544	0.913

3. Growth and mean size

Results of tagged sea urchins with time between tagging and collection of one year show an inflection and very slow growth of large sea urchins (Fig. 3). There is just one data point with an original diameter measurement smaller than 2.0cm but with a good spread of data values from 2.5cm out to 7.0cm. Only a few individuals >7.0 centimeters were tagged and recaptured. Eight growth models were explored to select ones with the most support based on Akaike's Information Criterion (Burnham & Anderson 2002). Two models with most support were the Gamma model (Ellers & Johnson 2009) and the Tanaka function (Tanaka 1982; Ebert 2013b). Models with little support were Dose response, Gaussian, Bertalanffy, Gompertz, Richards, and Logistic.

Use of Equation 1 with Tanaka parameters and mean diameters provides estimates of annual survival for each sample (Table 1). Estimates based on growth and mean diameters, the fraction of individual sea urchins age ≤1 year, and the coefficient of variation, CV, are related (Fig. 4) and are sensitive to the violation of the assumption that *S. purpuratus* in the Surfgrass Area at Sunset Bay, Oregon, represents a stationary population.

4. Growth used to determine flow through size classes

The final method for estimating survival is based on an analysis proposed by Van Sickle (1977) and uses 0.5cm intervals of the combined size distribution from the Surfgrass Area(Fig. 5). To be biologically reasonable survival values must not exceed 1.0 yr-1. From interval 0.01–0.50 up to 2.01–2.50cm the estimates of survival are unreasonable for at least two reasons. First, the numbers of small individuals in samples from 1964–2009 are the ones that show the greatest year-to-year variability and so farthest away from stationary size structure. Second, the estimates of growth of these small sea urchins are in the extrapolated region (Fig. 3). Starting with the interval 2.51–3.00cm, estimates other then 3.51–4.00cm, do not exceed 1.00. There is an increasing trend in survival estimates starting at 4.51–5.00 out to 7.01–7.50cm. This trend is not due to the choice of growth model because both the Tanaka and Gamma are similar over the selected range. Also, the summed size distribution probably is reasonably stationary for the larger sizes. What remains are the growth data. The results from 2007–'09 may not be a good approximation of overall growth from 1964–2009 or reflect the small number of individual recaptures of sea urchins with diameters greater the 7.0 centimeters. It also is possible that the trend of increasing annual survival rate is biologically real.

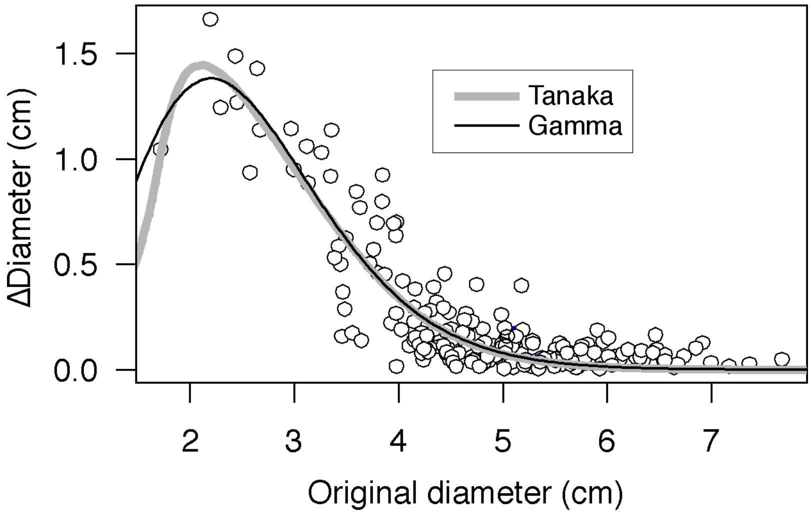

FIGURE 3. *Strongylocentrotus purpuratus* growth at the Surfgrass Area, Sunset Bay, Oregon, USA 2007–2009; calcein used in 2007 and tetracycline in 2008; $\Delta t = 1$ year for each tagging; combined N = 221; Tanaka function (SSE=3.832) f = 3.132±0.331(SE), d = 2.481±0.052(SE), a= 0.273±0.042(SE); Gamma model (SSE=3.793) κ= 5.283±0.646(SE), λ= 0.347±0.029(SE), α= 7.344±0.714; differences between the two models are evident at the smallest sizes but past original diameters of about 3cm the lines overlap and either model could be used.

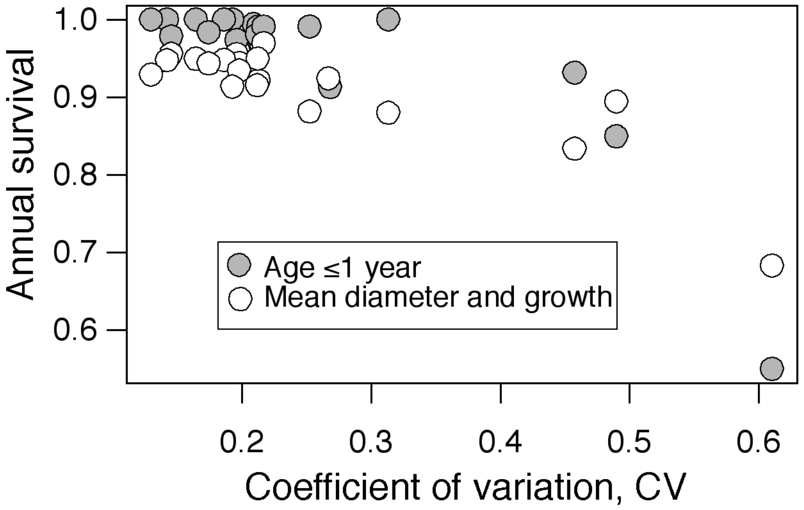

FIGURE 4. *Strongylocentrotus purpuratus* Surfgrass Area samples from 1964–2009. Annual survival estimates using (2) Fraction of individuals ≤ Age 1 and (3) Growth and mean size, plotted against the coefficient of variation of test diameter; unusual recruitment events result in an increase in CV, a decrease in mean size and hence an estimate of higher mortality. All methods reflect non-stationary size structure and actual survival may not be changing at all.

Survival estimates differ based on method (Table 2). The highest mean estimate of survival was obtained using the fraction of individuals Age≤1 year; the lowest estimate was from using mean diameter and growth. The associated estimates of ages attained by 5% of cohorts showed a range of 30 to 60 years and mean ages from 10 to 20 years. There is no good way of deciding which estimates best reflect the biology of *S. purpuratus* at Sunset Bay other than to conclude that it is a moderately long-lived species.

TABLE 2. Summary of survival estimates based on three methods; all estimates are for one year; P is mean survival yr-1 and annual mortality, M, is -ln(P) yr-1; 5% live to an age is ln(0.05)/(-M).

Statistic	Method		
	Age≤1	Mean and growth	VanSickle
N of cases	20	20	10
Mean survival, P yr-1	0.952	0.913	0.932
Std. error	0.023	0.014	0.024
M yr-1	0.049	0.091	0.07
5% live to age	61	33	43
Mean age (1/M)	20	9	14

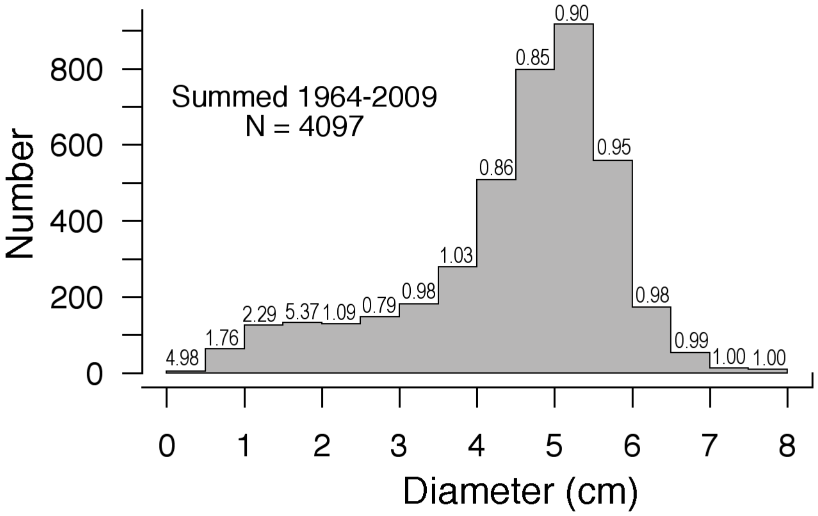

FIGURE 5. *Strongylocentrotus purpuratus* at the Surfgrass Area, Sunset Bay, Oregon, USA, size data summed; estimates of annual survival for each 0.5cm interval based on Van Sickle's method using Tanaka growth; there is a trend of increasing survival from the size category 4.0–4.5cm.

Discussion

There is no simple solution to the problem of estimating survival for sea urchins or other echinoderms with the possible exception of some stalked crinoids where individuals can be mapped (e.g. Syverson *et al.* 2015) or where density changes of cohorts can be followed (e.g. Beukema 1985; Lane & Lawrence 1980). For *S. purpuratus* at Sunset Bay, if just a single year is selected, it is difficult to know how representative an estimate of survival might be. For example, of the 20 size distributions from 1964–2009 six years had no sea urchins that were judged to be Age ≤1 year. Also, there were three years (1964, 1965, and 1994) where the survival estimate would now be judged to be too low so about 45% of the time a single sample would not be typical of overall survival. Similarly, using growth and mean size, five out of 20 samples had survival annual estimates less than 0.9 so 25% of the time a sample would have estimates now judged not typical. The obvious solution is to make certain that more than a single year is used to estimate survival. How many years are needed depends on the details of recruitment probability but even three years, the length of a typical research grant, probably are too few although if there is no substantial change in size structure, estimates may be reasonable.

Recruitment variability is not the only problem in estimating survival because there are occasional mortality events that can reset size structure. For example, intertidal *S. purpuratus* suffered a mass mortality along approximately 100km of the north-central California coast in August 2011 due to a toxic algal bloom (Jurgens *et al.* 2015). High temperatures have been suggested for the mass mortality of intertidal *S. purpuratus* in Southern California (Ebert 1983, 2013a) and increased mortality in central Oregon in May 1968 (Gonor 1968) was associated with measured internal body temperatures as high as 30°C. Reduced salinity associated with unusually intense rain events has been implicated in the elimination of intertidal *S. purpuratus* at Malibu in southern California (Hendler 2013) and in a section of Sunset Bay called the Boulder Field due to a storm in 1996 (Ebert 2013a).

Variable recruitment and unpredictable mortality events all contribute to keeping populations from attaining a stationary structure and hence interfere with estimating survival rates. There is no simple solution and so it is best to be cautious in interpreting studies particularly those based on a small number of years of study.

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