Inferring demographic processes from size-frequency distributions: Effect of pulsed recruitment on simple models

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Abstract.—The shape of a size-frequency distribution is the result of age- or size-specific rates of growth and survival, their variability, and seasonal and interannual variation in recruitment. Simulation of size distributions can be used to gain insight into the underlying processes that give rise to observed size structure of organisms in the field, but the utility of this approach depends critically on underlying assumptions. Incorrect judgment of the significance of assumptions can lead to erroneous conclusions concerning the causes of bi- or polymodal distributions.

Using the Brody-Bertalanffy growth model and a constant survival rate, bi- and polymodal distributions can be generated when recruitment is pulsed. Even with as many as 10 recruitment episodes per year, size distributions show several modes. A sampling of the literature indicates that most fish and marine invertebrates have pulsed rather than continuous recruitment; thus, when very little is known about a species, pulsed rather than continuous recruitment would be the better assumption when interpreting the shapes of size distributions.

Our simulations differ from those conducted by Barry & Tegner (1990) who assumed continuous and constant recruitment and focused on changing growth and survival parameters to explain bimodal size structure. These authors also suggested that their analysis was appropriate for interpreting the dynamics of red sea urchins *Strongylocentrotus franciscanus*. We have been documenting settlement of both red and purple (*S. purpuratus*) sea urchins. At La Jolla, California, neither species showed continuous settlement; rather, both species had pulses of settlement in spring 1990 and 1991.

Although age-specific variation in growth or mortality parameters can result in bimodal size distributions, it is more likely that such distributions are caused by seasonal pulses of recruitment.

For many organisms, size data are easy to gather and size-frequency distributions are common in the literature. In many cases, they provide the only clues to the underlying dynamics of growth, survival, and recruitment. Thus, 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 1950, Bhattacharya 1967, Young & Skillman 1975, Macdonald & Pitcher 1979). A second approach has attempted to use size data either to estimate mortality when growth parameters are known (e.g., Beverton & Holt 1956, Smith 1972, Van Sickle 1977ab, Ebert 1981 and 1987, Sainsbury 1982) or to estimate both growth and mortality parameters (e.g., Green 1970, Ebert 1973 and 1987, Saila & Lough 1981, Fournier & Breen 1983, Pauly 1987). A third approach has modeled size distributions to gain insight into the underlying processes that give rise to observed distributions (e.g., Craig & Oertel 1966, DeAngelis & Coutant 1982, Barry & Tegner 1990, Hartnoll & Bryant 1990). Simulations of size distributions are metaphors of the dynamic processes that give rise to actual size distributions. The utility of simulation depends critically on the underlying assumptions. If the significance of any of the assumptions is wrongly judged, one may be led to erroneous conclusions concerning underlying dynamics.

As an approach to explaining bimodal size distributions, Barry & Tegner (1990) presented a deterministic model for the development of size distributions that has seven assumptions: (1) Brody-Bertalanffy growth, (2) constant rate of mortality, (3) constant and continuous recruitment, (4) strict determinism for growth, so $\sigma=0$ for all sizes at an age, (5) strict determinism for survival, so $\sigma=0$ for numbers at an age, (6) population growth rate per individual, r, equal to 0, and (7) a stable size distribution equivalent to a stable age distribution. Bimodal size distributions are not possible with these seven assumptions, yet bimodality is commonly observed. Accordingly, one or more of the assumptions must be violated. Barry & Tegner focused on the assumptions concerning growth and survival and concluded that "...bimodality can develop only from an increase in survivorship with age or an increase in the growth coefficient with age, or both." In particular, they argued that size distributions of red sea urchins *Strongylocentrotus franciscanus* required age- or size-specific changes of the growth-rate constant, K, in the Brody-Bertalanffy equation, the mortality coefficient, Z, in an exponential survival curve, or both.

There are three issues that we would like to explore: (1) Possible causes of bimodal size distributions and, in particular, the consequences of pulsed recruitment, (2) applicability of the Barry & Tegner model to sea urchins in California, and (3) general applicability of the Barry & Tegner model.

Size-distribution simulation

We simulated several size distributions to show how the Barry & Tegner model works. Growth was modeled using the Brody-Bertalanffy equation for individual growth:

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

where S_t = size at time t after birth or settlement
S_∞ = asymptotic size
K = growth rate coefficient

$$b = \frac{S_\infty - S_R}{S_\infty} \tag{2}$$

S_R = size at t=0 when organisms begin to grow according to Eq. 1.

Sometimes Eq. 1 is written

$$S_t = S_\infty(1-e^{-K(t-t_0)}) \tag{3}$$

where t_0 = time at which size would be 0
$b = e^{Kt_0}$. $\tag{4}$

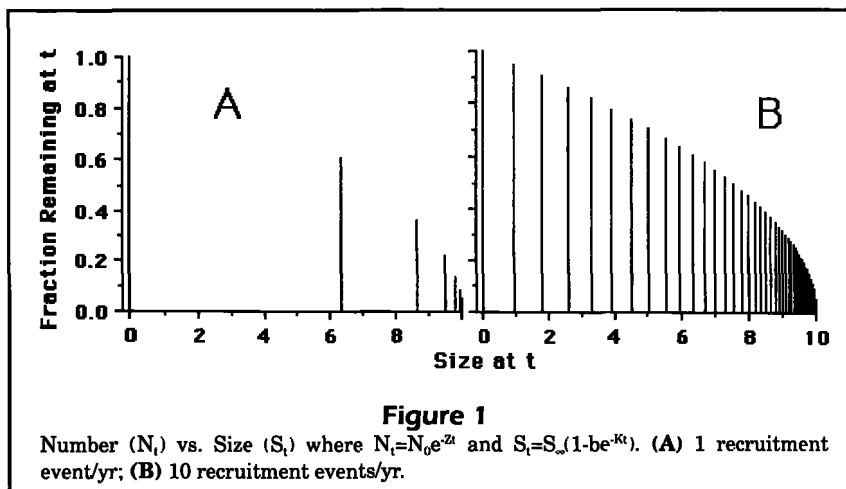Cohort survival was modeled so that the mortality rate was constant:

$$N_t = N_0e^{-Zt} \tag{5}$$

where N_t = number remaining in a cohort at time t
N_0 = initial number in a cohort
Z = mortality rate coefficient.

Equations 1 and 5 were used to generate a number-density distribution that was integrated over segments of arbitrary size to produce a size-frequency distribution. The first step was to calculate sizes at particular ages (Eq. 1) and then to estimate numbers in a cohort that survived to each age (Eq. 5). The number surviving to a specific size was generated using a constant time-interval and Z<K (Fig. 1). The size-intervals shorten because growth follows Eq. 1. For Fig. 1A, the time-interval between recruitment episodes is 1 unit, which, for purposes of this discussion, we call 1yr. Changing the time-interval for reproduction, that is, the number of evenly-spaced reproductive episodes/yr, changes the number and spacing of lines in the graph. In Fig. 1B we used 10 episodes/yr; that is, an interval of 0.1yr. In our simulation, we assumed that the population was periodically stable and stationary.

Stable and stationary structure for a population with pulsed recruitment means that demographic structure and number of individuals change between recruitment episodes but are the same across episodes. When the same times after recruitment episodes are compared, the age and size structures of the population are the same (stable structure) and the numbers of individuals are the same (stationary structure). The relationship between density and time would be saw-toothed, with an **average** slope of 0, but with increased numbers-at-recruitment and declining numbers up to the point of another recruitment episode. As the number of recruitment events increases, the height of each tooth becomes smaller until it is smooth when recruitment is continuous. The vertical lines in Fig. 1 represent not only the progression of a single cohort through time, but also cohorts that make up the stable and stationary population.

A size-frequency distribution was constituted by summing all lines within an arbitrary interval of 1.0 size units (Fig. 2). With just one reproductive episode/yr (Fig. 2A), size distribution is polymodal. The overall shape of the size distribution, which is formed by drawing an envelope around the distribution, has a negative slope. Over an increasing range of recruitment frequencies, the polymodal nature is preserved, so that with 10 episodes/yr (Fig. 2C) modes still are evident but the overall shape shows a positive slope. When there are 100 episodes/yr, size distribution approaches the continuous form used by Barry & Tegner:

Figure 1
Number (N_t) vs. Size (S_t) where $N_t=N_0e^{-Zt}$ and $S_t=S_\infty(1-be^{-Kt})$. **(A)** 1 recruitment event/yr; **(B)** 10 recruitment events/yr.

$$NS = \frac{N_0}{KS_\infty}\left(1-\frac{S_t}{S_\infty}\right)^{\left(\frac{Z}{K}-1\right)}. \tag{6}$$
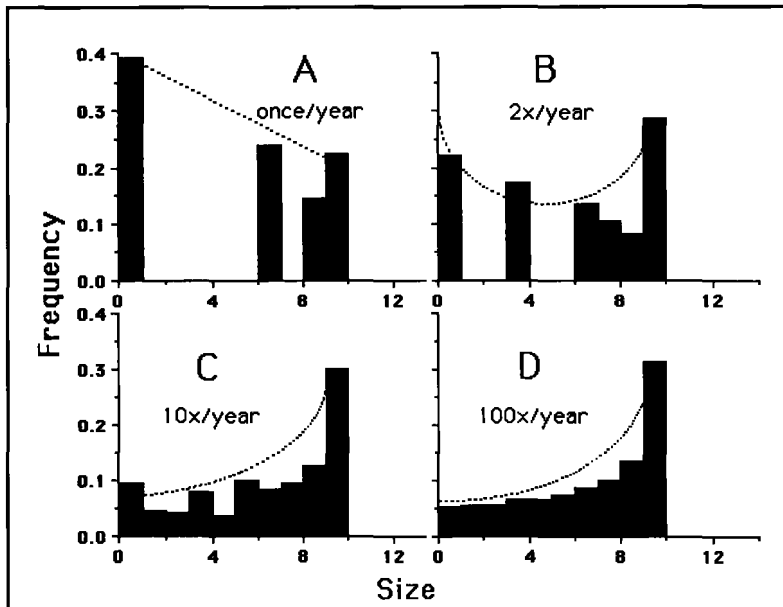
Figure 2

Integration of N_t vs. S_t over intervals of 1.0 size unit. Dotted line emphasizes general shape of the envelope of each distribution. (A) 1 recruitment episode/yr; envelope of the distribution has a negative slope. (B) 2 recruitment episodes/yr; envelope of the distribution has high points at smallest and largest sizes. (C) 10 recruitment episodes/yr; general envelope has a positive slope but has modes at small sizes. (D) 100 episodes/yr; envelope has a positive slope.

$$P(x) = \tfrac{1}{2} - r(a_1 t + a_2 t^2 + a_3 t^3) + \epsilon(x) \qquad (7)$$

$$x = \frac{s - \mu}{\sigma} \qquad (8)$$

$$r = \frac{e^{-x^2/2}}{\sqrt{2\pi}} \qquad (9)$$

$$t = \frac{1}{1 + Px} \qquad (10)$$

with $a_1 = 0.4361836$, $a_2 = -0.1201676$, $a_3 = 0.9372980$, $p = 0.33267$, and $\epsilon(x) < 10^{-5}$. The area under the normal curve, A, from s to s+Δs is

$$A = P(x)_{s+\Delta s} - P(x)_s. \qquad (11)$$

Areas under the normal curve for each cohort were reduced by multiplying each area, A, for a cohort by e^{-Zt} according to Eq. 5. The size-frequency distribution was produced by establishing a 1-unit size-interval and summing parts of all cohorts in each interval.

With one recruitment episode/yr (Fig. 3A), the distribution is polymodal. Because the cluster of individuals that are ≥1 yr is bi-
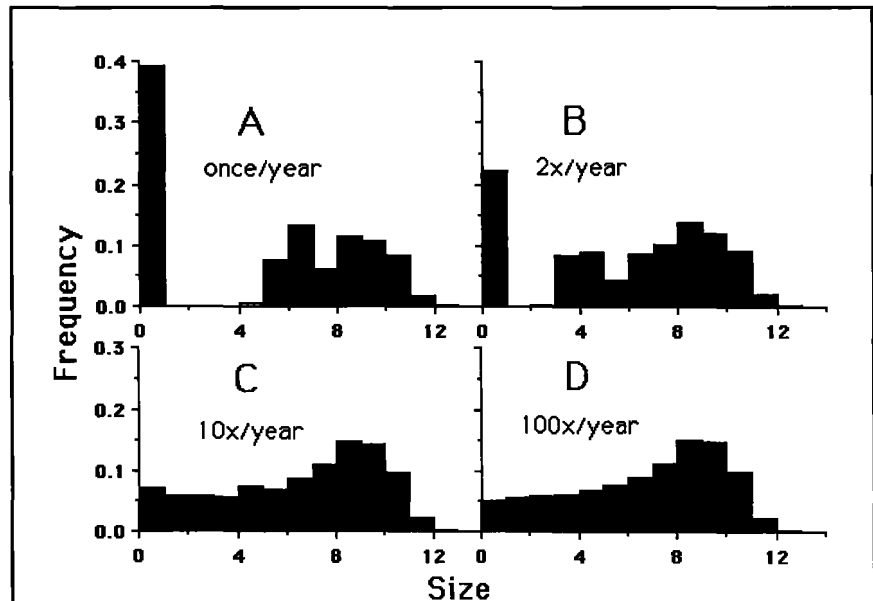
Simulated size distributions take on an appearance much closer to distributions seen in the field when individual sizes are distributed around mean size-at-age (Fig. 3). A coefficient of variation of 0.1 was used for simulation, so $\sigma = 0.1\mu$. Mean sizes were calculated using Eq. 1, and areas under the normal curve were estimated out to 4σ in units of $\sigma/10$. Areas for each size segment were determined by successive subtraction of terms obtained from a polynomial approximation of the area under the normal curve and based on a program for the normal distribution given by Poole & Borchers (1979), who used an algorithm from Hastings (1955) (Function 26.2.16 in Abramowitz & Stegun 1972). P(x) is the area under the normal curve from the mean, μ, to a size, s, given a standard deviation of σ:

Figure 3

Results of a simulation with Z=0.5, K=1.0, S∞=10.0, and s=0.1×mean. Simulations differ with respect to number of recruitment episodes/yr (range 1–100/yr). (A) polymodal with general envelope with negative slope; (B) polymodal with general negative slope; (C) polymodality still evident but envelope has a positive slope; (D) unimodal with general positive slope.

modal, it is clear that this distribution would always be bi- or polymodal. With two recruitment events/yr (Fig. 3B), the distribution again is polymodal and would always be so. With ten recruitment events/yr (Fig. 3C), the modes begin to disappear but the distribution still is weakly polymodal with modes at 0–1, 4–5, and 8–9 size units. With 100 recruitment events/yr (Fig. 3D), the distribution is unimodal. The general shapes are similar to the distributions in Fig. 2, with slopes that initially are negative (Fig. 3A) switching to positive (Fig. 3C, 3D). A combination of pulsed recruitment, coupled with a decaying exponential growth pattern and low mortality, can lead to size distributions with a wide range of shapes. A panoply of size-distribution shapes can be produced with identical values for Z, K, and S_∞ using different frequencies of recruitment.

Observed settlement of
S. franciscanus and *S. purpuratus*

Barry & Tegner (1990) used their model specifically to address bimodal size structure in red sea urchins *S. franciscanus*. We disagree with their assumption of continuous recruitment and base this on observed settlement data.

Starting in late February 1990, we deployed settlement collectors at a number of sites along the California coast. Wood-handled scrub brushes (model #0115 National Brush Co., Aurora IL) were used to evaluate temporal and spatial variability in settlement. Brushes were attached as pairs to a line with two pairs per line. The bottom pair of brushes was suspended 1m from the bottom, and the second pair was attached ~20cm farther up the rope. Brushes were tended on a weekly basis at sites within the California Bight and in northern California. One of the sites in southern California was off the end of the pier at Scripps Institution of Oceanography, La Jolla.

Following weekly collection, brushes were placed in a sonic cleaner with seawater for ~3 min to remove animals. Newly-metamorphosed sea urchins have a diameter of ~500 m; thus, following sonication, the water and sediment in the sonicator were strained through 436 m Nitex. Material retained by the screen was then examined using a dissecting microscope, and newly-settled sea urchins were identified and counted.

Settlement at Scripps Pier in San Diego County was confined to a pe-

riod of about 3 wk starting in late March 1990, and over a longer period in spring 1991 (Fig. 4). Timing of settlement was the same for both *S. purpuratus* and *S. franciscanus*. A few *S. purpuratus* settled in June 1990, but in terms of influencing the structure of a size-frequency distribution, settlement in 1990 can be considered a single event of short duration. Settlement in 1991 began in late February and continued into early June. The important point is that sea urchin settlement at Scripps Pier was seasonal. Settlement at other sites in California, as well as inside and outside kelp beds, all showed seasonal settlement (Ebert et al., in prep.).

Discussion

Bi- or polymodal size distributions and pulsed recruitment are common in the literature. We examined 69 papers that included larval distribution, settlement, or recruitment information for fish, molluscs, annelids, bryozoans, crustaceans, and echinoderms. Out of 216 species, only 8 could be considered to have continuous recruitment, and of these only five spider crab species (Hines 1982) appeared to have constant recruitment; that is, the same number/mo at all seasons. About 98% of the species failed to meet the assumption of constant and continuous recruitment made by Barry & Tegner (1990).

As shown by our simulations, pulsed recruitment produced bimodal distributions that were not transitory in the sense that distributions showed bimodality at all times between recruitment events. However, were a population characterized by pulsed recruitment, sampling could be done in such a manner that the relative magnitude of Z and K could be deduced from a simple
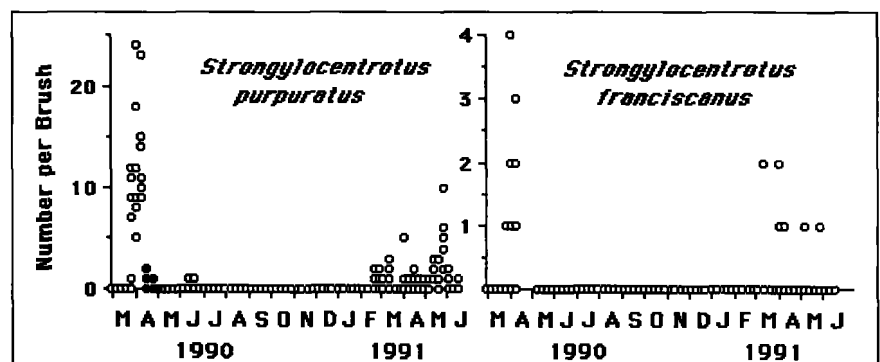

Figure 4
Settlement of purple and red sea urchins, *Strongylocentrotus purpuratus* and *S. franciscanus*, on eight scrub brushes: four suspended 1 m from bottom and four at 1.2 m off bottom at Scripps Pier, Scripps Inst. Oceanogr., La Jolla CA (32°52′N). Solid circles indicate animals not identified to species.

model such as Eq. 6. The changing shapes of the size-frequency distributions for a species with pulsed recruitment could be summed and so be made to approximate the shape that would be obtained with continuous recruitment. To obtain a reasonable approximation, it would be necessary to (1) take many evenly-spaced samples between recruitment events, and (2) weight the samples with the survival rate, e^{-Zt}, from the time of recruitment, t. Weighting could be accomplished if accurate estimates of density were known, which, of course, would be the same as knowing survival. An obvious variant would be the case in which the same area was sampled each time and all individuals were measured. Such a procedure would result in the largest N for the sample immediately following recruitment and the smallest N for the sample just prior to the next recruitment episode. All samples would be pooled before the size-frequency distribution would be constructed.

Approximation of a species with pulsed recruitment to a continuous form could be the same as distributions shown in Figs. 2 and 3. For example, if a species had a single pulse of recruitment and was sampled 10 evenly-spaced times during a year, and each sample was weighted according to the survival rate, then the summed frequency distribution would be C in Figs. 2 and 3. However, if size data were gathered in such a manner that weighting was not automatic, survival rate would have to be obtained by some other technique before size distributions could be summed to approximate continuous recruitment. Techniques for obtaining survival rate, the weighting factor, from size data include those presented by Ebert (1973, 1987), Saila & Lough (1981), Fournier & Breen (1983), and Pauly (1987). It must be noted that analysis of a series of size distributions to obtain the weighting factor would provide information on growth as well as survival, and so there would be scant motivation for constructing a summed distribution.

It is not possible to infer the causes underlying an observed size distribution from a single sample or even from several samples that are widely spaced in time. For example, bimodal size distributions can arise from intra-cohort (e.g., Shelton et al. 1979, Timmons et al. 1980) or inter-cohort (Johnson 1976) competition, and the simple models examined here and in Barry & Tegner (1990) demonstrate that similar size distributions can result from very different mechanisms. In a time-series of size distributions, when the smallest mode shifts through time, the simplest explanation for bimodality is pulsed recruitment (e.g., McPherson 1965, Hickman 1979, Dafni & Tobol 1986/87, Davoult et al. 1990). If sampling is adequate and the smallest mode of a bimodal distribution does not shift during the year (e.g., Gladfelter 1978), the most probable explanation

is continuous recruitment coupled with high mortality rates for the smallest animals and improved survival with increased size, which is a case that fits the explanation for bimodality provided by Barry & Tegner (1990). When size distributions are bi- or polymodal and are presented without a time-series (e.g., Tegner & Dayton 1981, Stein & Pearcy 1982, Wilson 1983), reasonable hypotheses can be formulated, but testing requires additional data.

There are numerous examples of pulsed recruitment for sea urchins in California. Size-frequency distributions gathered for purple sea urchins at Papalote Bay, Baja California, Mexico (31°42') (Pearse et al. 1970) may indicate multiple settlement events each year during 1962–69 because samples from January, April, and June–November all had a mode <1.0 cm (Pearse et al. 1970, Ebert 1983). However, if growth was very slow at Papalote Bay, as also indicated by the size-frequency distributions, a single settlement episode would explain the data because individuals with a mode at 0.5 cm were observed only in summer and fall samples.

Published size data for sea urchins at Whites Point (33°43'N) and Point Vicente (33°44'N) during 1966 and 1967 (Pearse et al. 1970) show recruitment pulses for both species of Strongylocentrotus and for Lytechinus. Recruitment was better in 1966 than in 1967, and small individuals were collected in September 1966 as well as in July and August 1967. Recruitment was not continuous at either Whites Point or at Point Vicente.

Finally, our results showing pulsed settlement for red and purple sea urchins corroborate the observation of a single spike of settlement at Naples Reef (34°25'N) off Santa Barbara in May 1986 (Rowley 1989) and the report by Harrold et al. (1991) of two recruitment events during a year in central California. The pulsed nature of recruitment means that analysis of size-frequency distributions of Strongylocentrotus spp. should not be based on a model that explicitly requires continuous and constant recruitment (Eq. 6).

We have demonstrated that by using fixed growth and survival parameters, it is possible to generate a wealth of size-distribution shapes merely by changing the number of recruitment episodes/yr. We have intentionally focused on this aspect of size-distribution shape because we believe that it forms the stumbling block to the application of the Barry & Tegner model. In effect, their model does not provide a convenient way of gaining insight into demographics because, in order to use it to divine the relative magnitude of parameters, it would be necessary to demonstrate the pattern of recruitment for the population being studied. Since the preponderance of field evidence indicates that recruitment generally is pulsed, one cannot "...draw inferences concerning the demographic dynamics of a population...simply by observing the shape of its size-

frequency distribution" (Barry & Tegner 1990). Furthermore, classifying populations as "growth dominated" or "mortality dominated," as these authors have done, introduces terms that obscure rather than illuminate the analysis of size distributions, much in the manner of r- and K-selection comparisons.

Size data should be part of every demographic study because they contain a record of the recent past history of a population. Such data ultimately can be used to estimate parameters, such as Z in Eq. 5, that frequently are difficult to obtain, or to test assumptions concerning annual variability in recruitment or mortality. There currently is no substitute for population studies that include not only size data but also independent estimates of growth and, where possible, survivorship.

Acknowledgments

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