

COMMENT

Limnol. Oceanogr., 48(5), 2003, 2070–2074
© 2003, by the American Society of Limnology and Oceanography, Inc.

Elucidating seagrass population dynamics: Theory, constraints, and practice

Seagrasses form important ecosystems in the coastal zone that provide valuable ecosystem services (Costanza et al. 1997). Growing evidence of widespread decline worldwide (Short and Wyllie-Echeverria 1996; Hemminga and Duarte 2000; Duarte 2002) has prompted interest in the early detection of change and the monitoring of seagrass beds. Most monitoring programs, however, are not very efficient at detecting change with sufficient anticipation because such change can either occur precipitously (e.g., Robblee et al. 1991) or be too gradual to be detected within the typically broad error margins of density and cover estimates used in most monitoring programs (Heidelbaugh and Nelson 1996). There is, therefore, a demand for approaches to quantify the components of seagrass population dynamics with the aim of allowing an evaluation of their status and an ecological forecast of possible future trends. A recent note published in *Limnology and Oceanography* (Ebert et al. 2002) calls into question the application of analyses of age distributions to predict population dynamics, as is being applied with increasing frequency in the literature (e.g., Peterson and Fourqurean 2001). With this comment, we would like to concur with their findings that published estimates of population growth rates derived from analysis of age structure can be in error if the underlying assumptions of the analyses are not met. However, we further argue that useful forecasts of population growth can indeed be gained from analyses of age distributions, but such forecasts should be used with caution until the validity of the assumptions implicit in the analyses is assured.

Population dynamics reflect the balance between immigration, emigration, recruitment, and mortality and the various factors that affect these gains and losses. For any closed population, the population growth rate per individual (r) is the difference between the per capita birth rate (recruitment, R) and death rate (mortality, M):

$$r = R - M \quad (1)$$

Knowing R and M , then, would allow for predictions of r . The bulk of the estimates of R and M for seagrass populations produced over the last 10 years have been derived through the use of age distributions and the so-called reconstructive techniques (Duarte et al. 1994). Reconstructive techniques are relatively simple to implement compared to other, more direct methods of measuring seagrass population dynamics (e.g., quadrat census, Short and Duarte 2001). Direct censuses have rarely been employed because of the multiple visits required, the substantial time required to mark shoots in very dense often deep stands, and the extended life span of many of the target seagrass species (e.g., *Posidonia*

spp., *Thalassia* spp., cf. Hemminga and Duarte 2000), which requires multiannual observational periods to record shoot births and deaths.

Because it is possible to age shoots in a seagrass population by counting leaf scars (Patriquin 1973; Duarte et al. 1994) it is possible to collect a sample of shoots from a population and evaluate the relative abundance of shoots of different age classes. The model generally used by seagrass ecologists to estimate M from this age structure data is

$$N_x = N_0 e^{-Mx} \quad (2)$$

where N_x is the number of shoots in age class x and N_0 is the number of shoots recruited into the population.

Ebert et al. (2002) join previous works (e.g., Jensen et al. 1996; Kaldy et al. 1999) and call into question such estimates of M , partly because of the assumptions underlying the application of Eq. 2. Most importantly, this analysis assumes a stable age distribution (and, therefore, that $R = M$) and age-independence of R and M . These assumptions have been acknowledged in seagrass applications, both as the method was proposed (Duarte et al. 1994) and applied (e.g., Durako and Duarte 1997; Peterson and Fourqurean 2001). This approach is not peculiar to seagrass populations, but has been applied (constrained by the same assumptions) to a wide variety of organisms (e.g., fisheries “catch curve” analysis, Ricker 1975; Quinn and Deriso 1999). Hence, the assumptions appear to be sufficiently well known—but, as Ebert et al. (2002) point out, there are cases in the literature where the ramifications of violations of these assumptions have not been recognized. Provided the assumptions and limitations of the approach are clearly appreciated, the conclusion of Ebert et al. (2002) that “age structure cannot be used to deduce survival and population growth” is extreme.

The method as formulated in Eq. 2 should only be applied to meadows that appear to have remained relatively steady in the past (i.e., $R \approx M$). On this point, we can agree with Ebert et al. (2002) that estimates derived from the reconstruction method of rapidly growing or rapidly declining populations are biased and that estimates of M are only reliable provided that the average r across the life span of the oldest individuals in the population ≈ 0 . As Ebert et al. (2002) point out, in the case where $r \neq 0$, Eq. 2 is not correct; rather

$$N_x = N_0 e^{-(M+r)x} \quad (3)$$

Referring to Eq. 1, Eq. 3 can be rewritten

$$N_x = N_0 e^{-Rx} \quad (4)$$

or, if $r \neq 0$, the slope of the regression of $\ln N_x$ versus x

multiplied by -1 is R , not M , thereby providing an estimate of the average recruitment rate. This can be easily confirmed by examining simulations presented in fig. 1 of Ebert et al. (2002).

But, since the methods explicitly assume that M and R have remained constant over the lifespan of the oldest individuals in the population, how then can this method be logically used to predict changes in r for the population? In fact, these key assumptions should be restated. In reality, using a regression approach to estimate slope of $\ln N_x$ versus x assumes that M and R have had no trend over the lifespan of the oldest shoots in the population, with year to year random variation around some mean value of M and R , which we will call \hat{M} and \hat{R} . Not only does the regression approach result in an estimate of \hat{R} , but it provides statistical confidence limits for this estimate.

Besides this estimate of a long-term average recruitment rate (\hat{R}), the age structure also yields an estimate of the recruitment for the year the population was sampled (R_0):

$$R_0 = \ln N_t - \ln N_{x>0} \quad (5)$$

where N_t is the total number of shoots in the population and $N_{x>0}$ is the number of shoots older than 1 year (Duarte et al. 1994; Short and Duarte 2001).

From each age distribution, then, come two estimates of R : R_0 and \hat{R} . If one assumes no trend in M over the lifespan of the oldest shoots in the population, there are three possible outcomes of a comparison of R_0 and \hat{R} :

1. If R_0 is not significantly different from \hat{R} , then the population's trajectory is not significantly different in the current year compared to the period representing the life spans of the oldest shoots in the population.
2. If $R_0 > \hat{R}$, then the population has grown faster in the current year than the long-term average r .
3. If $R_0 < \hat{R}$, then the population has grown slower in the current year than the long-term average r , thereby providing a diagnostic for trends in population growth.

Because the regression analysis provides confidence limits about \hat{R} , then the three cases above can be tested statistically (cf. Marbà et al. 1996). We note at this point that the confidence limits are dependent on the number of age classes, so that the method will derive more robust estimates for long-lived species. Provided the population remained steady ($r \approx 0$, $\hat{M} \approx \hat{R}$) over the past, then these comparisons identify populations in steady state and those expanding and declining for the current year, respectively. These inferences are possible because the approach compares the long-term mean M (\hat{M} ; equal to \hat{R} under the assumption of near steady state) to the present R , R_0 , not the long-term mean \hat{R} . In addition to the comparison of present recruitment (R_0) relative to the long-term mean recruitment (\hat{R}), ecologists can, through a residual analysis of the age class distribution against the assumed exponential decline in shoot number with increasing age (cf. Durako and Duarte 1997), detect particularly bad and good years for the population in the form of fewer or greater shoots than expected for a particular age class.

So, as Ebert et al. (2002) point out, most previously reported estimates (e.g., Durako 1994; Marbà et al. 1996; Pe-

terson and Fourqurean 2001) of population change (r) are inaccurate if $\hat{R} \neq \hat{M}$. Here, we point out that these previous studies have actually predicted whether the trajectories of the populations (i.e., r) have changed in the previous year compared to past years, if the assumptions of age-independent M and no trend in M over the period represented by the lifespan of the oldest shoots in the population hold. Only in seagrass beds that have been more or less stable for some time is it reasonable to assume that $r \approx 0$.

The analysis of Ebert et al. (2002) of the size of the bias in estimating M from age distribution data when $\hat{R} \neq \hat{M}$ corresponds to a worst-case scenario, since they chose to analyze a simulated population with $M = 1.7$, comparable to rates reported for only the fastest growing, most short-lived species. Slow-growing, long-lived species such as *Posidonia oceanica* and *Thalassia testudinum* exhibit M and R that are an order of magnitude less than this value (Marbà et al. 1996; Peterson and Fourqurean 2001), hence r for these species will generally be much lower than the -0.5 to 0.6 range used in the simulations of Ebert et al. (2002), and the magnitude of the bias will be much lower for slow-growing species. Yet, previously reported forecasts of net population changes are still biased even for slow-growing species, unless M was estimated independently from the age distribution.

There is some evidence, however, that natural seagrass populations can exhibit $r \approx 0$, and hence the reconstructive technique may indeed be useful to directly estimate M from age structure data in some instances. Whether seagrass stands may be in near steady state (i.e., whether $\hat{M} \approx \hat{R}$) is often difficult to assess, but there are indications that the assumptions of the application of reconstructive techniques to estimate M , R , and r are sometimes fulfilled. Shoot age distributions of *Posidonia oceanica* at la Fossa (SE Spain) examined in 1991 (Marbà et al. 1996) and revisited in 2001 (Marbà unpubl. data) were identical (Kolmogorov-Smirnov two sample test, $p > 0.05$, Fig. 1), suggesting a stable age distribution. The analysis of shoot age structure of a *Thalassia testudinum* meadow growing in a Mexican Caribbean lagoon in 1999 under the assumption that $\hat{R} = \hat{M}$ indicates $R_0 = 0.46 \text{ yr}^{-1}$ and $\hat{M} = 0.43 \pm 0.05 \text{ yr}^{-1}$, and, thus, $r \approx 0$ (data from Van Tussenbroek 2000). As estimated from repeated census data, the rate of change of mean shoot density (r) at the same meadow for the previous 6 years (corresponding to the median shoot age for the population) was not different from 0 ($-0.022 \pm 0.016 \text{ yr}^{-1}$, recalculated from Van Tussenbroek 2000), indicating that this population was in near steady state over the 6-yr period.

The various diagnostics possible from the examination of seagrass shoot age distributions provide useful assessments of the status of the stands and ecological forecasts—but not numerical predictions—of the future trends of the stands if the relation between the present year's R_0 and \hat{R} were to persist. Improved forecasts or predictions require direct estimates of dynamic population parameters. Ebert et al. (2002) echoed previous calls for the use of matrix models to estimate M and R (Jensen et al. 1996; Kaldy et al. 1999). Matrix models have been available to ecologists for decades (Leslie 1945), and yet none of the 806 published estimates of seagrass population dynamic parameters have been de-

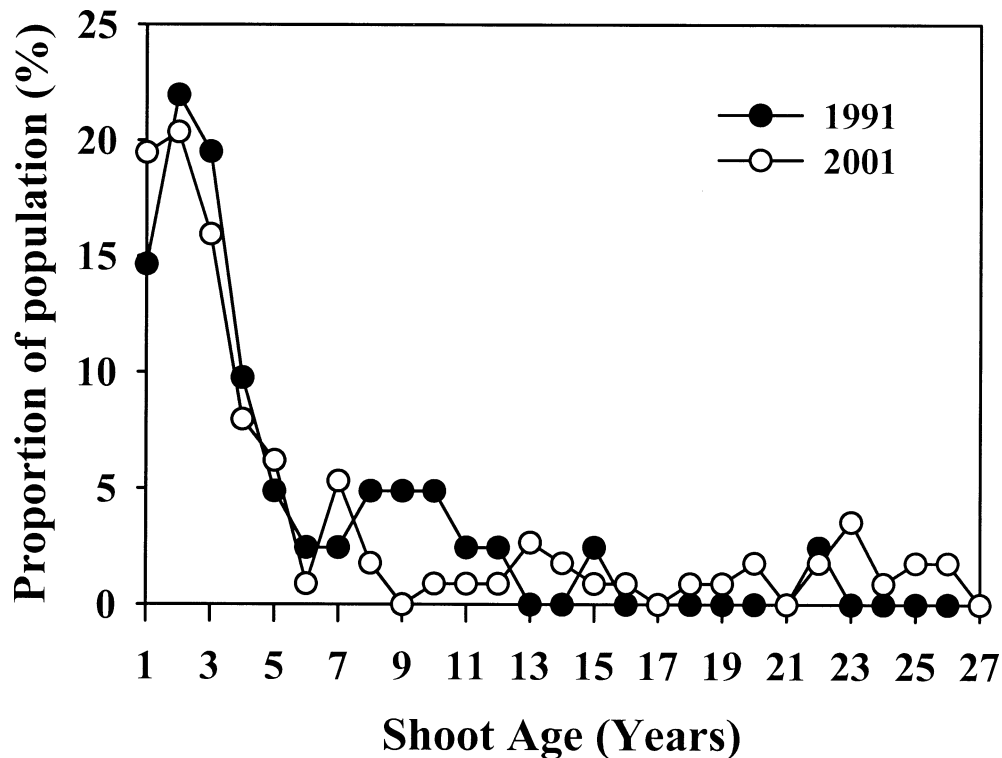


Fig. 1. The age distribution of shoots collected from the *Posidonia oceanica* stand at La Fosa (SE Spain) in 1991 and 2001.

rived through the use of matrix models, which cannot be charged to poor ecological training of seagrass scientists. The reasons for failure to apply matrix models to seagrass stands must lie elsewhere, and we argue that the key reason is that this technique is impractical for most seagrass populations because it requires the determination of different shoot stages relevant to population dynamics and the transition probabilities between them. Seagrasses are clonal organisms and the shoots are, therefore, modular units with rather similar properties, making it difficult to assign stages. There is some evidence of age-dependent population dynamics in seagrasses, particularly in reproduction (Duarte et al. 1997; Gallegos et al. 1992), so that matrix models could be formulated with age stages. However, in practical terms, this would require the excavation of the shoots to determine their age from leaf scars, which destroys the subjects of the investigation. If it were possible to age shoots without destroying them, it would be necessary to follow them from their birth to death, which takes decades in the long-lived species (Hemminga and Duarte 2000). Alternatively, in theory size may be used to characterize stages, as recommended by Ebert et al. (2002), but this is only reasonable whenever there is evidence of size dependence of events relevant to population dynamics, which is meager or nonexistent for seagrasses. The alternative suggestion of the use of ramet size is also impractical for plants that fragment rapidly, such as *Zostera muelleri* (Bearlin et al. 1999) because the size of the ramet becomes, through fragmentation, independent of age beyond a critical size (e.g., Marbà and Duarte 1998). Moreover, even if they did not fragment, elucidation of ramet

size also requires excavation. A further constraint is that, in practice, the collection of the data needed to feed matrix models involves the assumption of constant mortality rates over time and assumes age-independent mortality. This is because the evaluation of the transition probabilities by following particular shoots during their entire life span (e.g., up to 50 years in *Posidonia oceanica*) is difficult. In practice, this will be substituted—provided age could be determined without disruption of the shoots—by the estimation of transition probabilities for different age classes for a given year and then assuming that those transition probabilities hold for the entire life span of the population.

By following the birth and death of shoots in tagged populations, direct estimates of M , R , and r can be derived (Short and Duarte 2001), free of the assumptions of the application of Eq. 2. Direct censuses, however, are demanding of time and effort, for shoots have to be tagged individually in the field and relocated repeatedly. Moreover, individual tagging may only be practical for larger, longer lived species, such as *Posidonia oceanica* and *Thalassia testudinum*, and may be difficult in adverse environments, such as very deep or very turbid ones. Large-scale assessment of seagrass population dynamics through direct censuses is, however, possible. Therefore, we strongly advocate the use of direct censuses for estimating population trends whenever possible.

In conclusion, the present commentary extends the useful contribution of the analysis of Ebert et al. (2002) by identifying the slope of the semilogarithmic regression of the number of shoots per age class versus age as an estimate

of the long-term mean recruitment rate of the populations. In addition, we helped clarify what the assumptions and limitations of the use of age distributions to infer population dynamics are. Using age structure to estimate mortality rates in populations has the weaknesses eloquently demonstrated by Ebert et al. (2002). This procedure is, however, not peculiar to seagrasses but is widely used to examine the dynamics of other plant populations (e.g., mosses, Økland 1995; marsh plants, Sutherland and Walton 1990; bamboo, Taylor and Zisheng 1993; mangroves, Duarte et al. 1998, 1999; terrestrial trees, Szeicz and Macdonald 1995; Kelly and Larson 1997) and fish populations (e.g., larval sciaenids, Flores-Coto et al. 1998; tropical gobies, Kritzer 2002). In summarizing a similar debate about the utility of age structures to estimate mortality of benthic invertebrates, Valiela (1995; p. 97–98) concluded that “the assumptions do not always hold . . . but such calculations can give reasonable approximations.” Within the limits set by the assumptions of the technique, the parameters of population demographics derived from age distributions can indeed provide useful—but not definitive—indicators of the population status.

James W. Fourqurean¹

Department of Biology and Southeast
Environmental Research Center
Florida International University
Miami, Florida 33199

Núria Marbà and Carlos M. Duarte

IMEDEA (CSIC-UIB), Instituto Mediterráneo de
Estudios Avanzados
Miquel Marqués 21
07190 Esporles, Spain

References

- BEARLIN, A. R., M. A. BURGMAN, AND H. M. REGAN. 1999. A stochastic model for seagrass (*Zostera muelleri*) in Port Phillip Bay, Victoria, Australia. *Ecol. Model.* **118**: 131–148.
- COSTANZA, R., AND OTHERS. 1997. The value of the world's ecosystem services and natural capital. *Nature* **387**: 253–260.
- DUARTE, C. M. 2002. The future of seagrass meadows. *Environ. Conserv.* **29**: 192–206.
- , AND OTHERS. 1994. Reconstruction of seagrass dynamics: Age determinations and associated tools for the seagrass ecologist. *Mar. Ecol. Prog. Ser.* **107**: 195–209.
- , AND OTHERS. 1998. The relationship between mangrove (*Rhizophora apiculata*) seedling growth, nutrient status and sediment conditions in SE Asia. *Mar. Ecol. Prog. Ser.* **175**: 277–283.
- , U. THAMPANYA, J. TERRADOS, O. GEERTZ-HANSEN, AND M. D. FORTES. 1999. The determination of the age and growth of SE Asian mangrove seedlings from internodal counts. *Mangroves and Saltmarshes* **3**: 251–257.
- , J. S. URI, N. S. R. AGAWIN, M. D. FORTES, J. E. VERMAAT, AND N. MARBÀ. 1997. Flowering frequency of Philippine seagrasses. *Bot. Mar.* **40**: 497–500.
- 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., S. L. WILLIAMS, AND P. J. EWANCHUK. 2002. Mortality estimates from age distributions: Critique of a method used to study age distributions. *Limnol. Oceanogr.* **47**: 600–603.
- FLORES-COTO, C., A. SANCHEZ-ITURBE, F. ZAVALA-GARCIA, AND S. M. WARLEN. 1998. Age, growth, mortality and food habits of larval *Stellifer lanceolatus*, *Cynoscion arenarius* and *Cynoscion nothos* (Pisces: Sciaenidae), from the southern Gulf of Mexico. *Estuar. Coast. Shelf Sci.* **47**: 593–602.
- GALLEGOS, M. E., M. MERINO, N. MARBÀ, AND C. M. DUARTE. 1992. Flowering of *Thalassia testudinum* Banks ex König in the Mexican Caribbean: Age dependency and interannual variability. *Aquat. Bot.* **43**: 249–255.
- HEIDELBAUGH, W. S., AND W. G. NELSON. 1996. A power analysis of methods for assessing change in seagrass cover. *Aquat. Bot.* **53**: 227–233.
- HEMMINGA, M. A., AND C. M. DUARTE. 2000. Seagrass ecology. Cambridge Univ. Press.
- JENSEN, S. L., B. D. ROBBINS, AND S. S. BELL. 1996. Predicting population decline: Seagrass demographics and the reconstructive technique. *Mar. Ecol. Prog. Ser.* **136**: 267–276.
- KALDY, J. E., N. FOWLER, AND K. H. DUNTON. 1999. Critical assessment of *Thalassia testudinum* (turtle grass) aging techniques: Implications for demographic inferences. *Mar. Ecol. Prog. Ser.* **181**: 279–288.
- KELLY, P. E., AND D. W. LARSON. 1997. Dendroecological analysis of the population dynamics of an old-growth forest on cliff-faces of the Niagara Escarpment, Canada. *J. Ecol.* **85**: 467–478.
- KRITZER, J. P. 2002. Stock structure, mortality and growth of the decorated goby, *Istigobius decoratus* (Gobiidae), at Lizard Island, Great Barrier Reef. *Environ. Biol. Fish.* **63**: 211–216.
- LESLIE, P. H. 1945. On the use of matrices in certain population mathematics. *Biometrika* **33**: 183–212.
- MARBÀ, N., AND C. M. DUARTE. 1998. Rhizome elongation and seagrass clonal growth. *Mar. Ecol. Prog. Ser.* **174**: 269–280.
- , AND OTHERS. 1996. Growth and population dynamics of *Posidonia oceanica* in the Spanish Mediterranean coast: Elucidating seagrass decline. *Mar. Ecol. Prog. Ser.* **137**: 203–213.
- ØKLAND, R. H. 1995. Population biology of the clonal moss *Hylacomitrium splendens* in Norwegian boreal spruce forests. I. Demography. *J. Ecol.* **83**: 697–712.
- PATRIQUIN, D. 1973. Estimation of growth rate, production and age of the marine angiosperm *Thalassia testudinum* König. *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.

¹ Corresponding author (Jim.Fourqurean@fiu.edu).

Acknowledgments

This paper was improved by the comments of T.A. Ebert as well as two anonymous reviewers. This research was supported by the project Management and Monitoring of European Seagrass Ecosystems (M&M's) of the European Commission (contract EVK3-CT-2000-00044) and grant SAB2000-0082 from the Secretaría de Estado de Educación y Universidades, Ministerio de Educación, Cultura y Deporte, Spain. This is contribution #198 from the Southeast Environmental Research Center at FIU.

- QUINN, T. J. I., AND R. B. DERISO. 1999. Quantitative fish dynamics. Oxford Univ. Press.
- RICKER, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. **191**.
- 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.
- SHORT, F. T., AND C. M. DUARTE. 2001. Methods for the measurement of seagrass growth and reproduction, p. 155–182. In F. T. Short and R. G. Coles [eds.], Global seagrass research methods. Elsevier.
- , AND S. WYLLIE-ECHEVERRIA. 1996. Natural and human-induced disturbance of seagrasses. Environ. Conserv. **23**: 17–27.
- SUTHERLAND, W. J., AND D. WALTON. 1990. The changes in morphology and demography of *Iris pseudacorus* L. at different heights in a saltmarsh. Funct. Ecol. **4**: 655–659.
- SZEICZ, J. M., AND G. M. MACDONALD. 1995. Recent white spruce dynamics at the subarctic alpine treeline of north-western Canada. J. Ecol. **83**: 873–885.
- TAYLOR, A. H., AND Q. ZISHENG. 1993. Ageing bamboo culms to assess bamboo population dynamics in panda habitat. Environ. Conserv. **20**: 76–79.
- VALIELA, I. 1995. Marine ecological processes. Springer.
- VAN TUSSENBOECK, B. I. 2000. Frequency distributions and demographical analysis of seagrasses with special emphasis on *Thalassia testudinum* in a tropical reef lagoon. Biol. Mar. Mediterr. **7**: 147–151.

Rejoinder to Fourqurean et al. (2003)

Overall, Fourqurean et al. (2003) agree with our paper (Ebert et al. 2002) and accept that mortality rates cannot be estimated from age distributions unless the population growth rate per individual, r , is equal to 0. Also, we agree with part of the last line of their paper where these authors state that direct censuses should be used. This could be the end of our rejoinder except that the authors still want to use age structure data based on reconstructive methods to predict change in seagrass populations with all the implicit significance for decisions in seagrass management.

The modification Fourqurean et al. (2003) propose would not include an estimate of population growth rate per individual, r , but rather would attempt to decide, based on sampled age structure, whether the current year's recruitment rate of new shoots, R , had changed from a fixed recruitment rate, \hat{R} , of previous years. \hat{R} would be determined by a regression of the natural logarithm of number versus age as done in the standard reconstructive method; \hat{R} is the slope of the regression and includes both survival and population growth. A population could be growing or declining but would have to have attained a stable age distribution, which requires fixed rates of survival and reproduction, the year before sampling was done. So the year just before the time of sampling would have to be the year when a change in recruitment occurred. If R_0 is not the same as \hat{R} then the year just prior to the time of observation must have been the year when the rates changed. Is this reasonable? If rates changed, for example, over the past 3 or 4 years, what then? First, the age distribution at the time that \hat{R} was estimated would *not* be stable, and so population growth rate would be changing from year to year and unstable until new vital rates became fixed and a new stable age distribution attained. The assumptions of their proposed modification, though listed in their note, are so restrictive as to make the method of dubious utility and could lead to substantial errors in statements concerning seagrasses.

Fourqurean et al. (2003) say that forecasts based on their modification should be used with caution until the validity

of the assumptions implicit in the analyses are assured. Validating the method for each study would require having data on survival and reproduction that could be used to show that a stable age distribution had been attained a year prior to the year when they would apply their reconstructive method. How would this be done? Data would have to be gathered to estimate survival and reproduction independent of the standard reconstructive method, so population growth rate and a stable age distribution could be estimated and compared with the age distribution determined from the reconstructive method. If the estimated and observed stable age distributions were the same one year before the use of the reconstructive method, then their method probably could be used. Data gathered in the validation of the method they propose, however, would make their method unnecessary. Comparisons of observed and expected age distributions, however, can be useful even when they do not match (Doak and Morris 1999).

If the rates of survival and reproduction are fixed, attaining a stable age distribution may take much longer than the lifespan of the oldest individuals. It all depends on how far away the population is from a stable age distribution and on the details of age-specific rates of survival and reproduction. Populations can fluctuate simply because a stable age distribution has not been attained and can fluctuate even when the long-term trend is 0 growth (e.g., Bernardelli 1941). Details of the life table thus are very important, and differences in recruitment from one year to the next may or may not signify changes in the life table.

Concerning use of a decaying exponential survival model, Fourqurean et al. (2003) state that “this analysis assumes a stable age distribution (and, therefore, that $R = M$).” This quote shows that the authors confuse the difference between a stable age distribution and a stable age distribution with stationary structure. With a stable age distribution, r can be negative, positive, or zero. In contrast, in a stable age distribution with stationary structure, not only is age structure stable with a fixed proportion in each age class, but also r