

Mortality estimates from age distributions: Critique of a method used to study seagrass dynamics

Abstract—Age structure of seagrass samples has been used to estimate survival and recruitment and then used to estimate population growth rate. Survival rate can be estimated from age structure only if the population is neither growing nor declining ($r = 0$), so the age distribution is both stable and has stationary structure. If survival is estimated from age structure, it must be assumed that $r = 0$ or additional information about the population must be known. If a decaying exponential model is used for number (N) in each age class, $\ln N$ versus age has a slope of $-(M + r)$, and so an incorrect survival rate, $\exp(-M)$, would be estimated if $r \neq 0$. Simulations show that when $r > 0$, the slope of the regression of $\ln N$ versus age is too steep and hence mortality rate would be overestimated, and the reverse when $r < 0$. Ignoring the assumption of $r = 0$ is a fundamental flaw in many seagrass studies and calls into question the mortality and population growth rates that have been published.

Measuring demographic attributes is an established part of devising management plans as well as understanding patterns of life-history evolution. Seagrasses are important elements of near-shore environments, are declining worldwide (e.g., Orth and Moore 1983; Shepherd et al. 1989; Giesen et al. 1990; Robblee et al. 1991), and so have been a focus for approaches that can contribute to prediction of change. Population growth rates for seagrasses have been estimated based on morphological characteristics of short shoots, the meristem that produces leaves (Patriquin 1973; Tomlinson 1974), to develop an age-structured analysis (cf. Duarte et al. 1994). Age structure of seagrass samples is determined, and this is used to estimate survival and recruitment, so single samples of age structure are used to estimate population growth. The point of this note is to call attention to the assumption that must be made in analyses of age structure from single samples that makes the estimation of survival (or mortality) rates not possible in most cases, namely, that the population is stationary, neither increasing nor declining. If the assumption is made, the estimated mortality rate cannot be used to estimate a population growth rate other than 0. If the assumption is not made, mortality rate cannot be estimated unless the population growth rate is known. Ignoring the assumption of population growth rate per individual (r) equal to 0 is a fundamental flaw that calls into question the mortality and population growth estimates presented by Duarte and Sand-Jensen (1990), Gallegos et al. (1993), Duarko (1994), Duarte et al. (1994), Vermaat et al. (1995), Marbà et al. (1996), Duarko and Duarte (1997), Marbà and Walker (1999), and Petersen and Fourqurean (2001), as well as other research that uses observed age structure in samples to estimate mortality rate.

If a population is growing according to a fixed schedule of survival and fecundity, it will, eventually, change at a constant rate per individual, r , or with a finite growth rate,

λ , which is $\exp(r)$. When the total population is changing at this constant rate, λ , each age class of the population also is changing at this rate and will have a fixed proportion of individuals in each age class; the population has a stable-age distribution (Sharpe and Lotka 1911; Lotka 1924, any introductory ecology text such as Krebs 1994 or more specialized population books such as Ebert 1999 or Caswell 2000).

When age structure of a population is sampled at a single point in time and data are used to estimate survival, two assumptions must be made: (1) the population has achieved a stable-age distribution and (2) $r = 0$ (i.e., $\lambda = 1.0$), that is, the population has stationary structure. Neither assumption can be tested from a single sample, although if a sample is known to be from a newly established colony, then it would be best to assume that sufficient time has not elapsed for development of a stable-age distribution, and hence rates of survival should not be estimated. If it is reasonable to assume that a stable-age distribution has been attained, then it is necessary to deal with the assumption of stationary structure.

The age data gathered by seagrass biologists cited above can be expressed as fractions of the total population and are at best the terms of the stable-age distribution, C_x ,

$$C_x = \frac{l_x \lambda^{-x}}{\sum_{t=0}^{\omega} l_t \lambda^{-t}} \quad (1)$$

where l_x is the probability that a new individual is alive at time x starting with $l_0 = 1.0$. Rearrangement of Eq. 1 to isolate l_x is

$$l_x = \frac{C_x \sum_{t=0}^{\omega} l_t \lambda^{-t}}{\lambda^{-x}} = \lambda^x C_x \sum_{t=0}^{\omega} l_t \lambda^{-t} \quad \text{and} \quad (2)$$

$$l_{x+1} = \lambda^{x+1} C_{x+1} \sum_{t=0}^{\omega} l_t \lambda^{-t} \quad (3)$$

Survival probability from time x to $x + 1$ is

$$p_x = \frac{l_{x+1}}{l_x} \quad (4)$$

which, from Eqs. 2 and 3, is

$$p_x = \frac{C_{x+1} \lambda}{C_x} \quad (5)$$

In order to estimate survival (p_x in Eq. 5) it is necessary to have an estimate of λ or to assume that $\lambda = 1$ (i.e., $r = 0$). This problem is not new in ecology and has been discussed, among others, by Caughley and Birch (1971) and Michod and Anderson (1980) for mammal studies and Johnson et al.

(1994) for trees and is included in a discussion of seagrasses by Kaldy et al. (1999).

The survival model used by seagrass biologists cited above is a decaying exponential (Eq. 6), although any model of survival based on an observed age structure will have the same assumption of $r = 0$.

$$N_x = N_0 e^{-Mx} \quad (6)$$

where numbers (N) at age (x) are based on the estimated ages of short shoots in samples and M is called the instantaneous mortality rate and is related to p_x in Eq. 5,

$$p_x = e^{-M} \quad (7)$$

Eq. 6 can be written as a difference equation

$$N_{x+1} = N_x e^{-M} \quad \text{or} \quad N_{x+1} = N_x p_x \quad (8)$$

which can be compared with a rearranged Eq. 5

$$C_{x+1} = C_x p_x \lambda^{-1} \quad (9)$$

The slope of the regression in Eq. 8 is p_x but is $p_x \lambda^{-1}$ in Eq. 9 and shows that use of the regression model employed by many seagrass biologists does not address the assumption of stationary population structure. The regression model must be corrected to include population growth, and because $\lambda = e^r$ Eq. 6 can be written

$$N_x = N_0 e^{-(M+r)x} \quad (10)$$

which means that a regression of $\ln(N_x)$ versus x has a slope of $-(M+r)$ and so M cannot be determined without knowing r or vice versa.

The consequences of using Eq. 6 rather than Eq. 10 can be shown by a simulation using the Euler equation (Eq. 11) as a convenient way of estimating population growth, λ , and terms of the stable-age distribution:

$$\sum_{x=0}^{\omega} l_x m_x e^{-rx} = 1 \quad (11)$$

where l_x is the probability that a new individual age 0 is alive at time $= x$, m_x is the age-specific fecundity, and ω is the last age class of the life table.

The initial values for l_x in the simulation were selected so just one individual out an initial 1,000 would be alive at age 4 yr and the survival rate would be constant. Using Eq. 6,

$$1 = 1,000 e^{-M \times 4}$$

or $M = 1.7 \text{ yr}^{-1}$, which is within the range of slopes calculated for six tropical seagrass species (Vermaat et al. 1995). Values of l_x were calculated from Eq. 6 (Table 1) with $l_0 = 1.0$,

$$l_x = e^{-1.7x}$$

Age-specific fecundity was simplified by making all age classes the same and starting reproduction at age 1. If the population is not growing, then net reproductive rate per generation, R_0 , must be equal to 1.0. R_0 is related to l_x and m_x

$$R_0 = \sum l_x m_x \quad (12)$$

and so with a constant m_x ,

Table 1. Simulation of age structure with different rates of population growth; N_x values are the numbers in each age class out of 1,000 individuals and are the terms of the stable-age distribution, C_x , multiplied by 1,000. Note when $\lambda = 1.0$ (i.e., $r = 0$), l_x and N_x columns are in the same proportions and the l_x column is obtained by dividing all N_x values by N_0 , which is how an observed age distribution is converted to survival using Eq. 1 (Fig. 1).

Age (x)	l_x	m_x	C_x	N_x
Simulation 1, $r = 0$ ($\lambda = 1.0$)				
0	1.0	0	0.8177	818
1	0.183	4.484	0.1496	150
2	0.033	4.484	0.0270	27
3	0.006	4.484	0.0049	5
4	0.001	4.484	0.0008	1
Simulation 2, $r = 0.600$ ($\lambda = 1.821$)				
0	1.0	0	0.8997	900
1	0.183	8.968	0.0904	90
2	0.033	8.968	0.0090	9
3	0.006	8.968	0.0009	1
4	0.001	8.968	0.0001	0
Simulation 3, $r = -0.533$ ($\lambda = 0.587$)				
0	1.0	0	0.6915	691
1	0.183	2.242	0.2157	216
2	0.033	2.242	0.0663	66
3	0.006	2.242	0.0206	21
4	0.001	2.242	0.0058	6

$$m_x = \frac{1}{\sum l_x} \quad (13)$$

which is 4.484 (Table 1).

The terms of the stable-age distribution, C_x , were multiplied by 1,000 to simulate an actual distribution of ages similar to what would be gathered in the field as a single sample (Table 1). We call terms of this simulated distribution N_x . A plot of $\ln(N_x)$ versus x (Fig. 1) has a slope of -1.7 , which is the value used in the simulation. With $r = 0$, the correct survival rate can be estimated from successive terms of a measured age distribution as indicated in Eq. 11. This is, however, not the case for $r \neq 0$.

In the next simulations, survival rate was maintained at $\exp(-1.7)$ and fecundity was doubled for one simulation and reduced by one half for another (Table 1). Population growth rates again were determined using the Euler equation. The new values for r were 0.600 and -0.533 , respectively, and indicated rapid growth or rapid decline of the population. The new stable-age distributions differ from the distribution where $r = 0$, and so regressions of $\ln(N_x)$ versus x do not recover the correct values for survival. For the declining population estimated survival is too high, and for the increasing population estimated survival is too low. The slopes of the lines are $-(M+r)$ or

$$M = -(\text{slope} + r)$$

So for the increasing population with a slope of -2.3 and $r = 0.6$ $M = 1.7$, and for the declining population with a slope of -1.2 and $r = -0.5$ $M = 1.7$. If population growth rate is known, then M can be calculated.

N_x values can be used to calculate l_x values for the Euler

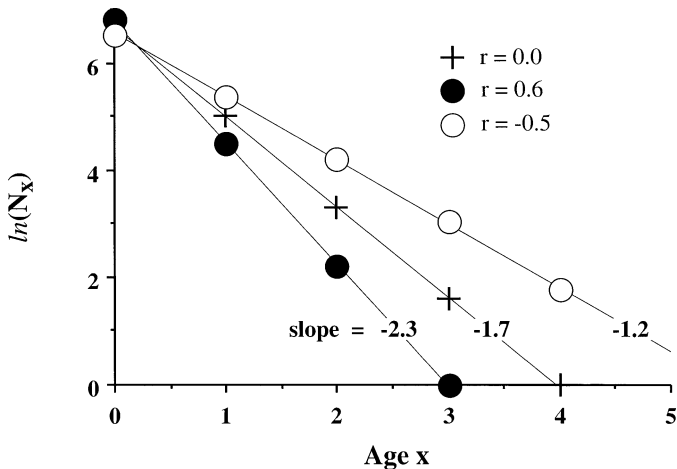


Fig. 1. Natural logarithm of terms of the stable-age distribution, N_x , versus age, x (Table 1). Slope is $-(M + r)$ in $N_x = N_0 e^{-(M+r)x}$. The slope of -1.7 is for $r = 0$, so $M = 1.7$, which is the correct value for the life table and is estimated from N_x only when the population is stationary. Slope = -2.3 is for a growing population ($r = 0.6$), and slope = -1.2 is for a declining population ($r = -0.5$). $M = -(\text{slope} + r)$, so for $r = 0.6$, $M = -(-2.3 + 0.6) = 1.7$, and for $r = -0.5$, $M = -(-1.2 - 0.5) = 1.7$. The slope must be corrected for population growth rate in order to estimate the correct value of M .

equation by dividing all elements of the column by N_0 , the number of age 0 individuals. When $r = 0$, correct values are obtained (Table 1), but this will not be true when $r \neq 0$ (Table 2). Estimating r from age structure when true values are for an increasing or decreasing population shows that in both cases the estimate of r is close to 0 rather than the true values. Misjudging r , however, is the expected result because, as shown above, to use age structure to determine survival, it is necessary to assume that $r = 0$, and so the assumed value is, indeed, the value recovered in the analysis rather than the true value. Peterson and Fourqurean (2001) show a mean of r close to 0 for their samples with a range of -0.2 to $+0.5 \text{ yr}^{-1}$. We suggest that it is not possible to tell whether this is actually how seagrass beds are changing or whether the result is due to an inappropriate calculation of survival or violation of other assumptions such as the assumption of fixed survival or reproductive rates.

The solution to the problem is to actually measure survival, which can be done by tagging or mapping individual shoots as has been done in other plant and algal studies (e.g., Bierzychudek 1982; Åberg 1992; Canales et al. 1994) and determining fate of shoots after some suitable period of time such as 1 yr. A solution to the problem of using age structure to estimate survival was proposed by Michod and Anderson (1980): measure at least one survival transition in a life cycle, such as from age 0 to age 1, as a way of correcting an age distribution to estimate l_x . For seagrasses it probably is better to recast the analysis as stage or size structured and to measure survival and reproduction of mapped individuals. Bearlin et al. (1999) suggest using ramets as individuals with size based on number of shoots. Ewanchuk (1995) used shoots as individuals and size based on width of blades. Measured loss and addition of new individuals, however an

Table 2. Effect of population growth on the estimate of population growth when l_x is calculated from a single sample of age structure.

Age (x)	l_x	m_x	C_x	N_x	est r
Simulation 4, correct $r = 0.600$ ($\lambda = 1.821$), est $r = -0.004$					
0	1.0	0	0.8997	900	1.000
1	0.183	8.968	0.0904	90	0.100
2	0.033	8.968	0.0090	9	0.010
3	0.006	8.968	0.0009	1	0.001
4	0.001	8.968	0.0001	0	0.000
Simulation 5, correct $r = -0.533$ ($\lambda = 0.587$), est $r = 0.003$ l_x from N_x					
0	1.0	0	0.6915	691	1.000
1	0.183	2.242	0.2157	216	0.313
2	0.033	2.242	0.0663	66	0.096
3	0.006	2.242	0.0206	21	0.030
4	0.001	2.242	0.0058	6	0.009

investigator chooses to define them, do not require the assumption of a stable-age distribution with stationary structure. The central point we wish to emphasize is that a sample of age structure by itself cannot be used to deduce survival and population growth. This point is especially critical to recognize when population growth rates of seagrasses are used in support of management decisions. We encourage our colleagues to focus attention on directly measuring survival of seagrasses in the field.

Thomas A. Ebert¹

Department of Zoology
Oregon State University
Corvallis, Oregon 97331-2914

Susan L. Williams

Bodega Marine Laboratory
P.O. Box 247
Bodega Bay, California 94923

Patrick J. Ewanchuk

Department of Ecology and Evolutionary Biology
Brown University
Providence, Rhode Island 02912

References

ÅBERG, P. 1992. A demographic study of two populations of the seaweed *Ascophyllum nodosum*. *Ecology* **73**: 1473–1487.

¹ Corresponding author (tebert@sunstroke.sdsu.edu).

Acknowledgments

This research was supported by the National Oceanic and Atmospheric Administration under grant NA36RG0469 through the Coastal Ocean Program and grant NA66RGO477, through the National Sea Grant College Program. The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its subagencies. The U.S. Government is authorized to reproduce and distribute this article for governmental purposes. Contribution 2154 from Bodega Marine Laboratory, University of California at Davis.

- BEARLIN, A. R., M. A. BURGMAN, AND H. M. REGAN. 1999. A stochastic model of seagrass (*Zostera muelleri*) in Port Phillip Bay, Victoria, Australia. *Ecol. Model.* **118**: 131–148.
- BIERZYCHUDEK, P. 1982. The demography of jack-in-the-pulpit, a forest perennial that changes sex. *Ecol. Monogr.* **52**: 335–351.
- CANALES, J., M. C. TREVISAN, J. F. SILVA, AND H. CASWELL. 1994. A demographic study of an annual grass (*Andropogon brevifolius* Schwartz) in burnt and unburnt savanna. *Acta Ecol.* **15**: 261–273.
- CASWELL, H. 2000. Matrix population models: Construction, analysis, and interpretation, 2nd ed. Sinauer.
- CAUGHLEY, G., AND L. C. BIRCH. 1971. Rate of increase. *J. Wildl. Manag.* **35**: 658–663.
- DUARTE, C. M., AND K. SAND-JENSEN. 1990. Seagrass colonization: Biomass development and shoot demography in *Cymodocea nodosa* patches. *Mar. Ecol. Prog. Ser.* **67**: 97–103.
- , AND OTHERS. 1994. Reconstruction of seagrass dynamics: Age determinations and associated tools for the seagrass ecologist. *Mar. Ecol. Prog. Ser.* **107**: 195–209.
- DURAKO, M. J. 1994. Seagrass die-off in Florida Bay (USA): Changes in shoot demographic characteristics and population dynamics in *Thalassia testudinum*. *Mar. Ecol. Prog. Ser.* **110**: 59–66.
- , AND C. M. DUARTE. 1997. On the use of reconstructive aging techniques for assessing seagrass demography: A critique of the model test of Jensen et al. (1996). *Mar. Ecol. Prog. Ser.* **146**: 297–303.
- EBERT, T. A. 1999. Plant and animal populations. Methods in demography. Academic.
- EWANCHUK, P. J. 1995. The relative importance of sexual versus asexual reproduction in eelgrass (*Zostera marina* L.) population growth. MS thesis, San Diego State University.
- GALLEGOS, M. E., M. MERINO, N. MARBÀ, AND C. DUARTE. 1993. Biomass and dynamics of *Thalassia testudinum* in the Mexican Caribbean: Elucidating rhizome growth. *Mar. Ecol. Prog. Ser.* **95**: 185–192.
- GIESEN, W.B.J.T., M. M. V. KATWIJK, AND C. DEN HARTOG. 1990. Eelgrass condition and turbidity in the Dutch Wadden Sea. *Aquat. Bot.* **37**: 71–85.
- JOHNSON, E. A., K. MIYANISHI, AND H. KLEB. 1994. The hazards of interpretation of static age structures as shown by stand reconstructions in a *Pinus contorta*–*Picea engelmannii* forest. *J. Ecol.* **82**: 923–931.
- KALDY, J. E., N. FOWLER, AND K. H. DUNTON. 1999. Critical assessment of *Thalassia testudinum* (turtle grass) aging techniques: Implication for demographic inferences. *Mar. Ecol. Prog. Ser.* **181**: 279–288.
- KREBS, C. J. 1994. Ecology: The experimental analysis of distribution and abundance, 4th ed. HarperCollins.
- LOTKA, A. J. 1924. Elements of physical biology. Williams and Watkins (reprinted and revised 1956 as Elements of mathematical biology, Dover).
- MARBÀ, N., C. M. DUARTE, J. CEBRIÁN, M. E. GALLEGOS, B. OLESEN, AND K. SAND-JENSEN. 1996. Growth and population dynamics of *Posidonia oceanica* on the Spanish Mediterranean coast: Elucidating seagrass decline. *Mar. Ecol. Prog. Ser.* **137**: 203–213.
- , AND D. I. WALKER. 1999. Growth, flowering, and population dynamics of temperate Western Australian seagrasses. *Mar. Ecol. Prog. Ser.* **184**: 105–118.
- MICHOD, R. E., AND W. W. ANDERSON. 1980. On calculating demographic parameters from age frequency data. *Ecology* **61**: 265–269.
- ORTH, R. J., AND K. A. MOORE. 1983. Chesapeake Bay: An unprecedented decline in submerged aquatic vegetation. *Science* **222**: 51–53.
- PATRIQUIN, D. 1973. Estimation of growth rate, production and age of the marine angiosperm *Thalassia testudinum* Konig. *Caribb. J. Sci.* **13**: 111–123.
- PETERSON, B. J., AND J. W. FOURQUREAN. 2001. Large-scale patterns in seagrass (*Thalassia testudinum*) demographics in south Florida. *Limnol. Oceanogr.* **46**: 1077–1090.
- ROBBLEE, M. B., AND OTHERS. 1991. Mass mortality of the tropical seagrass *Thalassia testudinum* in Florida Bay (USA). *Mar. Ecol. Prog. Ser.* **71**: 297–299.
- SHARPE, F. R., AND A. J. LOTKA. 1911. A problem in age distribution. *The London, Edinburgh, and Dublin Philosophical Magazine and Journal of Science, Series 6*, **21**: 435–438.
- SHEPHERD, S. A., A. J. MCCOMB, D. A. BULTHUIS, V. NERVERAUSKAS, D. A. STEFFENSEN, AND R. WEST. 1989. Decline of seagrasses. In A. J. Larkum, A. J. McComb, and S. A. Shepherd [eds.], *Biology of seagrasses*. Elsevier.
- TOMLINSON, P. B. 1974. Vegetative morphology and meristem dependence—the foundation of productivity in seagrasses. *Aquaculture* **4**: 107–130.
- VERMAAT, J. E., N. S. R. AGAWIN, C. N. DUARTE, M. D. FORTES, N. MARBÀ, AND J. S. URI. 1995. Meadow maintenance, growth and productivity of a mixed Philippine seagrass bed. *Mar. Ecol. Prog. Ser.* **124**: 215–225.

Received: 19 January 2001

Accepted: 16 October 2001

Amended: 26 October 2001