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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

= 0. Unless an age distribution is drawn from a population that has a stable age distribution with stationary structure, it cannot be used to deduce survival. This statement is not extreme, as Fourqurean et al. suggest; it is just the way populations work. Stating assumptions in a paper does not absolve authors from being bound by them.

We agree that nondestructive tagging of individuals might be more laborious than a single excavation to estimate age, but no cost–benefit comparison has been made. Certainly, postexcavation measurements are very time consuming. Also, the difficulties posed for tagging and resampling seagrasses are not as onerous as they suggest; most of the seagrass examples they cite grow in relatively shallow, clear tropical waters. Following cohorts of annual recruits by tagging is possible, but obtaining age-specific rates of survival and reproduction would require a long-term study. We also agree that digging plants to determine age and then tagging these individuals to determine survival probably would make the measured rates suspect, but there are other more appropriate methods for obtaining life-table data. For some species, shoots could be tagged without knowing initial age and age then determined following excavation after some time period, such as a year or less, in the field. Time periods shorter than 1 year would be appropriate for species where a dead shoot would decay so rapidly that age could not be determined after a year's time. Fourqurean et al. (2003) seem to believe that it is necessary to follow all tagged shoots from birth to death, but such is not the case if different ages are tagged. A single year's study can be used to estimate age-specific rates. They are correct, however, in pointing out that a study of 1 year measures rates that are specific to that particular year. This is, of course, why multiyear studies usually are considered necessary for species of interest (e.g., Horvitz and Schemske 1995; Lesica 1995; examples in Caswell 2001). Our contention is that a study that estimates survival rates for even just 1 year will be better than a study based on a single point in time.

Use of repetitive reconstructive analyses of age structure in samples taken over a period of several years could be used to estimate age-specific survival based on density changes of age classes. Size-based analysis is an alternative to an age-based analysis and is workable. Use of size has the advantage over age-based analysis of annual cohorts in that all transitions necessary for analysis can be obtained each year of a study following initial tagging. Different seagrass species may require different approaches because not all can be aged. The central point in all of these suggestions is that more than a single sample date is needed.

Fourqurean et al. (2003) are critical of size-based analyses, but it is worth pointing out that their Eq. 1 contains no size-specific information and so nothing would be lost by using size-structure or just a single size class so that tagged individuals would not be classified with respect to either size or age. The decaying exponential survival model, their Eq. 2, is appropriate for survival with no age effects, and total new recruits as used in their Eq. 1 do not partition reproduction by age of parent shoot. There may be age effects as Fourqurean et al. (2003) acknowledge, but these are not explicitly incorporated into analyses they have done. Explicit inclusion of age effects would move analysis either to the Euler equation or to matrix methods.

Fourqurean et al. (2003) end by pointing out that other workers use age structures to estimate survival rates and suggest that there is a ''debate about the utility of age structures to estimate mortality.'' We suggest that ''debate'' is not a correct word choice. Our note (Ebert et al. 2002) called attention to a mathematical error in the use of age structure to estimate survival and as such is not a debatable issue.

Thomas A. Ebert[1]

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

Susan L. Williams

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

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[1] Corresponding author (ebertt@science.oregonstate.edu).